

Variation in Rubisco content and activity under variable climatic factors

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Abstract The main objective of the present review is to provide a compilation of published data of the effects of several climatic conditions on Rubisco, particularly its activity, state of activation, and concentration, and its influence on leaf gas exchange and photosynthesis. The environmental conditions analyzed include drought, salinity, heavy metals, growth temperature, and elevated [O₃], [CO₂], and ultraviolet-B irradiance. The results show conclusive evidence for a major negative effect on activity of Rubisco with increasing intensity of a range of abiotic stress factors. This decrease in the activity of Rubisco is associated with down-regulation of the activation state of the enzyme (e.g., by de-carbamylation and/or binding of inhibitory sugar phosphates) in response to drought or high temperature. On the contrary, the negative effects of low temperature, heavy metal stress (cadmium), ozone, and UV-B stress on Rubisco activity are associated with changes in the concentration of Rubisco. Notably, in response to all environmental factors, the regulation of *in vivo* CO₂ assimilation rate was related to Rubisco *in vitro* parameters, either concentration and/or carboxylation, depending on the particular stress. The importance of the loss of Rubisco activity and its repercussion on plant photosynthesis are discussed in the context of climate change. It is suggested that decreased Rubisco activity will

be a major effect induced by climate change, which will need to be considered in any prediction model on plant productivity in the near future.

Keywords CO₂ · Drought · Heavy metals · Ozone · Photosynthesis · Salinity · Temperature · Water stress

Introduction

Abiotic stress is the principal cause of crop failure, decreasing the average yields of most major crops by more than 50 % and threatening the sustainability of agriculture worldwide. Crop productivity is primarily dictated by the plant carbon balance, which is determined from the difference between the rate of photosynthetic CO₂ assimilation and respiration. Within the photosynthetic process, ribulose-1,5-bisphosphate carboxylase/oxygenase (Rubisco) is the enzyme responsible of CO₂ fixation, the importance of which on the primary productivity has been estimated to be above 10¹¹ tons of atmospheric CO₂ being annually fixed (Field et al. 1998).

Engineering Rubisco to improve its catalytic capacity is envisaged as one of the most suitable means for improving global plant productivity and agricultural yields (Parry et al. 2013). In particular, increasing the carboxylase catalytic turnover rate and/or the ratio of carboxylation to the apparently futile oxygenation reaction would improve photosynthesis and yield (Whitney et al. 2011). Owing to its importance, significant knowledge has been gained over the past decades on the biochemistry and the molecular biology of Rubisco. It is now well established that *in vivo* Rubisco activity is rapidly regulated to control the flux through the photosynthetic carbon reduction cycle in response to fluctuations in the environment. This regulation

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consists in the spontaneous carbamylation of a lysine residue and the subsequent stabilization of the carbamate by Mg^{2+} ions (Cleland et al. 1998). Premature binding of RuBP to uncarbamylated Rubisco or binding of day- and night-time inhibitors results in inactive complex (Parry et al. 2008). Release of sugar phosphates from active and inactive Rubisco sites is catalyzed by the nuclear encoded enzyme Rubisco activase, the activity of which is modulated by stromal ATP/ADP and redox changes, thus facilitating carbamylation and regulating Rubisco activity according to the metabolic demands of photosynthesis (Portis 2003).

Although the mode of regulation is well established at the molecular level, much less is known on the precise modulation of Rubisco activity under varying environmental conditions, with apparently controversial results being published. For instance, there is discrepancy on the effects of drought on the Rubisco activity, with some studies showing no effect (Sharkey and Seemann 1989; Tezara et al. 1999), while other studies found it to be affected, hypothesizing that Rubisco activity plays a central role in the drought-induced depression of photosynthesis (Parry et al. 2002; Zhou et al. 2007). Most likely, the trigger of the decrease of the Rubisco activity depends on the severity and/or duration of the stress imposed (Flexas et al. 2006a; Galmés et al. 2011a). In addition, when activity is impaired, the precise underlying mechanisms (i.e., decreased Rubisco content, activation state, or presence of inhibitors) seem to depend on the species analyzed (Bota et al. 2004) and the rate of drought imposition (Flexas et al. 2006b). Other authors have suggested that decreased Rubisco activity under drought stress is a direct consequence of secondary oxidative stress, which in turn depends on the prevailing levels of irradiance (Zhou et al. 2007). With respect to other environmental stresses, there is much less information, although a similar lack of generalized patterns of response of Rubisco has been observed under conditions of salinity (e.g., Delfine et al. 1998; Feng et al. 2007; Singh et al. 2007), high temperature (e.g., Gesch et al. 2003; Kim and Portis 2005, Prasad et al. 2009), low temperature (Savitch et al. 2000; Aranjuelo et al. 2005; Zhou et al. 2006), increased O_3 (e.g., Fontaine et al. 1999; Di Cagno et al. 2001; Leitao et al. 2007), increased CO_2 (e.g., Sicher and Bunce 1997; Centritto and Jarvis 1999; Aranjuelo et al. 2011) increased UV (Correia et al. 2005) or heavy metal toxicity in soils (e.g., Chaffei et al. 2004; Dhir et al. 2009; Ying et al. 2010).

Improving our understanding on how Rubisco activity is regulated under varying environmental conditions is crucial to design the best Rubisco to be engineered to improve photosynthesis and yield under a climate change scenario. For instance, climate change perspectives predict increased temperature and CO_2 and decreased water availability in many areas of the world (Gornall et al. 2010). As

mentioned, the response of Rubisco to each of these three environmental conditions separately is not fully understood, for which there is still much to be learned before the effects of the three factors interacting together can be envisaged.

The aim of the present study was to compile a large dataset from the literature on the effects of environmental variables on Rubisco activity and its main components. Data analysis intends to answer the following questions: (i) is there a general pattern of response of Rubisco activity to each independent environmental factor? (ii) is there a common general response to all environmental factors? (iii) is it possible, with the data available, to have a hint of the regulatory mechanisms for environmentally induced down-regulation of Rubisco activity?, i.e., is it mostly regulated through decreased concentration, activation, or other factors? and (iv) what is the actual relationship between stress-induced decreases of Rubisco activity as determined *in vitro* and the *in vivo* down-regulation of gas exchange and photosynthetic activity?

Materials and methods

Data on the effects of eight environmental factors (drought stress, salinity, heavy metals, high and low growth temperatures, and elevated $[O_3]$, $[CO_2]$, and ultraviolet-B (UV-B) irradiance) on *in vitro* Rubisco parameters were compiled by surveying the peer-reviewed literature on the web of science (Thompson-ISI, Philadelphia, USA). Eight databases were created, one for each environmental factor, with the following data: (i) descriptive information (article, species, and environmental conditions regarding the treatment), *in vitro* Rubisco parameters (initial and total activities, carbamylation state, and concentration), and *in vivo* light-saturated net CO_2 assimilation rate (A_N).

Within each article \times species interaction, a control treatment was considered when plants were grown under optimal conditions. Although plant response to stress can be influenced by other factors related to plant developmental stage, duration of the stress and growth, and sampling conditions, those data were not considered during data analysis. Nevertheless, care was taken, during data extraction from original sources, to ensure minimal differences in these additional factors between control and non-control treatments.

Units for the initial and total Rubisco activities, as well as for Rubisco concentration, varied among studies, with unit interconversion being sometimes problematic or even impossible. Therefore, for comparative purposes, these parameters were expressed as a percentage of the control values. Consequently, for scaling purposes, A_N data were also transformed into percentage of the control values.

Data were arranged in averages extracted from tables, text, and/or figures of each article, and compiled into spreadsheets specific for each environmental factor. Then, data were classified according to arbitrarily established intensity degrees of stress, as explained below, and averages and standard errors calculated. All publications and species whose data have been used in the present review are listed in Table 1, classified according to the different environmental factors.

Drought is the environmental factor under which Rubisco has been characterized in more detail (Table 1). Comparing results from different studies and species is difficult because of interspecific differences in the response of photosynthesis to leaf water potential and/or leaf or soil relative water content, the parameters most commonly used to assess the degree of drought. In an attempt to solve this problem, the relationship between stomatal conductance (g_s) and photosynthesis has been used, since g_s has been described as a valid indicator of the intensity of drought stress (Flexas and Medrano 2002; Chaves et al. 2009). Therefore, only articles providing g_s values were considered in this database. Plants were grouped under mild, moderate, severe, and extreme drought stress when the g_s was above 70 %, between 70 and 40 %, between 40 and 10 %, and less than 10 % of control values, respectively.

For salinity studies, plants were grouped depending on the concentration of NaCl in the irrigation solution: mild stress when [NaCl] < 100 mM, moderate stress when [NaCl] was between 100 and 400 mM, and severe stress at [NaCl] > 400 mM.

The temperature databases consisted of data from plants grown (i.e., acclimated) either under low or high temperatures. Hence, the aim was to study the effects of the growth temperature, but not of the measuring temperature. Therefore, in vitro activities and in vivo gas-exchange data from both control and stressed treatments were measured at the same temperature (typically between 20 and 30 °C). This rule for comparable temperature of measurement was generalized for all databases.

For high-temperature stress, data were grouped under mild, moderate, and severe heat stress. To define the different intensities of stress, the absolute increase in Celsius degrees between the treatment and the control was multiplied by a factor considering the temperature achieved during the light period. This factor had a value of 1 when the temperature during the light period was <30 °C, 2 when this temperature was between 30 and 38 °C, and 3 when >38 °C. For mild, moderate, and severe heat stress intensities, the product between the maximum temperature factor and the absolute increase in Celsius degrees was <10, 10–20, and >20, respectively.

With respect to low-temperature stress, because the growth temperature in all control treatments was similar

(between 20 and 30 °C), the absolute decrease in Celsius degrees was directly used to define the two intensities of stress: mild-to-moderate stress when the temperature decrease <10 °C, and severe stress when the decrease >10 °C.

The search for literature reporting data on the effect of heavy metals on the in vitro Rubisco parameters showed that most experiments were performed on cadmium toxicity. Therefore, our review on heavy metal effects is mainly focused in studies dealing with Cd. Two different intensities of Cd toxicity were considered: mild/moderate, and severe stress intensities, which corresponded to [Cd] in the irrigation solution lower and higher than 50 μM, respectively.

Similar to heavy metals, data on O₃ were separated in two groups of intensity. Mild/moderate stress included [O₃] < 120 nL L⁻¹, whereas severe stress included studies where the plants were exposed to [O₃] > 120 nL L⁻¹. The data from articles dealing with elevated [CO₂] were separated into studies where elevated [CO₂] was <200 and >200 % than the corresponding ambient [CO₂] treatment. Finally, the low amount of data available on the effects of higher UV-B irradiance on the in vitro Rubisco parameters precluded its grouping under different intensities.

Statistical analyses

Univariate analysis of variance (ANOVA) was used to study the effect of the different stress intensities on the in vitro parameters. Significant differences between means were revealed by Duncan test ($P < 0.05$). These analyses were performed using the SPSS 12.0 software package (SPSS Inc., Chicago, IL, USA). Regression analyses were performed with the 11.0 Sigma Plot software package (Sigma, St Louis, MO, USA).

Results and discussion

Drought and salt stress

There is a general consensus that drought and salinity limit photosynthesis predominantly through increases in the leaf resistances to CO₂ transport, while metabolic impairment may occur when the intensity of stress becomes more severe (Flexas et al. 2004). In spite of this, variability of data on Rubisco parameters indicates that there is some controversy in literature, which has been attributed to differences in the velocity of stress imposition and to species-specific responses (Parry et al. 2002; Flexas et al. 2006a; Galmés et al. 2011a).

Data collected in this review essentially support the general consensus, with no significant or only minor

Table 1 List of articles and species used for the analysis of each environmental factor on the in vitro Rubisco parameters

Article	Species
Drought stress	
Aranjuelo et al. (2005)	<i>Medicago sativa</i>
Aranjuelo et al. (2007)	<i>Medicago sativa</i>
Bota et al. (2004)	<i>Nicotiana tabacum</i> , <i>Phaseolus vulgaris</i> , <i>Rhamnus alaternus</i> , <i>Rhamnus ludovici-salvatoris</i> , <i>Vitis vinifera</i>
Carmo-Silva et al. (2012)	<i>Gossypium barbadense</i>
Dias and Brüggemann (2010)	<i>Phaseolus vulgaris</i>
Erice et al. (2007)	<i>Medicago sativa</i>
Flexas et al. (2006b)	<i>Glycine max</i> , <i>Nicotiana tabacum</i>
Galmés et al. (2011a)	<i>Beta maritima</i> , <i>Cistus albidus</i> , <i>Diploaxis ibicensis</i> , <i>Hypericum</i> <i>baleaicum</i> , <i>Lavatera maritima</i> , <i>Limonium gibertii</i> , <i>Limonium</i> <i>magallufianum</i> , <i>Lysimachia minoricensis</i> , <i>Phlomis italica</i> , <i>Pistacia lentiscus</i>
Galmés et al. (2011b)	<i>Solanum lycopersicum</i>
Guo et al. (2007)	<i>Oryza sativa</i>
Hu et al. (2009)	<i>Cynodon dactylon</i>
Hu et al. (2010)	<i>Poa pratensis</i>
Inclán et al. (2005)	<i>Pinus halepensis</i>
Lal et al. 1996)	<i>Hordeum vulgare</i> , <i>Vicia faba</i>
Maroco et al. (2002)	<i>Vitis vinifera</i>
Pagter et al. (2005)	<i>Phragmites australis</i>
Singh and Usha (2003)	<i>Triticum aestivum</i>
Tezara et al. (2002)	<i>Helianthus annuus</i>
Vu and Allen (2009)	<i>Saccharum officinarum</i>
Zhou et al. (2007)	<i>Oryza sativa</i>
Salt stress	
Debez et al. (2006)	<i>Cakile maritima</i>
Delfine et al. (1998)	<i>Spinacia oleracea</i>
Dias et al. (2013)	<i>Lactuca sativa</i>
Feng et al. (2007)	<i>Oryza sativa</i>
Kasai et al. (1998)	<i>Agropyron elongatum</i>
Singh et al. (2007)	<i>Oryza sativa</i>
Soussi et al. (1998)	<i>Cicer arietinum</i>
Wang and Nii (2000)	<i>Amaranthus tricolor</i>
Zhu and Meinzer (1999)	<i>Atriplex lentiformis</i>
High-temperature stress	
Chauan et al. (2009)	<i>Triticum aestivum</i>
Dwyer et al. (2007)	<i>Panicum coloratum</i> , <i>Cenchrus ciliaris</i> , <i>Flaveria bidentis</i>
Erice et al. (2007)	<i>Medicago sativa</i>
Gesch et al. (2003)	<i>Oryza sativa</i>
Kim and Portis (2005)	<i>Arabidopsis thaliana</i>
Liu and Huang (2008)	<i>Agrostis stolonifera</i>
Olesen and Madsen (2000)	<i>Callitriche cophocarpa</i> , <i>Elodea canadensis</i>
Prasad et al. (2009)	<i>Sorghum bicolor</i>
Pushpalatha et al. (2009)	<i>Triticum aestivum</i>
Vu et al. (2001)	<i>Glycine max</i>
Vu et al. (2002)	<i>Citrus reticulata</i>
Vu (2005)	<i>Arachis hypogea</i>
Wang et al. (2010)	<i>Oryza sativa</i>
Xu and Huang (2001)	<i>Agrostis palustris</i>

Table 1 continued

Article	Species
Yamasaki et al. (2002)	<i>Triticum aestivum</i>
Low-temperature stress	
Alonso et al. (2008)	<i>Triticum aestivum</i>
Aranjuelo et al. (2005)	<i>Medicago sativa</i>
Cavaco et al. (2003)	<i>Paspalum dilatatum</i>
Pérez et al. (2005)	<i>Triticum aestivum</i>
Pérez et al. (2011)	<i>Triticum aestivum</i>
Pons (2012)	<i>Arabidopsis thaliana</i>
Savitch et al. (2000)	<i>Triticum aestivum</i>
Yamori et al. (2005)	<i>Spinacea oleracea</i>
Yamori et al. (2006)	<i>Spinacea oleracea</i>
Zhou et al. (2006)	<i>Cucumis sativus</i>
Heavy metal stress	
Chaffei et al. (2004)	<i>Solanum lycopersicum</i>
Dhir et al. (2011)	<i>Salvinia natans</i>
Jiang et al. (2009)	<i>Citrus grandis</i>
Krantev et al. (2008)	<i>Zea mays</i>
Li et al. (2010)	<i>Citrus grandis</i>
Mobin and Khan (2007)	<i>Brassica juncea</i>
Pietrini et al. (2003)	<i>Phragmites australis</i>
Ying et al. (2010)	<i>Picris divaricata</i>
Ozone stress	
Brendley and Pell (1998)	<i>Populus maximowizii x trichocarpa</i>
Dann and Pell (1989)	<i>Solanum tuberosum</i>
Degl'Innocenti et al. (2003)	<i>Trifolium repens, Trifolium pratense</i>
Di Cagno et al. (2001)	<i>Helianthus annuus</i>
Enyedi et al. (1992)	<i>Solanum tuberosum</i>
Fontaine et al. (1999)	<i>Pinus halepensis</i>
Gérant et al. (1996)	<i>Pinus halepensis</i>
Guidi et al. (2003)	<i>Phaseolus vulgaris</i>
Inclán et al. (2005)	<i>Pinus halepensis</i>
Kytöviita et al. (1999)	<i>Pinus halepensis</i>
Landry and Pell (1993)	<i>Populus maximowizii x trichocarpa</i>
Lehnherr et al. (1987)	<i>Triticum aestivum</i>
Leitao et al. (2007)	<i>Zea mays</i>
Leitao et al. (2008)	<i>Phaseolus vulgaris</i>
Lütz et al. (2000)	<i>Fagus sylvatica</i>
Pell et al. (1992)	<i>Populus maximowizii x trichocarpa</i>
Pell et al. (1999)	<i>Prunus serotina</i>
Pelloux et al. (2001)	<i>Pinus halepensis</i>
High CO ₂	
Alonso et al. (2008)	<i>Triticum aestivum</i>
Aranjuelo et al. (2009)	<i>Medicago sativa</i>
Bunce and Sicher (2003)	<i>Brassica oleracea</i>
Centritto and Jarvis (1999)	<i>Picea sitchensis</i>
Centritto et al. (1999)	<i>Prunus avium</i>
Erice et al. (2007)	<i>Medicago sativa</i>
Gesch et al. (2003)	<i>Oryza sativa</i>
Jacob and Greitner (1995)	<i>Scirpus olneyi</i>

Table 1 continued

Article	Species
Li et al. (1999)	<i>Quercus germinata</i> , <i>Quercus myrtifolia</i>
Pérez et al. (2011)	<i>Triticum aestivum</i>
Prasad et al. (2009)	<i>Sorghum bicolor</i>
Pritchard et al. (2000)	<i>Glycine max</i>
Rogers et al. (2001)	<i>Pinus taeda</i>
Sicher and Bunce (1997)	<i>Triticum aestivum</i> , <i>Hordeum vulgare</i>
Sicher and Bunce (2001)	<i>Solanum tuberosum</i>
Tezara et al. (2002)	<i>Helianthus annuus</i>
Vu et al. (1983)	<i>Glycine max</i>
Vu et al. (1987)	<i>Glycine max</i>
Vu et al. (1998)	<i>Oryza sativa</i>
Vu et al. (2001)	<i>Glycine max</i>
Vu et al. (2002)	<i>Citrus reticulata</i>
Vu (2005)	<i>Arachis hypogea</i>
Vu and Allen (2009)	<i>Saccharum officinarum</i>
High ultraviolet-B	
Allen et al. (1998)	<i>Brassica napus</i>
Bischof et al. (2000)	<i>Alaria esculenta</i> , <i>Laminaria solidungula</i> , <i>Monostroma arcticum</i> , <i>Palmaria palmata</i> , <i>Phycodrys rubens</i>
Correia et al. (2005)	<i>Zea mays</i>
He et al. (1993)	<i>Oryza sativa</i> , <i>Pisum sativum</i>
He et al. (1994)	<i>Oryza sativa</i> , <i>Pisum sativum</i>
Jordan et al. (1992)	<i>Pisum sativum</i>
Kulandaivelu and Nedunchezian (1993)	<i>Vigna sinensis</i>

changes in any of the Rubisco-related parameters under mild-to-moderate drought, followed by decreases in Rubisco activity at higher intensities of stress, when g_s was below 40 % of control treatment values (Fig. 1a). Initial and total Rubisco activities decreased by about 70 % under severe stress, although the carbamylation of Rubisco was not significantly modified. In principle, decreased activity with unequal change in carbamylation can be explained by decreased Rubisco content. However, this was not the case as the concentration of Rubisco under severe stress was not significantly different from that reported under nonstressed conditions (Fig. 1a). This suggests that, under severe drought, a percentage of the catalytic sites of Rubisco are blocked by tight-binding of inhibitors which decrease the concentration of sites catalytically available for carboxylation. An increase in the concentration of tight-binding inhibitors has been reported in several species under moderate-to-severe drought intensities (Parry et al. 2002; Carmo-Silva et al. 2010). The decrease in the CO₂ concentration at the sites of carboxylation in the chloroplastic stroma observed under moderate-to-severe drought intensities (Flexas et al. 2012), and the concurrent increase in the CO₂/O₂ ratio may lead to an increase in the production of misfire products, like D-glycero-2,3-diulose-1,5-

bisphosphate (Parry et al. 2008). This finding supports the view that carbamylation is not the only parameter modulating Rubisco activity and that the presence of unknown inhibitors can control the number of Rubisco sites that can be activated by carbamylation (Eichelmann et al. 2009).

There is evidence showing that decreased ATP limits RuBP production under drought stress (Tezara et al. 1999), and inhibitors binding to Rubisco sites may occur especially at subsaturating RuBP concentration. The interaction of Rubisco with tight-binding inhibitors has been hypothesized to prevent the degradation by proteases of the Rubisco not being used for in vivo catalysis, especially in stressed leaves (Parry et al. 2008). Nevertheless, this protection to proteolysis would not be sufficient under extreme drought intensities, when the concentration of Rubisco drops to about half of that measured under control conditions (Fig. 1a). However, under these extreme drought intensities, the initial activity (at about 50 % with respect to control values) decreases below total activity (Fig. 1a). This fact suggests that ca. 25 % of Rubisco becomes inactivated because of decarbamylation of catalytic sites, probably mediated by the lower CO₂ availability induced by further decreases in the stomatal and mesophyll conductances to CO₂ (Galmés et al. 2011a). The degree of deactivation of

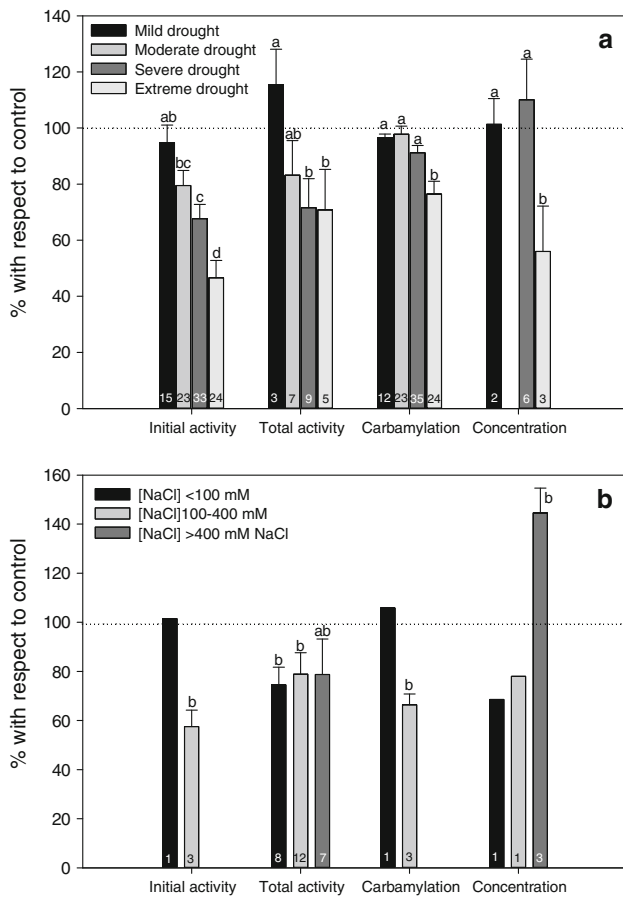


Fig. 1 Effect of **a** drought and **b** salt stress on Rubisco parameters. As for drought, four different intensities of stress were established according to the stomatal conductance (g_s) values expressed as a percentage of the control treatment. Mild stress $g_s > 70\%$; moderate stress $70\% < g_s < 40\%$; severe stress $40\% < g_s < 10\%$; extreme stress $g_s < 10\%$. As for salt stress, three different intensities were considered according to the concentration of NaCl in the solution used to irrigate the treated plants. Number of replicates is indicated at the bottom of each column. See Table 1 for articles and species considered in the analyses. Different letters denote statistically significant differences among different treatments through Duncan test ($P < 0.05$), being control treatment *a*

Rubisco sites in drought-stressed plants has been related to its functional type, which could explain, at least partially, the apparent discrepancies on the effects of drought on Rubisco in vitro parameters between different species (Galmés et al. 2011a).

The effects of soil salinity on plants have been divided into osmotic and ionic phases (Munns and Tester 2008). The osmotic phase is caused by a decrease in the soil and the intracellular water potential, and its consequences on the physiology of plants are similar to those triggered by drought stress (Munns and Tester 2008). With respect to photosynthesis, osmotic effects of salinity have been described to primarily affect leaf CO_2 diffusion through decreases of g_s and g_m (Flexas et al. 2004), thereby

potentially decreasing Rubisco activation because of decarbamylation of catalytic sites, as reported under moderate concentration of NaCl in the soil (100–400 mM) (Fig. 1b). Moreover, similar to the effects of mild drought stress, Rubisco carbamylation state was not affected at lower salt stress intensities ($[NaCl] < 100$ mM) (Fig. 1b), although decreases in the concentration of Rubisco have been reported (Delfine et al. 1998). This is clearly illustrated in Fig. 2a, where in rice subjected to salt stress, differences between initial and total activities become evident at moderate salt concentrations, but not at concentrations below 100 mM. However, data availability for some Rubisco parameters under salt stress is yet scarce, and more studies are required to confirm the trends described here.

At higher salt concentrations or under prolonged stress, the osmotic phase is followed by an ionic phase, when

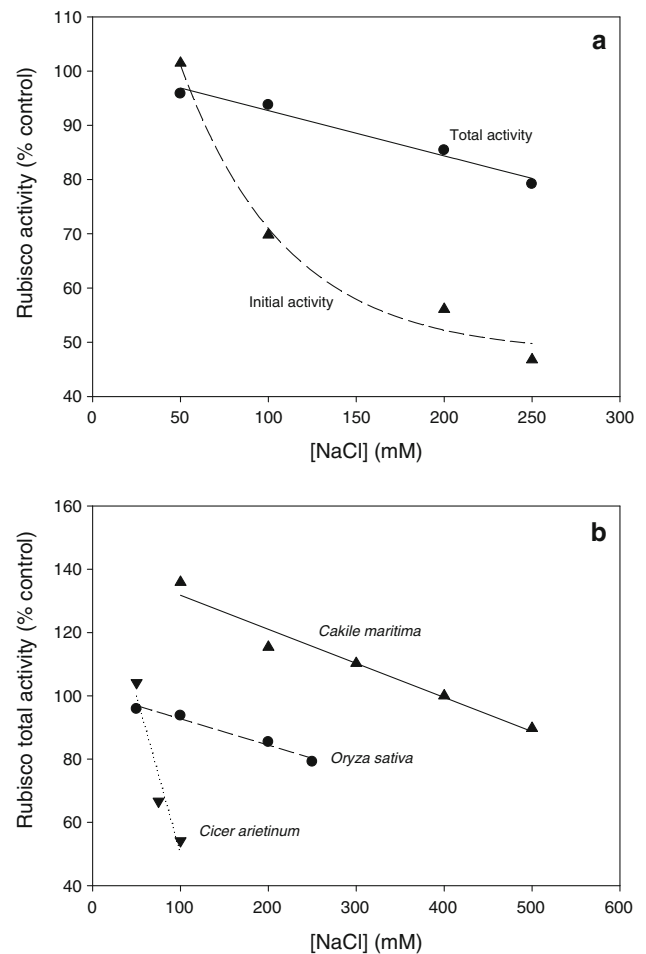


Fig. 2 **a** The relationship between the concentration of NaCl in the irrigation solution and the Rubisco total and initial activities of *Oryza sativa* (Feng et al. 2007). **b** The relationship between the concentration of NaCl in the irrigation solution and the Rubisco total activity, for three species differing in the tolerance to salt stress: *Cakile maritima* (high tolerance, from Debez et al. 2006), *O. sativa* (medium tolerance, from Feng et al. 2007), and *Cicer arietinum* (low tolerance, from Soussi et al. 1998)

metabolic impairment of the photosynthetic machinery is more likely to occur (Munns and Tester 2008). However, distinctions have to be made among species differing in their tolerance to salt stress. Hence, the effect of increasing soil salinity on the Rubisco total activity of the halophyte *Cakile maritima* is lower in comparison to rice and especially the glycophyte chickpea (Fig. 2b). Differences in the effects of salinity on the Rubisco activity among these species seem to be exclusively ascribed to their ability to control salt uptake by the roots and transport within the plant, and particularly to avoid salt accumulation to toxic levels in the cytosol and certain subcellular organelles like chloroplast (Flowers and Colmer 2008).

In vitro assays showed that Na^+ begins to inhibit most enzymes at concentrations around 100 mM (Greenway and Osmond 1972; Parida and Das 2005). Rubisco seems to be among the most sensitive enzymes, with sharp declines of its carboxylase activity starting even at lower salt concentrations in the assay media (Sivakumar et al. 2000). The precise biochemical causes of NaCl toxicity of Rubisco activity have yet to be explained, although it does not seem to be related to the disruption of the interaction between subunits. In fact, it has been reported that NaCl stimulated the oxygenase activity measured in vitro (Sivakumar et al. 2000). No difference in the sensitivity of Rubisco extracted from halophytes and glycophytes to NaCl has been documented yet (Sivakumar et al. 1998), unlike what has been observed for other enzymes (Munns et al. 2006).

A distinctive response between water and salt stresses at high stress intensities can be described for Rubisco concentration. Thus, while under drought it decreases, under salt stress it increases (Fig. 1). This increase in the content of Rubisco in response to extremely high concentration of NaCl, which is particular to halophyte plants and other photosynthetic organisms (Takabe et al. 1988), may be a compensatory mechanism for the reduced activation of Rubisco.

Growth temperature

Rubisco parameters were not significantly affected by mild heat stress, except for a slight (~20 %) decrease in total activity (Fig. 3a). This small decrease is likely to be due to increased inhibitors blocking Rubisco sites, given the minor decrease in the Rubisco concentration which would not explain the decrease in the total activity (Fig. 3a).

At moderate stress intensities, decreases in Rubisco activity became stronger, and correlated with decreases of the Rubisco concentration (Fig. 3a). Lower expression of Rubisco per area under heat stress has been reported in various species, concomitantly to decreases of its protein content (Vu et al. 2002; Pérez et al. 2011), and may be

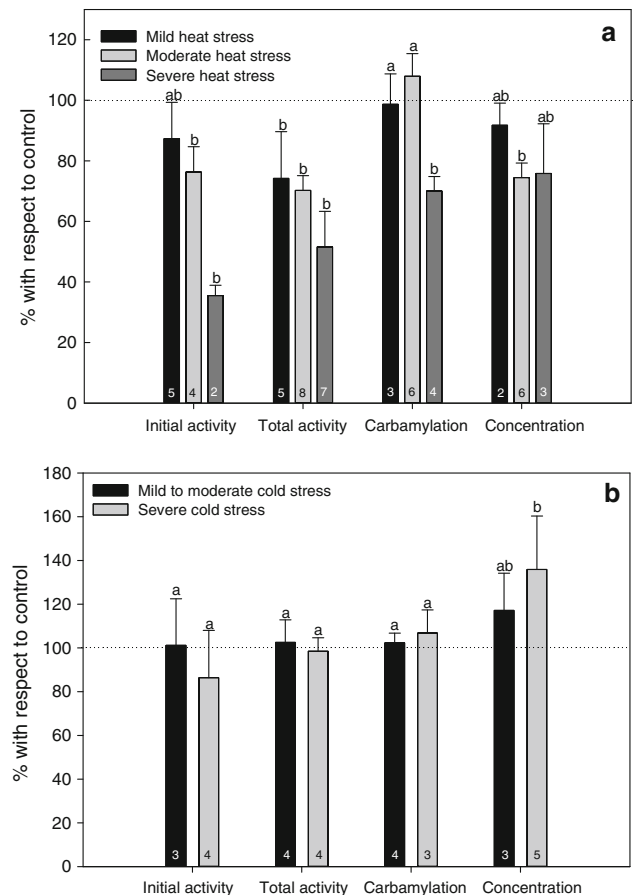


Fig. 3 Effects of **a** high- and **b** low-temperature stresses on Rubisco parameters. It is important to remark that high and low temperatures refer to the growth temperature and not to the measuring temperature. Data on Rubisco activity were measured at the thermal optimum (i.e., between 20 and 30 °C), and always at the same temperature as the respective control. As for high-temperature stress, to define the different intensities of stress, the absolute increase in Celsius degrees was multiplied by a factor considering the maximum temperature achieved during the treatment. This factor had a value of 1 when the maximum temperature was <30 °C, 2 when the maximum temperature was between 30 and 38 °C, and 3 when the maximum temperature >38 °C. For mild, moderate, and severe stress intensities, the product between the maximum temperature factor and the absolute increase in Celsius degrees was <10, 10–20, and >20, respectively. As for low-temperature stress, the absolute decrease in Celsius degrees was used to define the two intensities of stress: mild-to-moderate stress when the decrease <10 °C, and severe stress when the decrease >10 °C. Number of replicates is indicated at the bottom of each column. See Table 1 for articles and species considered in the analyses. Different letters denote statistically significant differences among different treatments through Duncan test ($P < 0.05$), being control treatment *a*

partly explained by changes in leaf anatomy, such as decreases in leaf mass area and the surface of chloroplasts facing the internal air spaces (Kogami et al. 2001; Yamori et al. 2005).

For the temperature-stress analyses, it should be highlighted that growth temperature was considered to be the

treatment while measurements of Rubisco activity were made at the same temperature for control and stress treatment plants. Inhibition of enzymatic activity tends to be reversible at mild-to-moderate supra-optimal temperatures, whereas at severely high temperatures inhibition tends to be irreversible (Haldimann and Feller 2004; Sharkey and Zhang 2010). Therefore, it is noteworthy that some parts of the effect of mild-to-moderate heat stress on Rubisco activity and carbamylation state could have been lost when performing the assays at an optimal temperature (Fig. 3a). Under severe heat stress, however, strong irreversible decreases in Rubisco initial (<40 %) and total activity (~50 %) are typically measured (Fig. 3a).

The decrease in total activity under severe heat stress is probably due to both decreased concentration of Rubisco and increased production of inhibitors (Fig. 3a). It has been shown that the production of side-products from RuBP by Rubisco is stimulated in heat stressed leaves (Sharkey et al. 2001; Kim and Portis 2006). However, it is not clear whether increased inhibitors production would result in a stronger inhibition *fallover*, because a faster release of inhibitors from Rubisco sites may occur at high temperatures (Schrader et al. 2006). Furthermore, at severe heat stress, Rubisco initial activity decreased to <40 % because of decreased carbamylation state (Fig. 3a). This result is in agreement with previous reports identifying Rubisco activase as one of the most heat-sensitive components of the photosynthetic apparatus (Feller et al. 1998; Salvucci et al. 2001), thus leading to Rubisco deactivation at moderate to extreme heat stress intensities. Whether the decline in Rubisco activation state at high temperature is due to limitation in the electron transport capacity rather than a consequence of a direct effect of heat on the integrity of Rubisco activase is still an unresolved question (Hikosaka et al. 2006; Sage and Kubien 2007; Yamori and von Caemmerer 2009). Deactivation due to decreasing CO₂ concentrations can be, in principle, discarded because leaf conductances tend to increase up to moderate heat-stress intensities, and because *starvation* CO₂ levels have not been documented even in plants exposed to extreme heat stress (Flexas et al. 2012).

According to the compiled data, the activity of Rubisco measured in vitro at non-stressful temperatures is not significantly affected by low growth temperatures (Fig. 3b). However, when growing at low temperature, the in vivo carboxylase capacity is diminished because of the direct effect of low temperature on the Rubisco kinetic constants, particularly the decreased carboxylase turnover rate (k_{cat}^c) (Sage 2002). In order to compensate for these effects, plants grown under severe cold stress have an increased concentration of Rubisco (Fig. 3b) (Hikosaka et al. 2006). The higher concentration of Rubisco occurs simultaneously with increments of its leaf mass area and leaf N content per area in plants grown at low temperature (Yamori et al. 2010). This

effect has also been described for other photosynthetic enzymes (Holaday et al. 1992). Other reported response mechanisms to low growth temperature include acclimation of Rubisco kinetic constants, which may compensate for some of the negative effects of decreased activity under low temperatures (Cavanagh and Kubien 2013).

Overall, the data compiled from the literature demonstrate that the regulation of Rubisco activity differs in plants grown at different temperatures. Heat stress causes a decline in the activity of Rubisco through alteration of the activity of Rubisco activase, concentration of catalytic sites and/or presence of inhibitors, depending on the intensity of the stress. The effects of cold stress on Rubisco were limited to a trend for an increased concentration when growth temperature was severely diminished. Irrespective of the observed trends, the species included in the analysis may differ in their optimum temperature for photosynthesis (Hikosaka et al. 2006), and therefore in their specific response to a given change in the growth temperature.

Heavy metals

Among the studies analyzing the effects of heavy metals on photosynthesis, and particularly on Rubisco, those using toxic concentrations of cadmium are by far the most abundant (Chaffei et al. 2004; Krantev et al. 2008; Ying et al. 2010).

Data from the literature show that Rubisco performance under Cd exposure is conditioned by the concentration of this toxic element in the media (Fig. 4). Rubisco initial activity is almost unchanged at Cd values below 50 μM. On the other hand, Rubisco initial activity is negatively affected after exposure to Cd concentration above 50 μM (Fig. 4). These changes in activity were explained, in some cases, by alterations in the concentration of Rubisco (Pietrini et al. 2003; Chaffei et al. 2004; Ying et al. 2010), although our compilation did not report significant differences in the concentration of the enzyme, when compared to control plants (Fig. 4).

Different mechanisms have been suggested to explain the influence of Cd on the Rubisco activity. An irreversible dissociation of the Rubisco large and small subunits has been observed under high Cd concentration, thus leading to total inhibition of the enzyme (Malik et al. 1992). Alternatively, it is likely that Cd²⁺ lowers carboxylase activity by replacing Mg²⁺ in its catalytic sites (Dias et al. 2013). Indeed, alteration of Rubisco kinetics, including a shift of activity toward RuBP oxygenation after binding to bivalent cations others than Mg²⁺ was described earlier (Christeller and Laing 1979; Robison et al. 1979). Another mechanism leading to decreased Rubisco carboxylase activity has been related to limited chlorophyll synthesis under Cd stress (Pietrini et al. 2003). Finally, it is not excluded that thiol

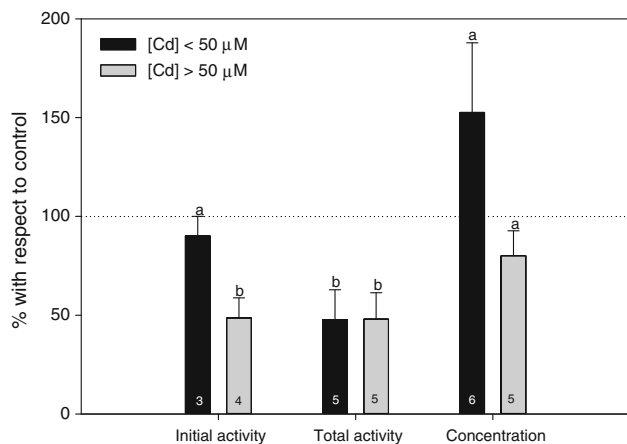


Fig. 4 Effects of the concentration of Cd^{2+} on the initial and total activity, and concentration of Rubisco. Number of replicates is indicated at the bottom of each column. See Table 1 for articles and species considered in the analysis. Different letters denote statistically significant differences among different treatments through Duncan test ($P < 0.05$), being control treatment *a*

residues of Rubisco activase could bind Cd, thus inducing Rubisco inactivation (Portis 2003).

The causes of the decline in the total activity that occurred at $[\text{Cd}] < 50 \mu\text{M}$ with no concurrent decreases in the concentration of Rubisco (Fig. 4) remains to be elucidated. Increased concentration of inhibitors in the low Cd treatment cannot be discarded, but it is unlikely that plants under low Cd increased the content of Rubisco sites and blocked them by enhancing the production of inhibitors. It is worth noting that the data shown in Fig. 4 are with a relatively low number of species, and data for initial and total activities came from species with different sensitivities to Cd toxicity, thus precluding conclusive trends on the effects of Cd on Rubisco in vitro. Indeed, similar to what occurred with salinity stress, the effects of heavy metals on Rubisco are species specific, and depend on the divergent strategies to cope with the toxicity of heavy metals. For instance, at $[\text{Cd}^{2+}]$ around $50 \mu\text{M}$, the hyper-accumulator *Picris divaricata* maintained Rubisco content at control levels (Ying et al. 2010), while a 50 % decrease in the Rubisco content was observed in *Solanum lycopersicum* (Chaffei et al. 2004).

There is very little information regarding the effect of other heavy metals on Rubisco performance (e.g., Al, Cr, Fe, Mn). From limited studies, it is clear that deleterious effects on Rubisco activity are not only dependent on the concentration, but also on nature of the toxic element (Jiang et al. 2009; Li et al. 2010; Dhir et al. 2011).

Atmospheric (O_3 and CO_2) and UV changes

The analysis of the compiled data on the effects of increased O_3 suggests a trend relatively independent of the

intensity of the stress (i.e., of the $[\text{O}_3]$). Thus, this trend can be summarized as a similar decrease in the initial and total activities up to about 70 % of the values measured under the control conditions, which can be explained by a similar decline in the concentration of Rubisco (Fig. 5a). This result is in accordance with the observed decline in the levels of *rbcS* and *rbcL* mRNA transcripts, and large subunit polypeptides in the O_3 -treated plants (see Dizenegrel 2001 and references therein). In addition, exposure to O_3 leads to increased oxidizing stress in the chloroplast (Pell et al. 1997), probably inducing the modification of Rubisco to an unstable form that may be rapidly degraded by proteases (Pell et al. 1994).

Although the concentration of Rubisco activase has been shown to decrease after O_3 exposure (Pelloux et al. 2001),

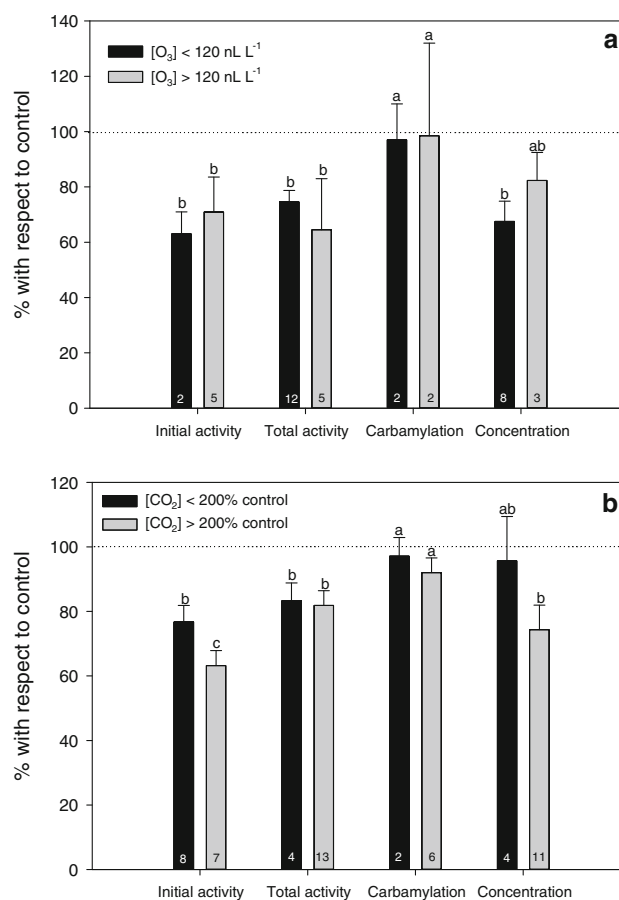


Fig. 5 Effect of the increase in the atmospheric concentration of **a** ozone and **b** CO_2 on Rubisco parameters. As for ozone stress, the different intensities were established according to the concentration of ozone in air: mild-to-moderate stress $< 120 \text{ nL L}^{-1}$, and severe stress $> 120 \text{ nL L}^{-1}$. As for CO_2 , two different intensities were established according to the concentration of CO_2 in the atmosphere of treated plants with respect to that measured under control conditions. Number of replicates is indicated at the bottom of each column. See Table 1 for articles and species considered in the analyses. Different letters denote statistically significant differences among different treatments through Duncan test ($P < 0.05$), being control treatment *a*

there is not a significant decrease in the carbamylation status of Rubisco in plants subjected to $[O_3]$ (Fig. 5a), possibly due to stable or increased ratio $[Rubisco]/[Rubisco\ activase]$. In spite of this general trend, the phytotoxic effects of O_3 on Rubisco activity and concentration have been described to vary depending on various factors, among them, being the species or even genotypes within a given species (Enyedi et al. 1992; Wittig et al. 2007), the developmental stage of the leaf, with the older leaves being more sensitive to the pollutant (Pell et al. 1997; Lütz et al. 2000), or the duration and timing of exposure (Pell et al. 1992; Landry and Pell 1993).

Compiled data analyzing the effects of $[CO_2]$ on Rubisco showed that plants exposed to high $[CO_2]$ decreased Rubisco activity, especially when $[CO_2] > 200\%$ (with respect to the control treatment; Fig. 5b). The lack of effect on the activation state and Rubisco content when plants were fumigated with $[CO_2] < 200\%$ suggests that Rubisco inhibitors may play a key role in the depleted carboxylation activity. According to Kane et al. (1998) and Pérez et al. (2011), under elevated $[CO_2]$, the production of Rubisco binding inhibitors is enhanced to protect Rubisco from proteolytic activity.

On the contrary, the analyses carried out on studies where plants were exposed to $[CO_2] > 200\%$ (with respect to the control treatment) showed that reduced Rubisco content is the primary driver in the regulation of Rubisco activity to high $[CO_2]$ (Fig. 5b). A key process conditioning the photosynthetic performance under elevated $[CO_2]$ is the capability of plants to adjust their C sink/source balance (Ainsworth et al. 2004). According to this hypothesis, when plants exposed to elevated $[CO_2]$ have limitations in increasing C sink strength, they decrease their Rubisco content and consequently photosynthetic rates to balance C source activity and sink capacity (Aranjuelo et al. 2013).

The limited number of articles in the literature reporting Rubisco in vitro data under different UV-B irradiances precluded executing a similar analysis to those performed with the other environmental factors. In spite of this, the compiled data demonstrate a general trend of a decreased activity due to a decline in the concentration of Rubisco (He et al. 1993; Allen et al. 1998), while the carbamylation state remained relatively stable (Jordan et al. 1992; Allen et al. 1998). Prolonged exposure to UV radiation has been shown to decrease the abundance of Rubisco subunit transcripts (Jordan et al. 1992) and to induce the formation of high molecular mass aggregates of Rubisco (Ferreira et al. 1996) through photomodification (Wilson et al. 1995) and photodegradation processes (Caldwell 1993). The decline in the concentration of Rubisco correlated positively with the decrease in A_N ($r^2 = 0.715$, $P < 0.01$, not shown), confirming previous suggestions that UV-induced

inhibition of photosynthetic CO_2 uptake is primarily because of changes in the carboxylase capacity (Lingakumar and Kulandaivelu 1993).

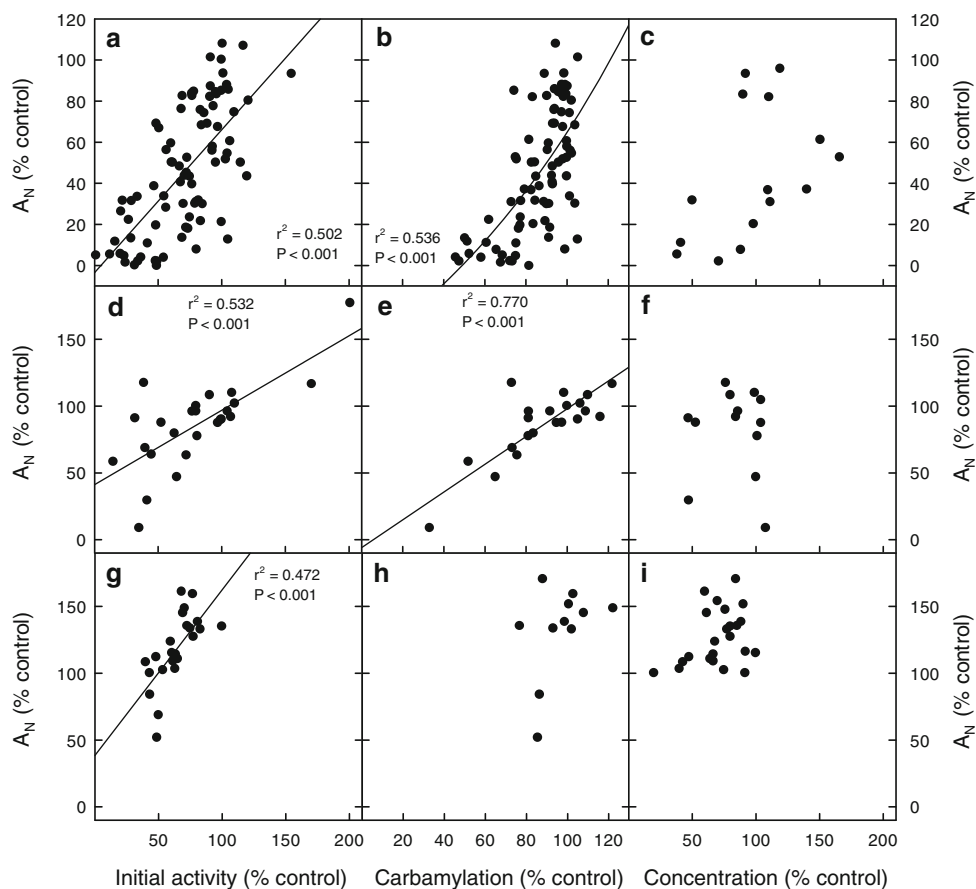
Drought, high temperature, and CO_2 effects on Rubisco activity may determine climate change impacts on the leaf CO_2 assimilation capacity

The nature of climate change has been typically summarized by higher atmospheric $[CO_2]$ and growing temperatures, and varying precipitation patterns potentially leading to more frequent and severe drought episodes (Gornall et al. 2010). The comprehension of how Rubisco responds to these main drivers of climate change and whether induced changes in Rubisco activity impact the photosynthetic capacity of plants is of pivotal importance to predict consequences of future climate on agriculture and natural ecosystems. According to data in Fig. 6, changes in Rubisco initial activity and carbamylation state induced by drought or increased growth temperature correlated positively with changes in A_N (expressed as a % of the control treatment values). These results suggest that the decrease in the photosynthetic capacity of plants induced by drought and heat stress is partially explained by changes in the activity and activation state of Rubisco in vitro.

Correlation analyses in Fig. 6g–i indicate that changes in A_N in response to increased $[CO_2]$ were significantly related to Rubisco initial activity, but not to its carbamylation state or concentration. A deeper analysis of these plots shows that regardless of the Rubisco parameters, most studies reported an increase in A_N under elevated $[CO_2]$. For instance, Rubisco initial activity decreased under elevated $[CO_2]$ in all the compiled studies, and the extent of this decrease partly determined the response of A_N (Fig. 6g). Although the increase in A_N under elevated $[CO_2]$ is caused, in a large proportion, by the higher intercellular CO_2 availability, the importance of Calvin cycle enzymes other than Rubisco (aldolase, sedoheptulose 1,7-bisphosphatase and transketolase) may have higher control coefficient on photosynthesis (Lefebvre et al. 2005; Uematsu, et al. 2012; Aranjuelo et al. 2013). It is remarkable that even with a 50 % reduction in the Rubisco content, plants exposed to elevated $[CO_2]$ were capable to maintain and/or increase A_N (Fig. 6i). Because under non- CO_2 limiting conditions plants have an excess of Rubisco, redistribution of the excess of N invested in Rubisco and partitioning to other organs and limiting processes results in increased capacity for CO_2 fixation (Ainsworth and Rogers 2007).

With regard to other environmental factors analyzed in this review, changes in A_N due to salt stress correlated well with changes in Rubisco carbamylation and concentration (Table 2). As for heavy metals and O_3 , changes in A_N only correlated with modifications of the Rubisco concentration.

Fig. 6 Relationship between the net CO₂ assimilation rate (A_N) and Rubisco initial activity (a, d, g), carbamylation (b, e, h), and concentration (c, f, i), under the following environmental conditions: drought (a, b, c), heat stress (d, e, f), and elevated CO₂ (g, h, i). All parameters are expressed in percentage with respect to the control values. Regression line, altogether with regression coefficient and significance level are indicated when the relationship was significant ($P < 0.05$)



Finally, in cold acclimated plants, the alteration of A_N was explained by increases in the initial activity (Table 2). A general trend is that the modification of the photosynthetic capacity under those environmental factors being categorized as phytotoxins (salt, heavy metals, and O₃) are mainly associated with alterations in the concentration of Rubisco, while changes in the activity/activation of the enzyme are responsible of the affected photosynthesis under water and temperature stresses and elevated CO₂.

Despite being beyond the scope of this article, the relevance of the interaction between the different environmental factors, associated with synergistic and antagonistic phenomena, needs to be mentioned. For instance, in wheat, it was observed that although elevated [CO₂] and temperature affected negatively the Rubisco content, the combination of both factors induced the stimulation of k_{cat}^c (Pérez et al. 2011). Similar interactive effects have been described among almost all environmental factors included in the present review (e.g., Kytöviita et al. 1999; Pelloux et al. 2001; Tezara et al. 2002; Aranjuelo et al. 2005), along with nutrient availability (e.g., Correia et al. 2005; Guo et al. 2007; Yamori et al. 2011), and they must be considered when extrapolating results to field conditions, where usually two or more stresses take place simultaneously.

In summary, the present analysis of the effects of individual stresses associated with climate change together with the scarce but valuable knowledge on the interactions of some of these stresses, strongly suggest that decreased Rubisco activity will be a major plant response to climate change conditions, which is currently often neglected but should be considered in prediction models on plant productivity in the near future.

Concluding remarks

Acclimation of the key enzyme Rubisco to cope with fluctuations in the environment may be of great importance for plant survival and crop yield. There are data reporting differential capacities of plants from different climates, different functional types, or branches of evolution, to acclimate. However, by compiling most of the existing data on Rubisco activity under variable abiotic factors, we have demonstrated the existence of some trends describing how Rubisco activity is affected by a range of abiotic stresses. The results reveal some common patterns of response regardless of the particular stress and demonstrate that significant reductions in the activity of Rubisco take place

Table 2 Regression coefficient (r^2) and level of significance (P) for the relationship between the percentage of change in the net CO_2 assimilation rate (A_N) and the percentage of change in the Rubisco in vitro parameters under the different environmental factors

Environmental factor	Initial activity	Carbamylation	Concentration
Drought	$r^2 = 0.502, P < 0.001$	$r^2 = 0.536, P < 0.001$	N.s.
Salinity	N.s.	$r^2 = 0.875, P < 0.05$	$r^2 = 0.912, P < 0.05$
High temperature	$r^2 = 0.532, P < 0.001$	$r^2 = 0.770, P < 0.001$	N.s.
Low temperature	$r^2 = 0.724, P < 0.05$	N.s.	N.s.
Heavy metals	N.s.	N.s.	$r^2 = 0.809, P < 0.001$
O_3	N.s.	N.s.	$r^2 = 0.842, P < 0.05$
CO_2	$r^2 = 0.472, P < 0.001$	N.s.	N.s.

N.s. nonsignificant ($P > 0.05$)

Table 3 Summary of the effects of the different environmental factors on the initial activity, carbamylation state, and concentration of Rubisco

Environmental factor	Mild/moderate stress			Severe/extreme stress		
	Initial activity	Carbamylation	Concentration	Initial activity	Carbamylation	Concentration
Drought	=	=	=	↓↓	↓	↓↓
Salinity	=	=	↓	↓↓	↓	↑↑ ^a
High temperature	↓	=	=	↓↓	↓	↓
Low temperature	=	=	↑	↓	=	↑
Heavy metals	=	N.a.	↑↑	↓↓	N.a.	↓
O_3	↓	=	↓	↓	=	↓
CO_2	↓	=	=	↓	=	↓

Mild or moderate versus severe or extreme intensities of stress were considered for each environmental stress, as described in “Materials and methods”, except for salinity, where moderate intensity was considered instead of severe intensity for the initial activity and the carbamylation state (due to the lack of data for these two parameters at severe intensities). All three data from a single reference by Kasai et al. (1998)

= Means 90–110 % with respect to control treatment, ↓ 60–90 %, ↓↓ <60 %, ↑ 110–140 %, ↑↑ >140 %, N.a. not available data

^a All three data from a single reference by Kasai et al. (1998)

when the intensity of the stress becomes severe (Table 3). Furthermore, the decreased state of activation of Rubisco (i.e., indicative of de-carbamylation and/or binding of inhibitory sugar phosphates) contributes to the loss of Rubisco activity particularly under drought and heat stress (Table 3). Finally, a significant relationship between Rubisco in vitro parameters and in vivo CO_2 assimilation was found for all environmental factors. For those factors related to soil toxicity (salt, heavy metals, etc.), to the atmosphere (O_3), or to solar irradiance (UV-B), the decrease in CO_2 assimilation with stress is associated with decreased Rubisco content (Table 2). For those factors which directly affect the availability of CO_2 for carboxylation (drought, $[\text{CO}_2]$), or high temperature extremes which directly affect chloroplast function, the results indicate that the reduction in CO_2 assimilation is strongly associated with reduced state of activation of Rubisco (e.g., which may occur by reduced level or function of Rubisco activation). In general, this down-regulation in Rubisco activity may occur through signal transduction processes as a consequence of the stress inhibiting some part of photosynthesis or subsequent acclimation to stress under the prevailing environmental conditions.

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