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Potential improvement of photosynthetic CO_2 assimilation in crops by exploiting the natural variation in the temperature response of Rubisco catalytic traits

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The enhancement of the photosynthetic capacity of crops by the expression of more efficient Rubisco versions has been a main target in the field of plant photosynthesis improvement. However, such an increase in the photosynthetic efficiency will depend on the environmental conditions and on the responsiveness of Rubisco to temperature and CO_2 availability. After an exhaustive compilation and standardization of the data published so far, a large natural variability in the thermal responses of Rubisco kinetic parameters in higher plant species was revealed. The variability observed was related to the photosynthetic type but a limited adaptation to the species thermal environment was found. We provide theoretical evidence that the existence of distinctive Rubisco responses to varying temperature and CO_2 concentration constitutes a promising avenue for increasing the photosynthetic capacity of important crops under future climatic conditions.

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Introduction

The enzyme ribulose-1,5-bisphosphate carboxylase/oxygenase (Rubisco) catalyzes the addition of CO_2 to ribulose-1,5-bisphosphate (RuBP), which is quantitatively the most significant reaction converting inorganic carbon to organic carbon, thereby sustaining the vast majority of food webs on Earth. Despite being one of the most studied proteins since its discovery in 1957 [1], some basic aspects of its catalytic functioning remain unresolved. Notoriously, we still cannot fully explain why one of the most important enzymes for life on the planet is incapable of differentiating between CO_2 and O_2 as the substrate. Some studies argue that Rubisco is fully optimized to give the best possible performance depending on the environment [2,3], and others suggest that the carboxylase–oxygenase duality of the enzyme has been a key factor in the atmospheric dynamics of Earth [4]. Even, a recent study indicates that Rubisco catalytic performance is not so promiscuous when compared to other chemically related enzymes [5•]. Either way, the reaction of Rubisco with O_2 leads to releasing part of previously fixed carbon and nitrogen through photorespiration, requiring an extra energy investment [6]. This imperfect discrimination between CO_2 and O_2, together with a relatively slow carboxylation turnover rate and a low affinity for CO_2 implies that photosynthetic organisms maintain Rubisco at very high concentrations to support autotrophy [7]. It is not, therefore, surprising that engineering Rubisco for better performance in terms of CO_2 fixation rates has been one of the main targets in the field of plant improvement in the last years [8•,9•,10,11,12••].

The estimates of theoretical models endorse the hopes of Rubisco improvement, predicting very significant increases in the photosynthetic capacity of crops if their native Rubisco was replaced by foreign naturally occurring Rubiscos displaying better catalytic properties [13,14]. An important research target is therefore to find more efficient naturally occurring versions of Rubisco, and to understand the molecular causes of the variability in the catalytic traits, allowing the design of the improved Rubiscos in the laboratory. The data available so far suggest that environmental temperature and availability of CO_2 and O_2 are the environmental factors that have induced changes along evolution in the catalytic properties of Rubisco when comparing species from contrasting ecology and phylogeny [14,15,16••]. Actually, the quantitative impact of Rubisco kinetic traits on the carbon fixation rate depends on temperature, $[CO_2]$ and $[O_2]$ at the enzyme catalytic sites. Hence, the predicted increase in the atmospheric $[CO_2]$ will favor RuBP carboxylation over oxygenation, but this effect will be lower in warmer temperatures, since the ratio of dissolved $[O_2]/[CO_2]$ in chloroplasts increases with temperature. Furthermore, temperature itself has also a direct impact on the catalytic performance of Rubisco. The maximum carboxylase turnover rate (k_{cat}^{c}) of Rubisco increases up to 50–60°C, while the Rubisco specificity factor ($S_{c/o}$) decreases and the Michaelis–Menten constant for CO_2 (K_c) increases with increasing temperature [17,18,19••]. Studies reporting temperature effects on the Michaelis–Menten constant for O_2 (K_o) show contradictory results, with K_o being almost independent of temperature in some cases, while increasing or even decreasing with increasing temperature in other cases [20,21–24,25••,26••]. Despite the general trends for k_{cat}^{c}, $S_{c/o}$ and K_c, differences in the thermal dependencies of Rubisco kinetics have been reported between different photosynthetic organisms, even among closely related species [18,19••,27]. Furthermore, the variation in Rubisco temperature responses has been shown to depend on species' climate and photosynthetic mechanism, with lower energy of activation (ΔH_a) for k_{cat}^{c} and K_c in C_4 compared to C_3 plants [19••,26••,27] and lower ΔH_a for k_{cat}^{c} in C_3 plants from cool habitats (C_3^{cool}) relative to C_3 plants from warm habitats (C_3^{warm}) [18]. Rubisco-limited CO_2 gross assimilation rate ($A_{Rubisco}$) modelled at varying temperatures and chloroplastic CO_2 concentrations (C_c) suggested improved photosynthetic performance of C_3^{cool} plants at lower temperatures, and C_3^{warm} plants at higher temperatures, especially at higher CO_2 concentration [19••]. However, these previous analyses were based on a limited number of species; thus, more data on the temperature response of Rubisco kinetics from a wider range of species are needed to confirm the observed trends.

The present review updates and summarizes the information on the thermal sensitivity of Rubisco catalytic traits across spermatophytes, including the recent large screening studies published during the last two years [16••,25••,26••,28], and evaluates the ecological constraints of trait variability and the potential capacity for crop CO_2 assimilation improvement under certain environmental conditions by introducing contrasting Rubisco variants.

Spanning the temperature response of Rubisco catalytic traits among Spermatophyta: evidence of adaptation in relation to the photosynthetic mechanism but limited adaptation to the thermal environment

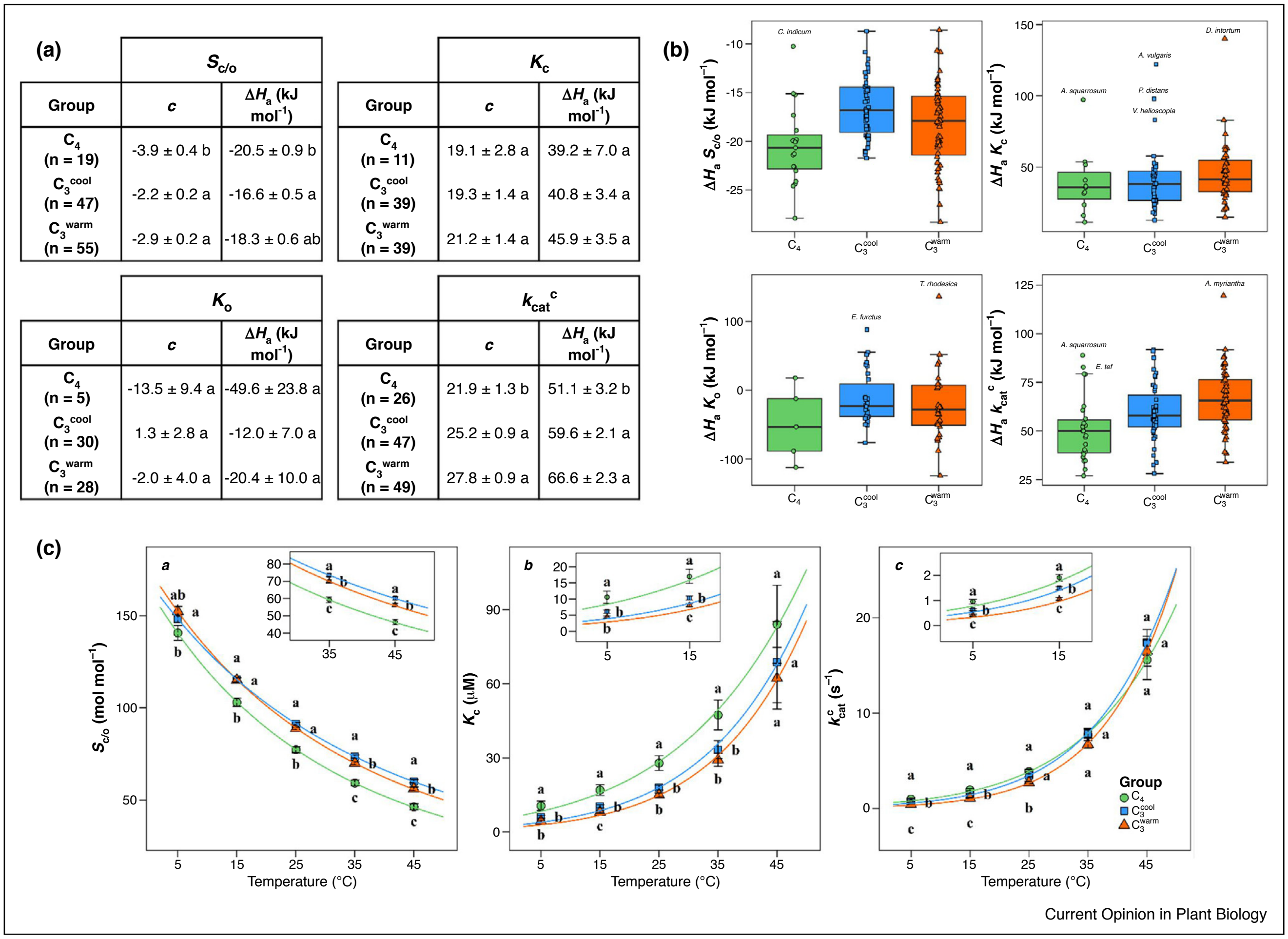
A total of 138 Spermatophyta species, for which at least one of the main Rubisco kinetic characteristics had been reported at three or more different temperatures in previous studies, were compiled, filtered, and standardized according to Galmés *et al.* [19••] to account for the effects of study-to-study methodological differences (Supplementary material). From these data, the energy of activation (ΔH_a) and the scaling constant (c) for the catalytic traits of Rubisco were obtained by applying an Arrhenius-type temperature response function [19••].

There was a large interspecific variability in ΔH_a for Rubisco catalytic traits, especially for K_c, K_o, and k_{cat}^{c}, across the compiled data, even within C_4 species, C_3^{warm} species, and C_3^{cool} species (Figure 1a,b). Despite this ample variability, significant differences were observed when comparing group averages. In particular, Rubisco in C_4 species has lower $S_{c/o}$ values than those in C_3 species at the range of studied temperatures, and also higher thermal sensitivity (more negative ΔH_a) for $S_{c/o}$ than Rubisco in C_3^{cool} (Figure 1a,c), while C_4 Rubisco has higher values than C_3^{warm} Rubisco at temperatures ≤25°C and lower thermal sensitivity (lower ΔH_a) for k_{cat}^{c} than both C_3^{cool} and C_3^{warm} Rubiscos. The same differences in Rubisco thermal dependency responses between C_4 and C_3 species were already observed in previous studies [19••,26••,27]. However, in contrast to these previous studies, no significant differences were observed between C_4 and C_3 Rubiscos in ΔH_a for K_c, although C_4 species possess K_c values higher than those reported for C_3 species at physiologically relevant temperatures. These results indicate that a significant increase in the number of species included in the present analysis evened out the differences in K_c temperature responses among species with different photosynthetic type.

Overall, the present analysis strengthens the evidence that C_4 and C_3 species evolved towards different temperature sensitivities of Rubisco kinetics, as suggested before [16••,27], with C_4 Rubiscos having a 18% larger ΔH_a for $S_{c/o}$ and 20% smaller ΔH_a for k_{cat}^{c} (Figure 1a). We also found a positive relationship between ΔH_a for $S_{c/o}$ and ΔH_a for k_{cat}^{c} ($P < 0.001$, $r^2 = 0.102$, data not shown) that has not been previously observed in smaller sets of data [19••]. This may indicate that the widely assumed trade-offs between these Rubisco catalytic traits at 25°C ($S_{c/o}$ decreases like the square root of k_{cat}^{c}) [2,3,16••] vary with temperature, and that contrasting relationships are principally possible. This fact is a critical cornerstone to find natural versions of Rubisco of particular interest for future attempts to engineer this enzyme for contrasting environmental conditions. For engineering foreign Rubiscos into crops, the outliers of these relationships as well as those displaying extreme behavior (Figure 1b) are of particular interest.

The comparison of the temperature sensitivity of Rubisco kinetics between C_3^{cool} and C_3^{warm} species revealed no differences in ΔH_a for any kinetic parameter (Figure 1a, c), even though some significant differences were found in the average values at discrete temperatures (e.g. higher k_{cat}^{c} in C_3^{cool} species at temperatures ≤25°C and higher $S_{c/o}$ in C_3^{cool} species at temperatures ≥35°C, compared with C_3^{warm} species). These results are in contrast to Galmés *et al.* [18], who obtained a lower ΔH_a for k_{cat}^{c} in C_3^{cool} compared with C_3^{warm} species. Also, we found non-significant relationship between the species optimum growth temperature and ΔH_a for all kinetic traits, except for $S_{c/o}$ ($P < 0.02$, $r^2 = 0.12$, data not shown) indicating a higher temperature sensitivity of this

Figure 1



(a)

	$S_{c/o}$	
Group	*c*	ΔH_a (kJ mol^{-1})
C_4 (n = 19)	-3.9 ± 0.4 b	-20.5 ± 0.9 b
C_3^{cool} (n = 47)	-2.2 ± 0.2 a	-16.6 ± 0.5 a
C_3^{warm} (n = 55)	-2.9 ± 0.2 a	-18.3 ± 0.6 ab

	K_c	
Group	*c*	ΔH_a (kJ mol^{-1})
C_4 (n = 11)	19.1 ± 2.8 a	39.2 ± 7.0 a
C_3^{cool} (n = 39)	19.3 ± 1.4 a	40.8 ± 3.4 a
C_3^{warm} (n = 39)	21.2 ± 1.4 a	45.9 ± 3.5 a

	K_o	
Group	*c*	ΔH_a (kJ mol^{-1})
C_4 (n = 5)	-13.5 ± 9.4 a	-49.6 ± 23.8 a
C_3^{cool} (n = 30)	1.3 ± 2.8 a	-12.0 ± 7.0 a
C_3^{warm} (n = 28)	-2.0 ± 4.0 a	-20.4 ± 10.0 a

	k_{cat}^c	
Group	*c*	ΔH_a (kJ mol^{-1})
C_4 (n = 26)	21.9 ± 1.3 b	51.1 ± 3.2 b
C_3^{cool} (n = 47)	25.2 ± 0.9 a	59.6 ± 2.1 a
C_3^{warm} (n = 49)	27.8 ± 0.9 a	66.6 ± 2.3 a

Current Opinion in Plant Biology

Thermal dependencies of *in vitro* Rubisco kinetic traits from Spermatophyta. Species were classified according to their photosynthetic mechanism (C_3 vs. C_4) and C_3 species were further classified as warm ($T_{growth} \geq 25$ °C), and cool-temperature ($T_{growth} < 25$ °C) species according to their optimum growth temperature (T_{growth}). Estimates of T_{growth} were obtained from literature or assigned according to their climate of origin as in Galmés *et al.* [18,19••]. The arbitrary threshold of 25 °C was used to separate cool and warm C_3 as in analogous studies [18,19••,40].

Rubisco kinetic data compilation of Galmés et al. [18,19••] was extended with new data from recent studies [16••,25••,26••,28], overall reporting Rubisco kinetic traits at three or more different temperatures for a large number of Spermatophyta species. All original data were corrected using the formulation already described by Galmés *et al.* [18,19••] to account for differences in the assay buffer composition that affected the ionic strength and the acidity constant of dissolved CO_2 (pK_a,CO_2), as well as for differences in the CO_2 and O_2 solubilities used, in order to remove the effects of study-to-study differences in Rubisco kinetic assays.

(A) Mean and standard error of the activation energy (ΔH_a) and the scaling constant (*c*) for each group of species after fitting the corrected Rubisco kinetic traits obtained from the original data at the different temperatures assayed in each study by the Arrhenius-type temperature response function, according to Galmés *et al.* [19••] (Supplementary material). Only the initial rising part was fitted in the case of $k_{cat}{}^{c}$ as the data above the thermal optimum were missing in most cases. Poor fits with $r^2 < 0.7$ were eliminated from the analysis. In the case of the species reported by more than one study, an average for each species Rubisco thermal dependencies was obtained before calculating the mean and the standard error for each group of species. Different letters indicate statistically significant differences ($P < 0.05$) between the three groups of species. After normality (Anderson-Darling test) and homogeneity of variances (Levene's test) were confirmed, means were compared by the analysis of variance (ANOVA) followed by Duncan's test. For those data whose normality or homogeneity of variances was not confirmed, Kruskal–Wallis test with Bonferroni correction for multiple comparison was done instead of the ANOVA. $S_{c/o}$, Rubisco specificity factor; K_c, K_o, semi-saturation constants for CO_2 and O_2, respectively; $k_{cat}{}^{c}$, the maximum carboxylase turnover rate; *n*, number of species for each Rubisco catalytic constant and group.

(B) Box plots depiction of ΔH_a for Rubisco kinetic traits of each group of species. The horizontal lines represent the median, and the box and whisker represent the 25 to 75 percentile and minimum to maximum distributions of the data, respectively. Single points out of this range represent the values considered outlayers (*Chrysanthellum indicum* – ΔH_a for $S_{c/o}$; *Agriophyllum squarrosum*, *Artemisia vulgaris*, *Puccinellia distans*, *Euphorbia helioscopia* and *Desmodium intortum* – ΔH_a for K_c; *Elymus farctus* and *Tephrosia rhodesica* – ΔH_a for K_o; *A. squarrosum*, *Eragrostis tef* and *Artemisia myriantha* - ΔH_a for $k^c{}_{cat}$).

(C) Arrhenius-type temperature response fits for $S_{c/o}$, K_c and $k_{cat}{}^{c}$. Circles, squares and triangles represent mean values for C_4, $C_3{}^{cool}$ and $C_3{}^{warm}$ species at each temperature, respectively; bars represent standard errors, and different letters indicate statistically significant differences parameter at warmer environments. Therefore, these data collectively suggest limited adaptive changes in Rubisco kinetic temperature sensitivity in response to the species thermal environment. Despite the slight trend for a higher thermal sensitivity of Rubisco kinetic traits in C_3^{warm} relative to C_3^{cool} species (Figure 1a), these differences are statistically not significant, indicative that factors other than the environmental temperature may have shaped thermal Rubisco adaptation. However, we also note that the recent large-scale screening studies have investigated Rubisco over a very limited thermal range, that is 20–30°C in Orr *et al.* [25••]. This limitation is particularly relevant for k_{cat}^{c} that has a thermal optimum at 50–55°C [18]. Furthermore, the current dataset is dominated by crops whose origin is, in most cases, warm environments, while the current distribution of their cultivation has been frequently shifted to cooler temperate regions. In crops, breeding has also resulted in multiple hybridizations and polyploidization and combinations of Rubisco large and small subunits that do not necessarily occur in Nature. Given that small subunits can play a critical role in Rubisco catalytic traits [29], crop breeding history itself might have resulted in the loss of adaptive signal in Rubisco traits. In fact, a significantly lower thermal sensitivity of k_{cat}^{c} in crops relative to wild species was obtained in the present dataset, and also higher $S_{c/o}$ and lower K_c, K_o and/or k_{cat}^{c} were obtained at discrete temperatures for crop versus wild species (data not shown). Future studies mapping Rubisco component origin and analyzing the effects of Rubisco small subunits on the temperature response of different catalytic traits are needed to test this hypothesis.

Remarkable is the wide variability of data regarding the thermal sensitivity of K_o, including positive and negative ΔH_a values ranging from -124 to 136 kJ mol^{-1} in the present dataset (Figure 1b). Although the amount of data of ΔH_a for K_o have significantly increased in comparison to previous compilations of the thermal sensitivity of Rubisco kinetics [19••], a large variability was also observed even for the same species across different studies, suggesting the presence of methodological problems which preclude obtaining reliable data. Actually, compared to the rest of the kinetic traits, the fit of K_o values to Arrhenius-equation was much poorer (32 out of 91 species with $r^2 < 0.7$ for K_o and 17 out of these 32 species with $r^2 < 0.2$). Most K_o values included in this dataset were obtained indirectly from the inhibition of the carboxylase activity between two different O_2 concentrations using the radiolabel method [25••,26••]. Only the values of K_o in Badger and Collatz [21] and in Lehnherr *et al.* [23] were based on the oxygen-electrode method and these studies showed positive values of ΔH_a for K_o, which is also the case of data from *in vivo* estimations [19••]. Recently, Boyd *et al.* [30•] used both radiolabel (indirect method for K_o determination) and membrane inlet mass spectrometry (MIMS; direct method for K_o determination) to study the temperature response of Rubisco kinetics in *Arabidopsis* and obtained positive and almost identical values for the ΔH_a for K_o with both methods. To elucidate whether the discrepancies in K_o temperature responses are due to true interspecific variability or caused by methodological artefacts, more direct measurements about the thermal sensitivity of the oxygenase activity of Rubisco in contrasting species are required. Under specific environmental conditions, like high temperature and drought stress, the oxygenase activity of Rubisco in C_3 species is enhanced, becoming a major determinant for the plant carbon balance. Therefore, having reliable information of thermal sensitivity of K_o is a critical factor for modelling the photosynthesis response to future climatic conditions.

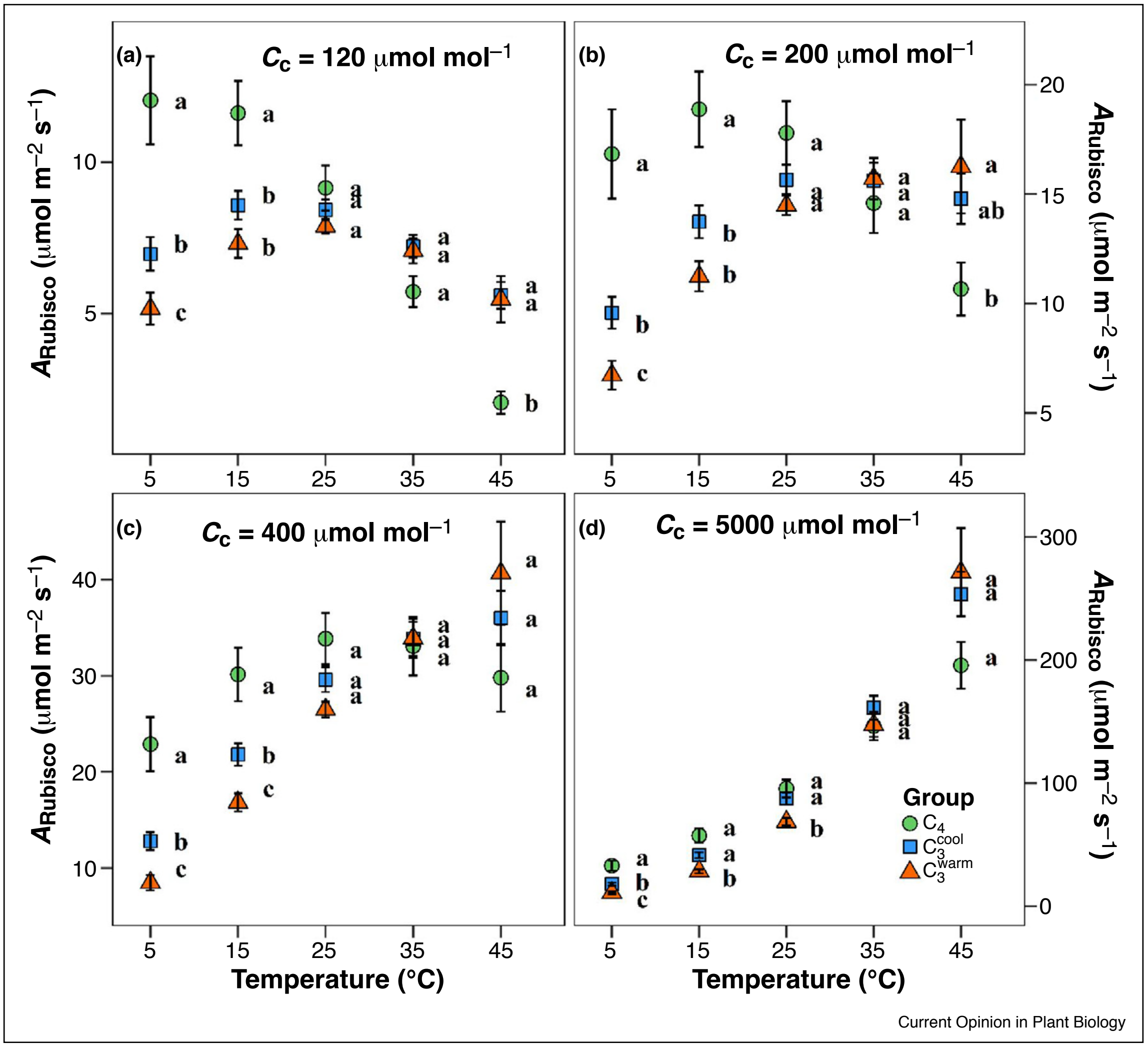
Modelling the assimilatory potential of contrasting Rubisco variants indicates that large improvements may be achieved in the photosynthetic capacity of crops under varying environmental conditions

The simulation analysis based on the kinetic traits from all species included in this compilation demonstrates that Rubisco adaptation to temperature can lead to significant differences in the Rubisco-based assimilatory potential ($A_{Rubisco}$) among different groups (Figure 2). For instance, Rubisco from C_3^{cool} species provides higher $A_{Rubisco}$ than C_3^{warm} Rubisco at lower temperatures, independently of the chloroplastic CO_2 concentration (C_c). But, contrarily to the results of Galmés *et al.* [19••], $A_{Rubisco}$ of C_3^{warm} species was not significantly higher than that of C_3^{cool} species at elevated temperatures.

Compared with Rubisco from C_3 species, C_4 Rubisco provided a significantly lower assimilatory potential at temperatures higher than 35°C and at lower C_c (120–200 µmol mol^{-1}), and significantly higher assimilatory potential at lower temperatures, irrespective of C_c (Figure 2). The result was maintained when considering the different C_4 subtypes, although PCK subtype tend to present higher $A_{Rubisco}$ than NAD-ME and NADP-ME subtypes at the range of studied temperatures (data not shown), in accordance with previous reports [16••]. This surprising finding may be due to the higher thermal sensitivity of $S_{c/o}$ and the lower thermal sensitivity of k_{cat}^{c} in C_4 Rubiscos (Figure 1a), and indicates a poor performance of C_4 Rubisco at high temperatures when

(Figure 1 Legend Continued) ($P < 0.05$ according to either one-way ANOVA followed by Duncan's test or Kruskal–Wallis test with Bonferroni correction. The latter statistical test was used when data normality or homogeneity of variances was not confirmed) between the three groups of species at each temperature. Since the temperatures used to measure Rubisco catalytic constants were different across the compiled studies, the Arrhenius-type equations were further used to calculate the discrete values of each trait at 5, 15, 25, 35 and 45 °C for each species.

Figure 2



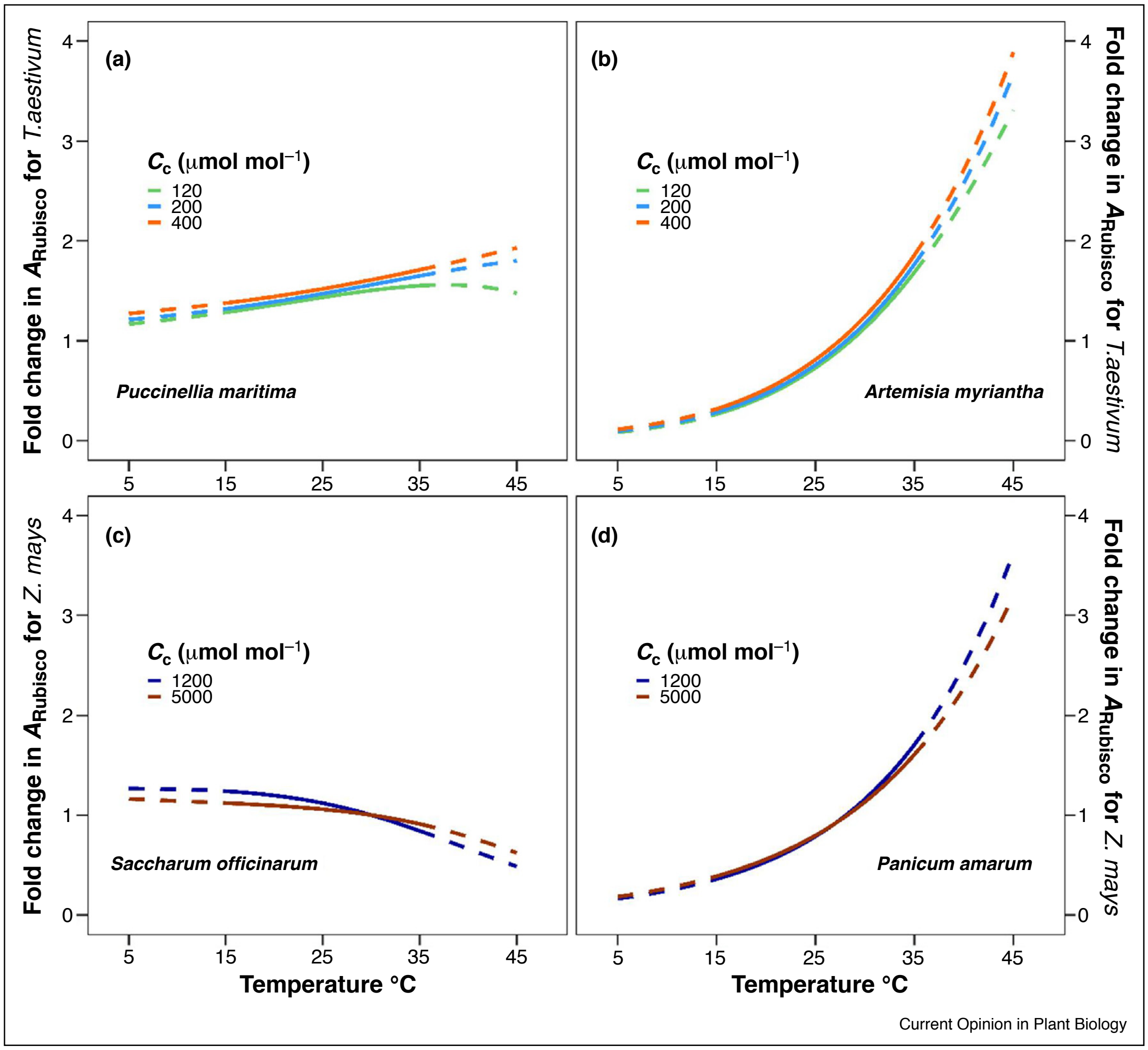
Current Opinion in Plant Biology

Modelling the effect of different temperature responses of Rubisco kinetic traits in C_3^{cool} (blue squares, n = 32), C_3^{warm} (red triangles, n = 28) and C_4 (green circles, n = 13) on the Rubisco-limited gross assimilation rate ($A_{Rubisco}$) at chloroplastic CO_2 concentrations (C_c) of 120 (*a*), 200 (*b*), 400 (*c*) and 5000 (*d*) μmol mol^{-1}. The photosynthesis model of Farquhar *et al.* [41] was used to model $A_{Rubisco}$ at the different temperatures and C_c, using the values for the temperature dependence parameters of $S_{c/o}$, K_c, K_o and k_{cat}^c for all species in the compiled database (Supplementary material, only species with the explained variance of trait vs. temperature response curve fits, r^2, equal or greater than 0.7 were included in the analysis) and a leaf Rubisco content of 2 g m^{-2} (equivalent to a concentration of 29 μmol catalytic sites m^{-2}). The species reported by Sharwood *et al.* [16••] were modelled by using the effective Michaelis-Menten constant for CO_2 under 21% O_2 ($K_c^{air} = K_c(1+[O_2]/K_o)$ instead of individual values of K_c and K_o in the photosynthesis model [41]. Gross assimilation was simulated here to avoid confounding effects of mitochondrial respiration. Although k_{cat}^c has a thermal optimum, typically at 50 °C or higher [18], in this analysis we only use the activation energy for the initial rising part due to lack of the higher temperature estimates of k_{cat}^c for the bulk of the recent screening studies. $A_{Rubisco}$ represents the potential estimate of photosynthesis rate supported by a given set of Rubisco characteristics under RuBP-saturated conditions. Different values of C_c were chosen to represent a typical C_c of a non-stressed C_3 plant (200 μmol mol^{-1}), a drought-stressed C3 plant (120 μmol mol^{-1}), a non-stressed C_3 plant under increased atmospheric CO_2 (400 μmol mol^{-1}) and a possible C_c for a C_4 plant (5000 μmol mol^{-1}). Circles, squares and triangles represent mean values for C_4, C_3^{cool} and C_3^{warm} species at each temperature, respectively; bars represent standard errors, and different letters indicate statistically significant differences ($P < 0.05$ according to either one-way ANOVA followed by Duncan's test or Kruskal–Wallis test with Bonferroni correction. The non-parametric test was used when data normality or homogeneity of variances was not confirmed) between the three groups of species for each temperature.

operates outside the range of chloroplastic CO_2 concentrations where it has evolved, but a generalized improvement in the performance over C_3 Rubisco at low temperatures. This is an important outcome, suggesting that the improvement of the photosynthetic capacity in C_3 species by transferring C_4 Rubiscos will generally only succeed at temperatures ≤15°C, contrary to what was previously suggested by Sharwood *et al.* [11,16••]. The former study claimed that Rubisco of some C_4 graminoid species might be of potential benefit to C_3-photosynthesis under current and future atmospheric CO_2 pressures at temperatures equal or higher than 25°C. However, Sharwood *et al.* [11,16••] only compared the assimilatory potential of these C_4 monocot Rubiscos with the assimilatory potential of tobacco and wheat Rubisco, and, as mentioned above, there is a wide variability in Rubisco catalytic traits among C_3 species, even a large study-to-study variability for the same species; therefore, it is necessary to be cautious when generalizing modeling responses based on a limited number of species. The effects of Rubisco replacements vary in dependence on the native and alien Rubisco characteristics, and it is possible to find unique alien/native Rubisco pairs where photosynthesis improvement occurs under different environmental conditions out of the observed general trends for C_3 and C_4 Rubiscos (see Figure 3). Overall, this simulation analysis clearly demonstrates that future attempts to increase the photosynthetic capacity by means of Rubisco design must consider the climatic conditions in which the target species will be cultivated, in particular, the prevalent thermal environment and the existence of processes limiting or promoting the transfer of atmospheric CO_2 to the sites of carboxylation.

The high variability in the thermal dependency of Rubisco kinetics across Spermatophyta allows testing

Figure 3



Fold change of the Rubisco-limited gross assimilation rate ($A_{Rubisco}$) of *Triticum aestivum* (*a, b*) and *Zea mays* (*c, d*) after replacement of the native Rubisco by foreign Rubiscos of *Puccinellia maritima* (*a*), *Artemisia myriantha* (*b*), *Saccharum officinarum* (*c*) and *Panicum amarum* (*d*). The photosynthesis model of Farquhar *et al.* [41] was used to model $A_{Rubisco}$ at the different temperatures and physiological concentrations of chloroplastic CO_2 (C_c) for the C_3 and the C_4 species, considering the Rubisco temperature parameters for each species (Supplementary material) and a constant leaf Rubisco content of 2 g m^{-2}.

how much A_{Rubisco} would change in two important crops, wheat and maize, if their native Rubisco were replaced by Rubiscos exhibiting the most extreme temperature responses. As for wheat, Rubisco from *Puccinellia maritima*, a C_3^{cool} species, would result in higher A_{Rubisco} especially at elevated temperatures (Figure 3a). The replacement of wheat Rubisco by that from *Artemisia myriantha*, a C_3^{warm} species, would result in a higher CO_2 assimilation capacity at temperatures above 30°C (Figure 3b). Among C_4 plants, Rubisco from *Saccharum officinarum* and from *Panicum amarum* would allow increasing A_{Rubisco} of maize at low and high temperatures, respectively (Figure 3c,d). These results demonstrate that there is place for CO_2 fixation improvement in C_3 and C_4 crops by engineering Rubisco.

Current status of Rubisco transplantation in crops

Although the replacement of the gene coding for the Rubisco large subunit (*rbcL*) of tobacco with foreign versions from phylogenetically close species has been successful, the scientific community has yet failed to engineer a foreign Rubisco sustaining, at least, the *in vivo* CO_2 assimilation rates of the native Rubisco [10,31]. This is mainly related to the inability to express sufficient amount of functional Rubisco, due to problems in the biogenesis, folding and assembly of foreign versions [32]. We focus on spermatophytes because the vast majority of available data, in particular, those provided by the screening studies, correspond to this group. Although Rubisco from other domains of life might have unique characteristics [18,19••,33–36], replacement and successful expression of functional Rubisco to result in a positive net carbon gain under current atmospheric CO_2 conditions is currently only feasible among higher plants [12••,37••]. Recently, large advances in understanding Rubisco biogenesis and repair have been achieved [38] and future efforts will continue in this direction [12••]. Moreover, for having success in the increase of the *in vivo* CO_2 assimilation rates by transplantomic plants with more efficient Rubisco versions at warmer temperatures, it must be also necessary to take into account the thermal stability of Rubisco activase [18,39•].

Conclusion

The comprehensive analysis of the data available so far demonstrates a high variability in the thermal dependence of Rubisco catalytic traits among higher plants. Part of this variability is related to the photosynthetic type, but only a limited adaptation to the climatic origin of the species has been observed due to large within group variation among species from different thermal environments. Nevertheless, the extensive variability includes a number of unique species whose Rubisco kinetic traits display a distinctive response to varying temperature and CO_2 concentration. The simulation of the benefits of using these specific Rubisco versions in future attempts to improve the photosynthetic capacity of important crops for global food security offers highly promising revenues in changing climates.

Conflict of interest statement

Nothing declared.

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Appendix A. Supplementary data

Supplementary material related to this article can be found, in the online version, at doi:https://doi.org/10.1016/j.pbi.2019.05.002.

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- • of special interest
- •• of outstanding interest

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