

Short communication

A mechanistic evaluation of photosynthetic acclimation at elevated CO₂

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Abstract

Plants grown at elevated $p\text{CO}_2$ often fail to sustain the initial stimulation of net CO₂ uptake rate (A). This reduced, acclimated, stimulation of A often occurs concomitantly with a reduction in the maximum carboxylation velocity ($V_{c,\text{max}}$) of Rubisco. To investigate this relationship we used the Farquhar model of C₃ photosynthesis to predict the minimum $V_{c,\text{max}}$ capable of supporting the acclimated stimulation in A observed at elevated $p\text{CO}_2$. For a wide range of species grown at elevated $p\text{CO}_2$ under contrasting conditions we found a strong correlation between observed and predicted values of $V_{c,\text{max}}$. This exercise mechanistically and quantitatively demonstrated that the observed acclimated stimulation of A and the simultaneous decrease in $V_{c,\text{max}}$ observed at elevated $p\text{CO}_2$ is mechanistically consistent. With the exception of plants grown at a high elevated $p\text{CO}_2$ (> 90 Pa), which show evidence of an excess investment in Rubisco, the failure to maintain the initial stimulation of A is almost entirely attributable to the decrease in $V_{c,\text{max}}$ and investment in Rubisco is coupled to requirements.

Abbreviations: A , net CO₂ uptake ($\mu\text{mol m}^{-2}\text{s}^{-1}$); A_{tmv} , theoretical maximum A for given conditions of I , T_{leaf} , elevated $p\text{CO}_2$ and the $V_{c,\text{max}}$ and J_{max} observed at current $p\text{CO}_2$ ($\mu\text{mol m}^{-2}\text{s}^{-1}$); c_a ambient CO₂ concentration ($\mu\text{mol mol}^{-1}$); c_i , CO₂ concentration in the substomatal cavity ($\mu\text{mol mol}^{-1}$); I , photosynthetic quantum flux density ($\mu\text{mol m}^{-2}\text{s}^{-1}$); J_{max} , maximum *in vivo* rate of electron transport ($\mu\text{mol m}^{-2}\text{s}^{-1}$); $p\text{CO}_2$, partial pressure of CO₂; m , gradient of a correlation; T_{leaf} , leaf temperature (°C); $V_{c,\text{max}}$, maximum *in vivo* rate of ribulose 1,5 bisphosphate-saturated carboxylation ($\mu\text{mol m}^{-2}\text{s}^{-1}$); WIMOVAC, Windows Intuitive Model of Vegetation response to Atmosphere and Climate Change.

Keywords: acclimation, C₃ photosynthesis, elevated carbon dioxide, modelling, Rubisco

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Introduction

Growth at elevated $p\text{CO}_2$ leads to the stimulation of net CO₂ uptake (A). As plants acclimate to growth at elevated $p\text{CO}_2$ they often fail to sustain the initial, and for given conditions, maximal stimulation of A (Gunderson & Wullschleger 1994; Curtis 1996; Drake *et al.* 1997). Acclimation of the photosynthetic apparatus to growth at elevated $p\text{CO}_2$ can involve several responses (Sage 1994; Sage *et al.* 1989; Ziska *et al.* 1991; van Oosten

et al. 1994; Nie *et al.* 1995; van Oosten & Besford 1995; Osborne *et al.* 1997; Rogers *et al.* 1998). However, a decrease in the amount of active Rubisco is the most consistently observed trait of photosynthetic acclimation (Long & Drake 1992). Commonly, this decrease in the maximum carboxylation velocity ($V_{c,\text{max}}$) of Rubisco occurs concomitantly with an elevated $p\text{CO}_2$ acclimated, stimulation in A (Drake *et al.* 1997). This study mechanistically evaluates the importance of an observed decrease in $V_{c,\text{max}}$ in causing the failure of plants acclimated to growth at elevated $p\text{CO}_2$ to attain their

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maximum theoretical A (A_{tm}) at their given elevated $p\text{CO}_2$. An increase in A at elevated $p\text{CO}_2$ is possible even if there is a reduction in $V_{c,max}$, provided that the increase in A due to elevated substrate concentration (c_i) and increased competitive inhibition of oxygenation is greater than the effect of the reduction in $V_{c,max}$ (Long & Drake 1992). However, there has been no quantitative study that examined the wide range of experimental evidence to ensure that this assumption holds true for plants that have acclimated to growth at elevated $p\text{CO}_2$.

We obtained 48 sets of leaf gas-exchange parameters from 24 studies encompassing a range of species and growth conditions and used the model of Farquhar *et al.* (1980) to answer three questions.

1 In plants acclimated to elevated $p\text{CO}_2$, is the observed reduction in $V_{c,max}$ mechanistically consistent with the reported acclimated stimulation of A ?

2 Does the decrease in $V_{c,max}$ observed in these plants account for the less than theoretically maximal stimulation of A at elevated $p\text{CO}_2$?

3 Is there an over investment in Rubisco in plants acclimated to growth at elevated $p\text{CO}_2$?

Materials and methods

Data acquisition

A computerized literature search was rejected, based on the experience of Wullschleger (1993), in favour of manually searching journals for studies that provided the parameters necessary for our calculations. Several relevant reviews were used as a starting point (Long & Drake 1992; Gunderson & Wullschleger 1994; Sage 1994; Curtis 1996; Drake *et al.* 1997; Saxe *et al.* 1998). Studies were selected solely on the basis of providing enough information to determine values for; A , I , T_{leaf} , $p\text{CO}_2$ and $V_{c,max}$ at current and elevated $p\text{CO}_2$. Where necessary $V_{c,max}$ and, where possible, J_{max} were calculated from the response of A to c_i following the procedure of Wullschleger (1993) and incorporating the temperature correction of McMurtrie & Wang (1993).

Calculations and assumptions

The WIMOVAC system (Humphries & Long 1995; Long *et al.* 1996) was used to simulate the effects of elevated $p\text{CO}_2$ on photosynthesis. The equations used to model leaf photosynthesis, based on those described by Farquhar *et al.* (1980), are listed in Long & Drake (1992) with the exception of the term for electron transport rate that can be found in Evans & Farquhar (1991). For a wide range of C_3 species stomatal conductance appears to interact with CO_2 uptake to maintain a c_i which is a

constant proportion of the ambient concentration of CO_2 (c_a). In plants grown in the present atmosphere c_i is maintained at 70% of c_a (Wong *et al.* 1979; von Caemmerer & Farquhar 1981; Long & Drake 1992). Drake *et al.* (1997) found that the mean and range of c_i/c_a were nearly identical for plants grown at current and elevated $p\text{CO}_2$. They concluded that although the stomatal conductance is reduced at elevated $p\text{CO}_2$, this does not by itself limit photosynthesis. Therefore, in our model c_i was assumed to be 70% of growth $p\text{CO}_2$. Following McMurtrie & Wang (1993) dark respiration was assumed to be $1 \mu\text{mol m}^{-2} \text{s}^{-1}$.

Wullschleger (1993) analysed A/c_i curves from 109 species and observed a strong correlation between $V_{c,max}$ and J_{max} . When there was insufficient information to determine J_{max} , the regression equation; $J_{max} = 29.1 + 1.64 V_{c,max}$ (Wullschleger 1993) was used to estimate J_{max} . As a test, we correlated the data obtained for the prediction of $V_{c,max}$ using the quoted J_{max} and the estimated J_{max} . There was an extremely strong correlation ($r^2 = 0.998$, $t_{(2)25} P < 0.001$) and near 1:1 relationship ($m = 0.99$) between results obtained using the quoted and estimated J_{max} values. The estimated value of J_{max} was used only to facilitate prediction of $V_{c,max}$ when J_{max} could not be determined from available data. This method was not used for generating J_{max} values used in the correlation of predicted and observed J_{max} .

For each data set we entered values for I , T_{leaf} , $p\text{CO}_2$, $V_{c,max}$ and J_{max} obtained at current $p\text{CO}_2$ and then used WIMOVAC to predict A at current $p\text{CO}_2$. Without adjusting the photosynthetic parameters entered for current $p\text{CO}_2$ we used WIMOVAC to predict the minimum $V_{c,max}$ necessary to support the observed acclimated stimulation in A at the given elevated $p\text{CO}_2$. This value was termed predicted $V_{c,max}$. This process was repeated to predict the minimum J_{max} necessary to support the observed stimulation in A . We also used WIMOVAC to calculate the A that could be attained at the given elevated $p\text{CO}_2$ if there were no change in any of the photosynthetic parameters observed under current $p\text{CO}_2$, i.e. no acclimation. This value, termed A_{tm} , represents the maximum theoretical A attainable at a given elevated $p\text{CO}_2$ for current $p\text{CO}_2$ conditions of I , T_{leaf} , $V_{c,max}$ and J_{max} . The A_{tm} is analogous to A observed when plants developed at current $p\text{CO}_2$ are measured at elevated $p\text{CO}_2$ (initial stimulation).

Statistical analysis

Linear correlation and the Student's t -tests associated with Fig. 1 were performed as described by Zar (1999).

Table 1 List of species, growth conditions and source of datasets used for determination of predicted $V_{c,max}$ (all) and J_{max} (*).

Species	CO ₂ fumigation	Cofactor	<i>n</i>	Reference
<i>Acacia mangium</i>	CE		1	Ziska <i>et al.</i> (1991) *
<i>Agrostis capillaris</i>	OTC	N-supply	2	Davey <i>et al.</i> 1999) *
<i>Betula pendula</i>	CE		1	Pettersson & McDonald (1992)
<i>Brassica oleracea</i>	GH		1	Sage <i>et al.</i> (1989)
<i>Chenopodium album</i>	GH		1	Sage <i>et al.</i> (1989)
<i>Duchesnea indica</i>	OTC		1	Osborne <i>et al.</i> (1997) *
<i>Eucalyptus tetrodonta</i>	CE		1	Eamus <i>et al.</i> (1995)
<i>Glycine max</i>	GH	N-supply, age	4	Sims <i>et al.</i> (1998a) *
	CE		1	Sims <i>et al.</i> (1998b)
<i>Gossypium hirsutum</i>	GH		1	Wong (1979)
<i>Liquidambar styraciflua</i>	GH		1	Fetcher <i>et al.</i> (1988) *
<i>Lolium perenne</i>	OTC	N-supply	2	Davey <i>et al.</i> (1999) *
<i>Nerium oleander</i>	GH		1	Downton <i>et al.</i> (1980)
<i>Nicotiana tabacum</i>	CE		1	Masle <i>et al.</i> (1993)
<i>Phaseolus vulgaris</i>	GH		1	Sage <i>et al.</i> (1989)
	CE		1	Socias <i>et al.</i> (1993)*
	GH		1	von Caemmerer & Farquhar (1984)
<i>Pinus ponderosa</i>	OTC		1	Tissue <i>et al.</i> (1999) *
<i>Pinus radiata</i>	OTC	age	2	Turnbull <i>et al.</i> (1998) *
<i>Pinus taeda</i>	FACE	season	2	Ellsworth <i>et al.</i> (1998) *
	FACE		1	Ellsworth <i>et al.</i> (1995)
	FACE	month	4	Myers <i>et al.</i> (1999) *
<i>Populus euramericana</i>	CE		1	Gaudillère & Mousseau (1989) *
<i>Populus grandidentata</i>	OTC	CO ₂ exposure	2	Curtis & Teeri (1992)
<i>Psychotria limonensis</i>	CE		1	Ziska <i>et al.</i> (1991)
<i>Quercus myrtifolia</i>	OTC		1	Li <i>et al.</i> (1999) *
<i>Scirpus olneyi</i>	OTC	month	2	Jacob <i>et al.</i> (1995)
<i>Solanum tuberosum</i>	GH		1	Sage <i>et al.</i> (1989)
<i>Tabebuia rosea</i>	CE		1	Ziska <i>et al.</i> (1991) *
<i>Trifolium repens</i>	OTC	N-supply	2	Davey <i>et al.</i> (1999) *
<i>Triticum aestivum</i>	CE	time of day	2	Rogers (1998)
	FACE	leaf position	3	Osborne <i>et al.</i> (1998)

CE, controlled environment; GH, green house; FACE, free-air CO₂ enrichment; OTC, open-top chamber.

Results and discussion

Although there was a mean $\approx 30\%$ acclimated stimulation of A with growth at elevated $p\text{CO}_2$ ($t_{(2)47}$, $P < 0.001$), as expected (Drake *et al.* 1997), the A observed was $\approx 10\%$ ($t_{(2)47}$, $P < 0.05$) lower than the A_{tm} (Fig. 1). This acclimated stimulation of A at elevated $p\text{CO}_2$ occurred in parallel with a $\approx 20\%$ reduction in $V_{c,max}$ ($t_{(2)47}$, $P < 0.001$), J_{max} was largely unaffected by growth at elevated $p\text{CO}_2$ (Fig. 1). For 48 datasets, encompassing 26 species grown at a range of partial pressures of CO₂ and including seasonal, temporal, developmental and nutritional variation (Table 1), WIMOVAC predicted the minimum $V_{c,max}$ and J_{max} that would be required to support the observed A .

There are three possible results and subsequent conclusions that can be drawn from a comparison of

observed and predicted values of $V_{c,max}$ and, analogously, J_{max} (Fig. 2). (i) Observed $V_{c,max}$ is less than predicted $V_{c,max}$. The model was used to predict the minimum $V_{c,max}$ capable of sustaining the observed A . Therefore, if the observed $V_{c,max}$ is less than this predicted minimum possible $V_{c,max}$ then according to the Farquhar model (Farquhar *et al.* 1980), the observed $V_{c,max}$ would be mechanistically incapable of sustaining the reported stimulation of A . (ii) Predicted $V_{c,max}$ is less than observed $V_{c,max}$, i.e. there is more active Rubisco present than is required to achieve the reported A . This would be indicative of an over investment in Rubisco, a finding recently reported for wheat grown at elevated $p\text{CO}_2$ (Theobald *et al.* 1998). (iii) Predicted and observed values of $V_{c,max}$ are identical. The amount of active Rubisco is matched to the requirement for the observed

A. However, it would not rule out the possibility that Rubisco activity may be tightly regulated to match an, as yet, unidentified rate-limiting step.

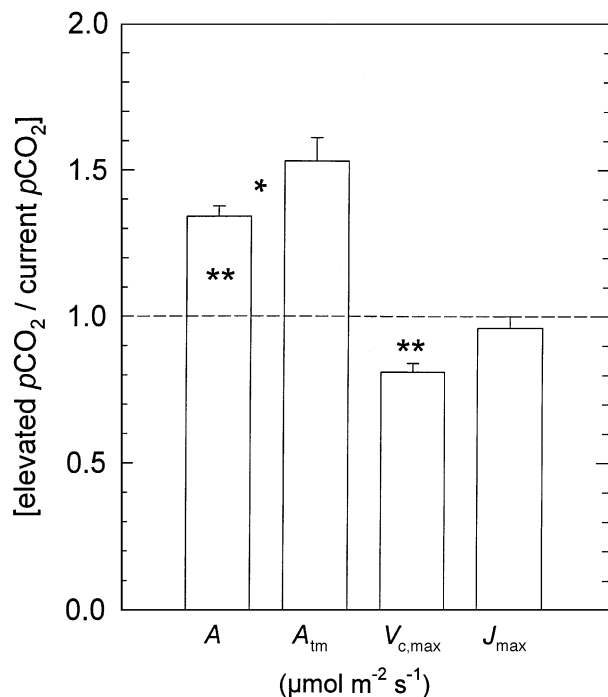
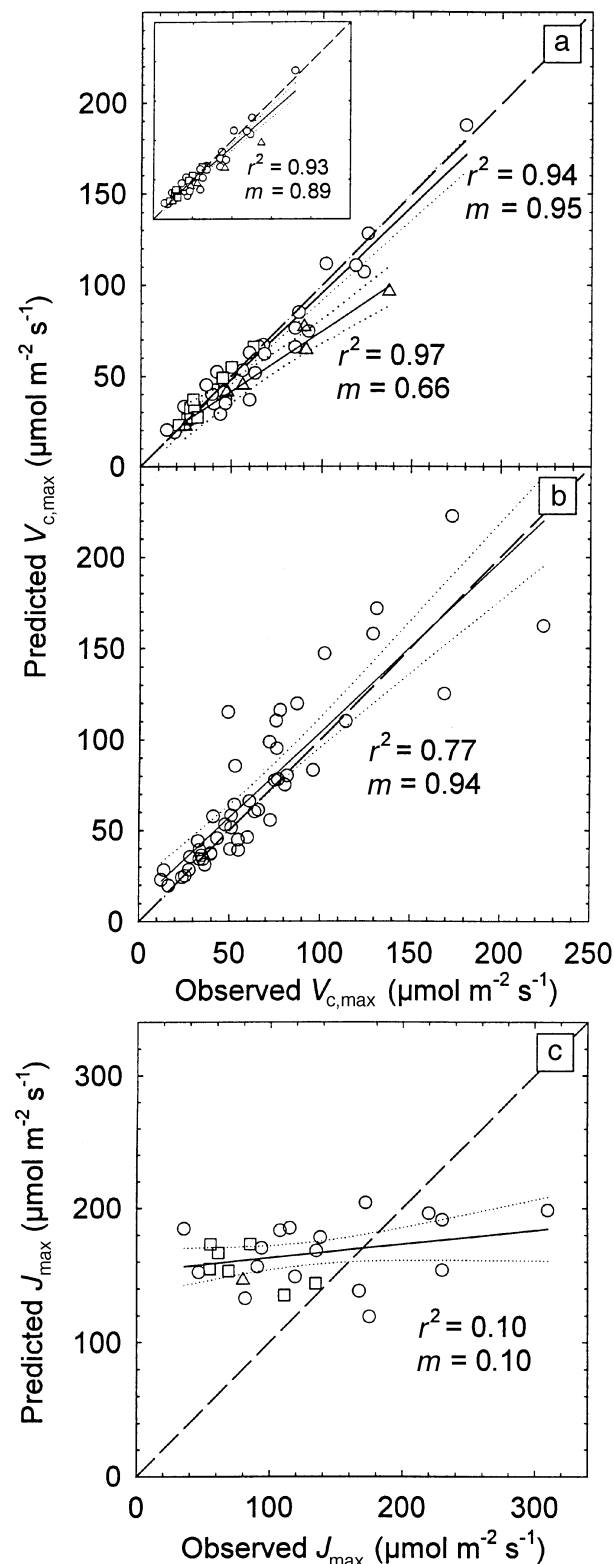


Fig. 1 Observed net CO₂ uptake (A), theoretical maximum A (A_{tm}), maximum carboxylation rate of Rubisco ($V_{c,max}$) and the maximum rate of electron transport (J_{max}) in plants acclimated to elevated pCO_2 as a proportion of that in plants at current pCO_2 . Bars show mean ratio \pm SE ($n=48$, except J_{max} where $n=26$). For the comparison between the A and A_{tm} at elevated pCO_2 relative to that at current pCO_2 $*(t_{(2),47}, P < 0.05)$ and for comparison between the relative level of a parameter at elevated pCO_2 (bar) to the level the same parameter at current pCO_2 (broken line) $** (t_{(2),47}, P < 0.001)$.

Fig. 2 Predicted $V_{c,max}$ correlated against observed $V_{c,max}$ for (a) elevated pCO_2 and (b) current pCO_2 , and predicted J_{max} correlated against observed J_{max} (c) for the range of species and growth conditions shown in Table 1. The minimum $V_{c,max}$ (a and b) or J_{max} (c) required to support the observed A at a given pCO_2 was predicted using the WIMOVAC system to stimulate C₃ photosynthesis as described by the Farquhar model (Farquhar *et al.* 1980). The insert in (a) shows correlation of predicted and observed values of $V_{c,max}$ at elevated pCO_2 for all the data in the study. The axes labels and the axes scale for the insert are the same as for main figure (a). The solid lines show the correlation, the dotted lines show the 95% confidence intervals for the correlation, and the broken lines show the one-to-one line. The symbols denote the elevated pCO_2 at which the measurements were made; squares, ≈ 55 Pa; circles ≈ 70 Pa and triangles > 90 Pa; m = gradient of the correlation.

There was a strong correlation between observed and predicted $V_{c,max}$ at elevated pCO_2 ($r^2=0.93$; $t_{(2),46}$, $P < 0.001$; Fig. 2a, insert) but no correlation between the



predicted and observed values of J_{\max} at elevated $p\text{CO}_2$ ($r^2=0.10$; $t_{(2),25}$, $P>0.05$; Fig. 2c). As expected, Fig. 2c shows that in isolation a decrease in J_{\max} could not account for the reduced stimulation of A in plants acclimated to elevated $p\text{CO}_2$, the nonsignificant correlation prevents any further meaningful discussion of this Figure.

The gradient of the correlation in Fig. 2a (insert; $m=0.89$) indicates that there is a $\approx 10\%$ over-investment in Rubisco at elevated $p\text{CO}_2$. The degree of acclimation of A is also $\approx 10\%$ ($A_{\text{tm}} - A$, Fig. 1). In isolation these data would suggest that the decrease in A at elevated $p\text{CO}_2$ does not result from a decrease in $V_{c,\max}$. Figure 2b shows a significant correlation ($r^2=0.77$, $t_{(2),46}$, $P<0.001$) and near 1:1 relationship ($m=0.94$), indicating that at current $p\text{CO}_2$ the amount of active Rubisco is coupled tightly to requirements (Fig. 2b). Considered in conjunction with the $\approx 20\%$ decrease in $V_{c,\max}$ at elevated $p\text{CO}_2$ (Fig. 1), these findings rule out the possibility that the apparent $\approx 10\%$ excess of Rubisco present after acclimation to elevated $p\text{CO}_2$ (Fig. 2a, insert) may have been sufficient to account for A prior to acclimation.

A closer analysis of the data in Fig. 2a reveals that the gradient of the correlation is influenced strongly by studies where a highly elevated $p\text{CO}_2$ (>90 Pa) was used (denoted by triangles, Fig. 2). Woodrow (1994) demonstrated that without acclimation, plants growing at a $p\text{CO}_2$ of 100 Pa would theoretically have an excess of Rubisco 10% greater than plants growing at 70 Pa. If these high-elevated $p\text{CO}_2$ studies, with a greater theoretical preponderance for excess Rubisco, are omitted from the correlation, the gradient increases and the 1:1 line falls within the 95% confidence interval (Fig. 2a). This suggests that the observed decrease in Rubisco activity (Fig. 1) is largely responsible for the reduced stimulation of A at elevated $p\text{CO}_2$ (Fig. 1). Correlating the high-elevated $p\text{CO}_2$ studies in isolation resulted in a significant correlation ($r^2=0.97$, $t_{(2),4}$, $P<0.001$) with a gradient indicative of a substantial over-investment in Rubisco ($m=0.66$; Fig. 2a). Removal of the high-elevated $p\text{CO}_2$ data had a negligible ($\pm <2\%$) effect on the parameters reported in Fig. 1 and no effect on the reported statistics.

This exercise has demonstrated three features of photosynthetic acclimation to elevated $p\text{CO}_2$.

1 The acclimated stimulation in A observed with growth at elevated $p\text{CO}_2$ is mechanistically and quantitatively consistent with a simultaneous decrease in photosynthetic capacity ($V_{c,\max}$).

2 With the exception of the studies at high-elevated $p\text{CO}_2$ (>90 Pa), the observed decrease in $V_{c,\max}$ is almost entirely responsible for the less than maximal stimulation of A in plants acclimated to growth at elevated $p\text{CO}_2$.

3 At highly elevated $p\text{CO}_2$ there is evidence of a considerable over investment in Rubisco which suggests that at highly elevated $p\text{CO}_2$ other factors may contribute to the acclimation of A . However, for the majority of studies where $p\text{CO}_2$ is increased two-fold or less above current levels there is no evidence for an over-investment in Rubisco.

Conclusions

This study suggests mechanistically and quantitatively, for a wide range of species and growth conditions, that the failure of C₃ plants to sustain the initial stimulation in A with growth at double current $p\text{CO}_2$ is largely attributable to a loss of active Rubisco. However, these results also suggest that at highly elevated $p\text{CO}_2$ (>90 Pa) other factors may begin to limit A . Although considerable advances have been made in recent years, the current mechanism (Drake *et al.* 1997; Moore *et al.* 1999) seeking to describe the process that results in photosynthetic acclimation at elevated $p\text{CO}_2$ remains incomplete and is still challenged by emerging studies (Makino *et al.* 1998; Theobald *et al.* 1998; Stitt & Krapp 1999). Our work has reinforced the importance of understanding this mechanism and the role it plays in determining ecosystem responses to climate change.

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