PLANT WATER USE

Global water use efficiency saturation due to increased vapor pressure deficit

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The ratio of carbon assimilation to water evapotranspiration (ET) of an ecosystem, referred to as ecosystem water use efficiency (WUE$_{eco}$), is widely expected to increase because of the rising atmospheric carbon dioxide concentration (C_a). However, little is known about the interactive effects of rising C_a and climate change on WUE$_{eco}$. On the basis of upscaled estimates from machine learning methods and global FLUXNET observations, we show that global WUE$_{eco}$ has not risen since 2001 because of the asymmetric effects of an increased vapor pressure deficit (VPD), which depressed photosynthesis and enhanced ET. An undiminished ET trend indicates that rising temperature and VPD may play a more important role in regulating ET than declining stomatal conductance. Projected increases in VPD are predicted to affect the future coupling of the terrestrial carbon and water cycles.

The rapid rise of atmospheric CO_2 concentration (C_a) has led to substantial changes in global terrestrial carbon (C) and water cycles, including an increase in the net assimilation of C through photosynthesis (A) and/or a decrease in transpiration (T) through declining stomatal conductance (g_s) (*1*–*3*). Although the theoretical importance of rising C_a in regulating plant water use efficiency (WUE, which is equal to A/T), a metric reflecting the trade-off between C gain and water loss, has been recognized since the 1970s (*4*), its underlying mechanisms remain debatable (*5*, *6*). Studies based on free-air CO_2-enrichment experiments have found increases in A and decreases in g_s across C3 and C4 plants, resulting in enhanced plant WUE (*6*–*8*). Mathias and Thomas (*9*) showed an ~40% increase in the intrinsic WUE of trees due to rising C_a based on a global database of tree-ring isotopic discrimination. At the ecosystem level, numerous studies have reported a substantial increase in ecosystem WUE (WUE$_{eco}$) over various biomes and scales (*10*, *11*), with a 48 ± 22% increase at the global scale (*12*). Previous studies have focused on quantifying the magnitude of increased WUE$_{eco}$ (*11*–*13*). To date, few studies have reported on WUE$_{eco}$ trends in response to the environmental forcings at the global scale.

Increased WUE$_{eco}$ is believed to result from the CO_2 fertilization effect that enhances gross primary productivity (GPP) through photosynthesis and reduces water loss through evapotranspiration (ET) because of declining g_s (*6*, *13*). The determinants of WUE$_{eco}$ (WUE$_{eco}$ = GPP/ET) are highly dependent on vegetation types and are influenced by environmental changes (*9*, *14*). Increasingly, vapor pressure deficit (VPD) is recognized as the most important atmospheric forcing after C_a because it imposes water stress on photosynthesis (*9*, *11*, *15*). Recently, a meta-analysis of eddy covariance (EC) observations and simulations of satellite-driven models indicated a weakening response in plant growth since 2000 due to rising VPD and/or nutrient limitation (*15*–*17*). At the same time, climate warming and increasing leaf area index (LAI) may intensify the ET response, which in turn will down-regulate the WUE$_{eco}$ increase (*18*). Additional constraints on WUE$_{eco}$ might stem from the stoichiometric availability of nitrogen (N) and phosphorus (P), which could slow plant growth due to the progressive nutrient limitation of CO_2 fertilization (*17*, *19*, *20*). Unfortunately, it remains unknown how these multifaceted factors affect global WUE$_{eco}$ (*16*).

Here, we found that global WUE$_{eco}$ has saturated since 2001 due to increased VPD. To examine the trends in WUE$_{eco}$ of global terrestrial ecosystems, estimates of GPP, ET, and WUE$_{eco}$ were achieved using 24 machine learning (ML) approaches (supplementary text S1 and figs. S1 to S8) by fusing the FLUXNET in situ observations of CO_2 and water vapor fluxes, satellite-derived observations, and climate reanalysis data (table S1). The range and median values for all models are presented to show the uncertainties in the analysis. We examined how climate change and elevated C_a interactively affect the underlying processes of GPP and ET, as well as gl WUE$_{eco}$.

Results and discussion

Changes in WUE$_{eco}$

Average global terrestrial WUE$_{eco}$ over the study period (1982–2016) was 1.96 g C kg^{-1} H_2O (table S2), which is determined by a total CO_2 uptake of 1155.57 g C m^{-2} $year^{-1}$ through photosynthesis and water loss of 541.04 kg H_2O m^{-2} $year^{-1}$ through ET. In response to the 18% rise in C_a (i.e., from 341 to 403 ppm) between 1982 and 2016, the overall global WUE$_{eco}$ increased significantly (trending slope = 0.0005 g C kg^{-1} H_2O $year^{-1}$, $P = 0.03$), as did GPP and ET, which increased at rates of 1.42 ± 0.48 g C m^{-2} $year^{-2}$ and 0.7 ± 0.15 kg H_2O m^{-2} $year^{-2}$, respectively. The significant increase in WUE$_{eco}$ was mainly due to a significant trend during 1982–2000 (0.0022 g C kg^{-1} H_2O $year^{-1}$, $P < 0.001$); thereafter, WUE$_{eco}$ exhibited no significant trending (0.0005 g C kg^{-1} H_2O $year^{-1}$, $P = 0.38$). The Michaelis-Menten model indicates that the global WUE$_{eco}$ saturated during 2001–2016 and stabilized at ~1.96 g C kg^{-1} H_2O (Fig. 1A).

The apparent saturation in global WUE$_{eco}$ during 2001–2016 was most likely due to the adverse forcing of continued VPD rise, as evidenced by a significant correlation between [C_a/VPD] and WUE$_{eco}$ ($r = 0.65$, $P < 0.001$, fig. S9A), but with little evidence of saturation due to vegetation regrowth or land cover change (supplementary text S2 and figs. S10 to S12). WUE$_{eco}$ is physically regulated by VPD, which suppresses ecosystem CO_2 fertilization through g_s controlling the inward diffusion of CO_2 (*1*), i.e., $A = g_s \bullet (c_a - c_i)$, where $(c_a - c_i)$ represents the difference between the ambient and leaf intercellular mole fractions of CO_2 and the outward diffusion of H_2O, i.e., $T = 1.6 \bullet g_s \bullet (e_i - e_a)$, where $(e_i - e_a)$ represents the difference between leaf intercellular and ambient water vapor pressure and is commonly substituted by atmospheric VPD (*11*). The strong influence of [C_a/VPD] on WUE$_{eco}$ was consistent in both the Northern Hemisphere ($r = 0.44$, $P = 0.008$; fig. S9B) and the Southern Hemisphere ($r = 0.66$, $P < 0.001$; fig. S9C). Concurrently, the increasing rate of GPP slowed by a factor of 2.14 (2.96 ± 0.55 g C m^{-2} $year^{-2}$ during 1982–2000 compared with 1.38 ± 1.15 g C m^{-2} $year^{-2}$ during 2001–2016), whereas the rate of ET increase declined by a factor of 1.65 (1.19 ± 0.15 kg H_2O m^{-2} $year^{-2}$ during 1982–2000 compared with 0.72 ± 0.28 kg H_2O m^{-2} $year^{-2}$ during 2001–2016) (Fig. 1B). Our finding of the saturation of WUE$_{eco}$ increase at the global scale was corroborated by ecosystem scale FLUXNET observations: 71% of the EC sites demonstrated a WUE$_{eco}$ increase with a higher median trend during 1997–2000, whereas only 51% of the EC sites showed WUE$_{eco}$ increases with a lower median trend after 2000 (Fig. 1C).

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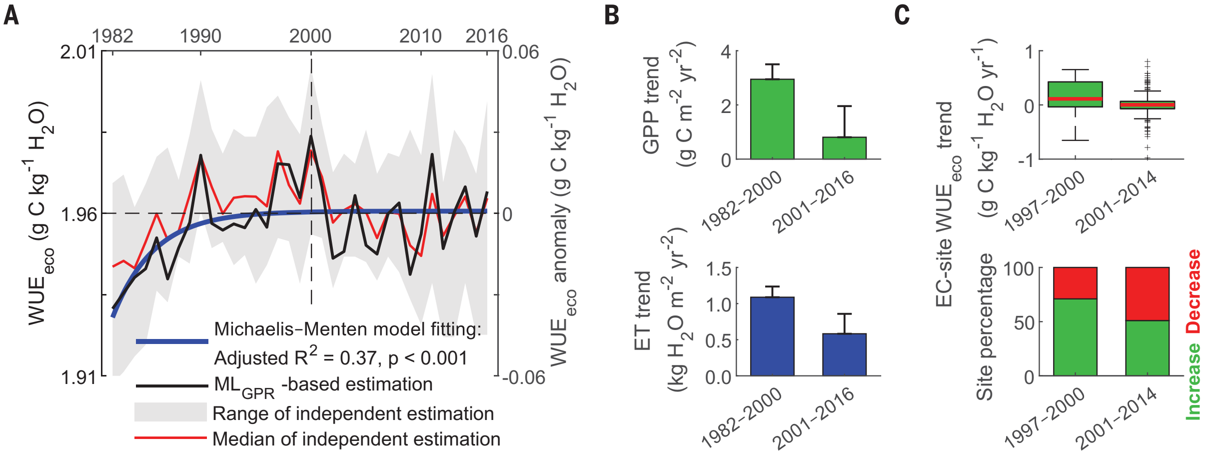

Fig. 1. Changes in WUE_{eco} and its determinants (GPP and ET) over vegetated lands during 1982–2000 and 2001–2016. (**A**) Changes in WUE_{eco} from an ensemble of 24 ML algorithms and Michaelis-Menten model fitting to the optimal estimation using ML Gaussian process regression (i.e., the ML_{GPR}) model. (**B**) Annual rates of change (trend) in gridded estimates of GPP and ET from 24 ML algorithms. (**C**) Box statistics describing changes in the rate of WUE_{eco} and corresponding percentages of increase and decrease among EC sites obtained from the global FLUXNET network.

Significant increases in WUE_{eco} across global biomes during 1982–2000 were primarily due to increases in the Northern Hemisphere (Fig. 2A and table S2). From 1982 through 2000, the Northern Hemisphere showed a stronger increase in GPP than did the Southern Hemisphere (Fig. 2B). By contrast, ET in the Northern Hemisphere showed a smaller increase than that of the Southern Hemisphere. During 2001–2016, although GPP in the Northern Hemisphere increased, the continuously strong ET responses, which were strikingly above 53°N (Fig. 2C), down-regulated WUE_{eco}, resulting in an insignificant WUE_{eco} trend in the Northern Hemisphere (supplementary text S3 and figs. S13 and S14) and apparent saturation over global terrestrial ecosystems. Significant decreasing trends for GPP and ET were observed in Africa and parts of South America. Among the five major biomes, divergent changes in WUE_{eco} were observed, with a noticeable decline in shrublands, grasslands, and croplands during 2001–2016, whereas forests and savannas showed insignificant trends over the study period 1982–2016 (fig. S15).

Climate change impacts on ecosystem CO_2 uptake

Our GPP estimates based on an ensemble of 24 ML algorithms show that ecosystem photosynthesis also slowed down after the year 2000 (Fig. 3A). Our analysis based on six independent GPP products (table S3) revealed a similar pattern (Fig. 3A). Stepwise regression analysis indicated that 72% of the variance in GPP was attributed to climate change and rising C_a, with effective coefficients of 0.66, 1.07, and –1.02 for air temperature (T_a), C_a, and VPD, respectively (Table 1). This implies that the enhancement effect of CO_2 fertilization and the net negative effect of climate change jointly influence ecosystem CO_2 uptake over global terrestrial ecosystems. Given the complex direct and indirect interactions among the effective variables (e.g., T_a and VPD), partial least-squares structural equation modeling analysis achieved consistent results, with path coefficients of 0.5, 0.82, and –0.81 for T_a, C_a, and VPD, respectively, providing additional evidence for the stronger VPD constraint than T_a enhancement of global GPP (fig. S16).

To futher examine the underlying interactive effects of these three factors (i.e., the physical effects of [C_a/VPD] to WUE_{eco} and the positive factor of T_a), we combined these factors with the form of [$T_a \times C_a$/VPD], which explained 74% of the variance in GPP, as evidenced by the well-matched changing trajectories between GPP and [$T_a \times C_a$/VPD] (Fig. 3A). This implies that the combined effects of [$T_a \times C_a$/VPD] dominate photosynthesis. After removing the positive effect of C_a, [T_a/VPD] increased before 2000 but declined throughout the remaining period, concurrent with the slowdown in GPP and LAI increases (fig. S17) (*21*, *22*) that appears to have down-regulated WUE_{eco}.

The negative effects of increasing VPD almost completely offset the positive effects of CO_2 fertilization on WUE_{eco} of global terrestrial ecosystems (Fig. 3B), which is more pronounced in the Southern Hemisphere (–0.95 VPD versus 0.74 C_a) than in the Northern Hemisphere (–0.61 VPD versus 0.77 C_a) (Table 1). Furthermore, rising T_a imposed a 0.73 positive effect on ecosystem CO_2 uptake in the Northern Hemisphere but not in the Southern Hemisphere. The combination of these influences resulted in more robust increases in GPP in the Northern Hemisphere than in the Southern Hemisphere (*23*). Consequently, global WUE_{eco} trends were dominated by changes in the Northern Hemisphere throughout the study period. Extensive decreases in [T_a/VPD] were observed over the land areas below 53°N from the period 1982–2000 to the period 2001–2016 (Fig. 3C). This led to consistent decreases in GPP, thus slowing the rate of WUE_{eco} increase. By contrast, areas north of 53°N showed increased [T_a/VPD], which has enhanced GPP, but has also enhanced ET to a much greater extent, resulting in a declining WUE_{eco} (fig. S14). This finding is inconsistent with the view that WUE_{eco} in high latitudes responds positively to rising T_a (*24*). The stronger response of ET to rising T_a than GPP may be an important factor in the down-regulation of WUE_{eco}.

The combined effect of [$T_a \times C_a$/VPD] was consistent among the five major biomes, showing the strongest effect on shrublands (78%) and the weakest effect on savannas (35%) (Table 1). For forests, grasslands, and croplands, the effect varied from 45 to 76% due to the positive effects of increasing T_a and the negative effects of increasing VPD on GPP. Precipitation had a positive effect on GPP on the global scale, particularly in savannas and grasslands, and the overall impact was greater in the Southern Hemisphere than in the Northern Hemisphere. This finding corresponds well with the extensive droughts that have occurred in the Southern Hemisphere in recent decades (*25*). Enhanced CO_2 uptake was previously assumed to be associated with increasing photosynthetically active radiation (PAR) at the ecosystem to biome scale (*16*, *26*). However, our study did not detect a strong PAR

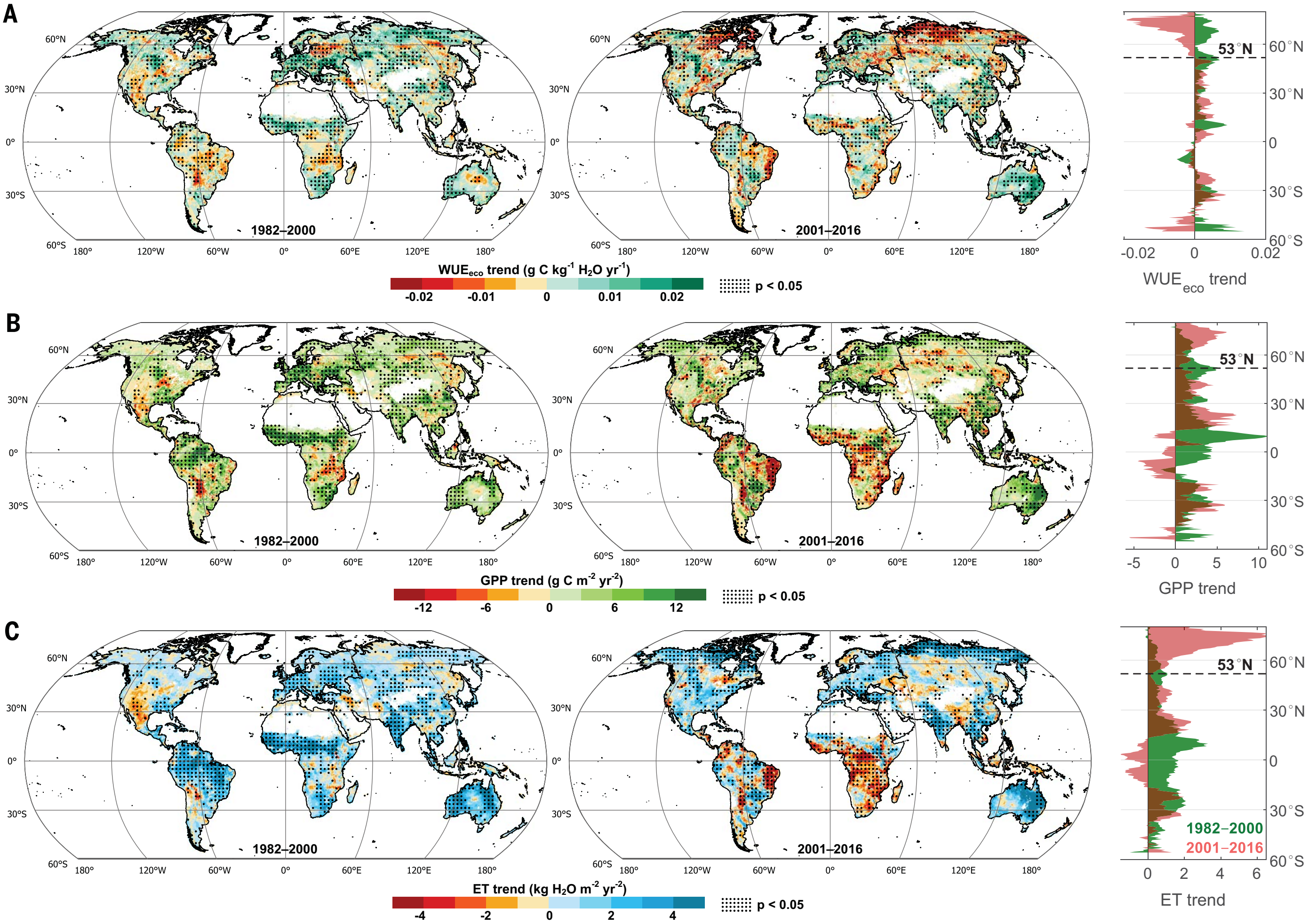

Fig. 2. Global patterns in trends of WUE$_{eco}$ and its determinants, GPP and ET, over 1982–2000 and 2001–2016. (**A**) WUE$_{eco}$. (**B**) GPP. (**C**) ET. The changing trends are calculated on a per-pixel basis (0.5 × 0.5°) over time and dotted if statistically significant ($P < 0.05$). Trends aggregated by latitude are illustrated in the far right panels, where recent trends during 2001–2016 (red) are compared with past trends during 1982–2000 (green).

effect at the global scale. Instead, increasing PAR exhibited a negative impact on GPP of shrublands in the Southern Hemisphere, likely because excessive increases in PAR can elevate VPD and thus reinforce water stress on vegetation (*15, 25*). Plants must open their stomata to allow CO_2 molecules to diffuse into the chloroplast stroma for ongoing photosynthesis. Once the moist interior of the leaf is exposed to the drier air, vapor pressure inside the stomata will decrease, resulting in the counteraction of CO_2 fertilization (*9*). This indicates that although CO_2 fertilization imposes a substantial effect on global biome WUE$_{eco}$, this enhancement is down-regulated by the ET response (*27*).

Climate change impacts on ecosystem ET

There has been an intense debate over whether CO_2 fertilization reduces g_s, and thereby decreases ET and enhances WUE$_{eco}$ (*6, 28*). However, consistent with 26 global ET products derived from different mechanistic models and ML algorithms (table S3), our estimates based on 24 ML models indicate that global ET over vegetated lands has increased significantly (Fig. 4A), with a stronger increase during 1982–2000 and a weaker increase during 2001–2016. On the basis of an ET decomposition model developed from the Penman-Monteith equation (*18*), ET showed a significant positive correlation with transpiration (fig. S18), indicating that the increasing trends in ET were significantly associated with a rise in transpiration, including sparsely vegetated areas north of 53°N (fig. S19). This increasing rate in ET also corresponded to the increasing rate in GPP across EC sites ($r = 0.62$, $P < 0.001$; Fig. 4B). This suggests that the saturation in global WUE$_{eco}$ during 2001–2016 was synchronously attributable to reduced GPP and increased ET, largely driven by increases in transpiration. Consistent with the currently prevailing view that CO_2 fertilization reduces plant g_s (*7, 8*), significant decreases in canopy g_s over the global biomes from 1982 to 2016 were observed in this study (fig. S20) and were inferred to reduce ecosystem ET (*6, 11*). However, this school of thought fails in considering the strong response of ET due to climate warming (e.g., north of 53°N). Other similar studies did not detect widespread g_s reductions (*9, 10*). In this case, ecosystem ET was expected to increase according to the approximately linear relationship of ET with g_s and VPD (see supplementary equation 5). Thus, we challenge the view that g_s-induced ET decline favors soil water conservation and enhances plant water-deficit resistance in arid ecosystems (*29, 30*). Instead, we propose that the negative effects of the continuous increase in VPD associated with global warming counteract the effects of CO_2 fertilization, thereby impairing plant growth, as evidenced by satellite-derived observations of vegetation browning (*21, 22*).

Oligotrophication

There is controversy over whether elevated C_a depresses WUE$_{eco}$ by inducing stoichiometric limitation of CO_2 uptake by N and P (i.e., oligotrophication) and/or their disequilibrium

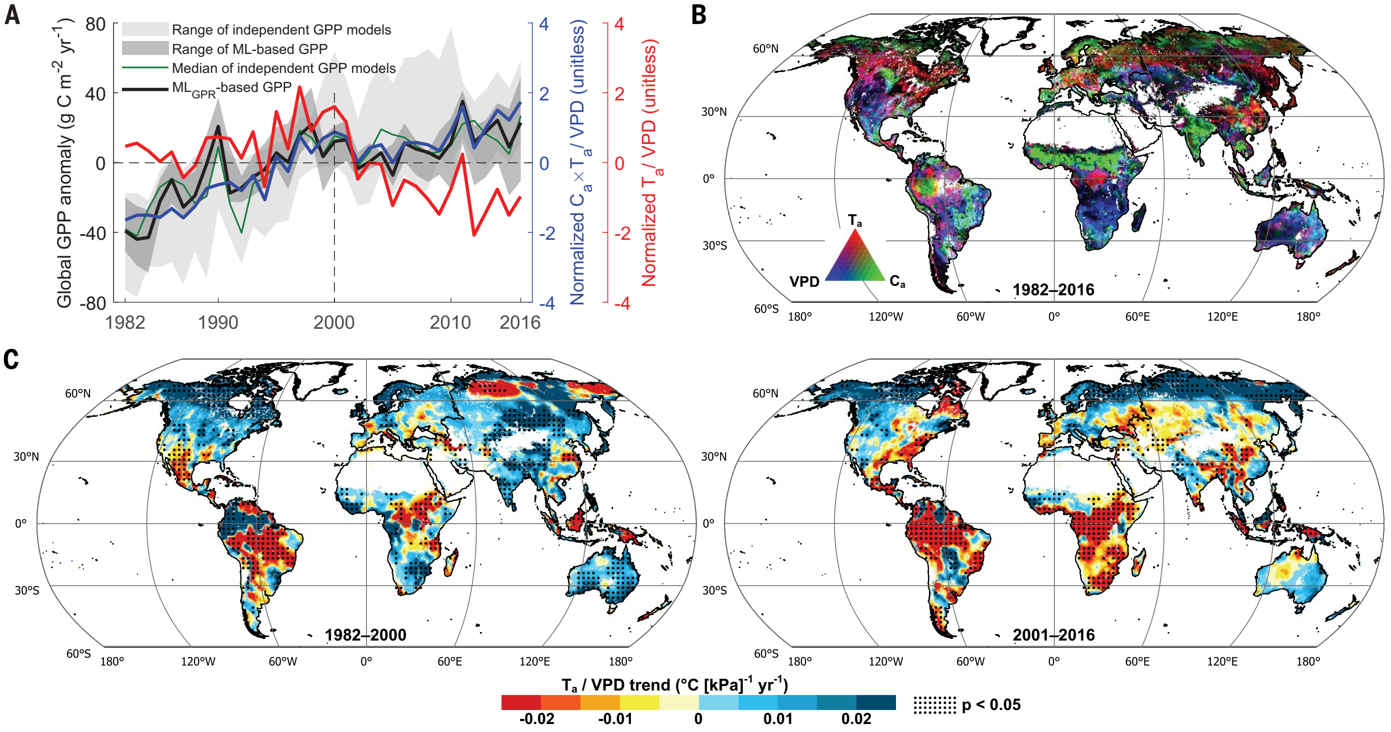

Fig. 3. Changes in GPP resulting from the combined effects of T_a, C_a, and VPD. (**A**) Changes in global GPP estimates based on an ensemble of 24 ML algorithms of this study and independent GPP products against driving factors of [$T_a \times CO_2$/VPD] and [T_a/VPD]. (**B**) Spatial patterns of composited RGB image of T_a, CO_2, and VPD covariance with GPP over global vegetated lands. (**C**) Changes in the spatial patterns of trends in [T_a/VPD] during the periods 1982–2000 and 2001–2016; trends are dotted if statistically significant ($P < 0.05$).

Table 1. Changes in GPP due to the effects of LAI and environmental variables, independently and interactively, over the globe, the Northern Hemisphere (NH), the Southern Hemisphere (SH), and the five major vegetation types in the period 1982–2016. The relationships between environmental variables and GPP were calculated using stepwise regression analysis, where the environmental variables were normalized by subtracting the mean of each term and dividing by the standard deviation for cross-comparison of the effective coefficients. A higher absolute coefficient value indicates a stronger effect on promoting or diminishing GPP changes. The relationships of GPP with LAI and combined environmental variables, i.e., [$T_a \times C_a$/VPD], were quantified with a statistical measure of R^2. For the excluded variables through stepwise regression analysis, correlation analysis was individually implemented to indicate a significantly positive or negative effect on GPP changes in cases with a significance level of 0.05.

Driving factors		GPP changes							
		Globe	NH	SH	Forests	Shrublands	Savannas	Grasslands	Croplands
Effects of LAI	R^2	0.80	0.84	0.61	0.61	0.19	0.62	0.85	0.87
Effects of environmental variables	C_a	1.07	0.77	0.74	0.93	0.99		+	0.80
	T_a	0.66	0.73		0.68	+		0.71	0.57
	PAR			–		–0.34		–0.33	
	P_r	+		+			0.40	+	
	VPD	–1.02	–0.61	–0.95	–0.79	–0.34	–		–0.55
	Adjusted R^2	0.72	0.81	0.59	0.66	0.84	0.14	0.49	0.77
Effects of [$T_a \times C_a$/VPD]	R^2	0.74	0.82	0.51	0.45	0.78	0.35	0.62	0.76

with widespread changes in N deposition input to ecosystems (19, 20). With the effective coefficient of CO_2 fertilization separated from the linear regression analysis (Fig. 3B), we examined the effects of CO_2 fertilization in relation to leaf N and P limitations. First, we examined changes in foliar N and P concentrations using observations of various tree species collected from 410 sites during 1990–2016, and found that 20.7 and 22.7% of the sites showed a significant decline in leaf N and P, respectively (17). However, we did not identify any significant relationships between changes in leaf N and P concentrations and the effects of CO_2 fertilization (Fig. 5A). Second, we examined disequilibrium quantified by the ratios of foliar N resorption efficiency (N_{RE}) and P resorption efficiency (P_{RE}) (i.e., N_{RE}/P_{RE} ratios) (31). We did not find significant decreases in the effects of CO_2 fertilization linked to the N_{RE}/P_{RE} ratios deviating from the equilibrium state (i.e., N_{RE}/P_{RE} = 1) (Fig. 5B). To examine the potential influence of scale mismatches between upscaled GPP estimates and site-level

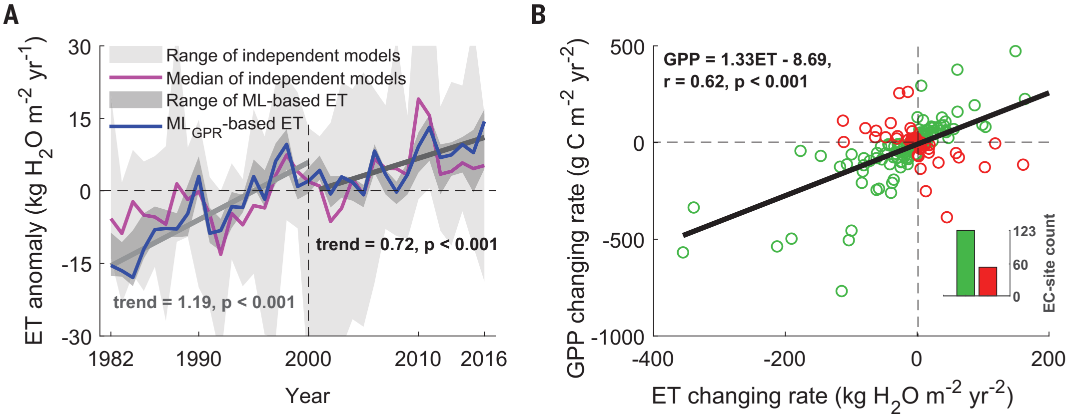

Fig. 4. Changes in ET over global vegetated lands during 1982–2016. (**A**) Comparisons between the ML-based ET estimates and 26 ET products used in previous studies. (**B**) Relationship between changing rates in ET and GPP derived from global FLUXNET observations collected in the period 1997–2014, where green circles represent ET and GPP showing consistent directions and red circles represent those showing inconsistent directions.

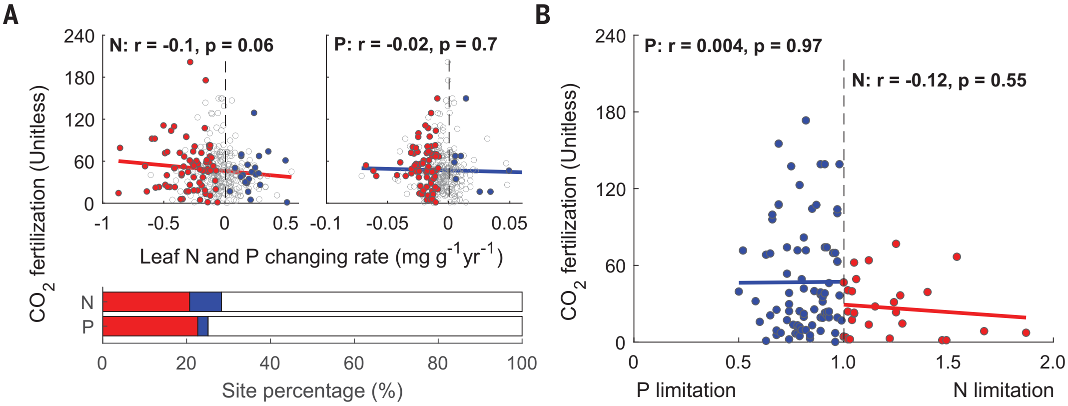

Fig. 5. Responses of CO_2 fertilization to nutrient limitations by N and P. (**A**) Relationship between changing rate in leaf N and P concentrations and C_a coefficients separated from the linear regression analysis, where the percentage of sites with significant changes ($P < 0.05$) in leaf N and P concentrations are stacked as red (decrease) and blue (increase) bars. (**B**) Relationship between N_{RE}/P_{RE} ratios and C_a coefficients.

N and P data, we conducted the same analysis with finer-resolution flux estimates to analyze the effect of nutrient limitations and found similar results (supplementary text S4 and fig. S21). Previous studies suggested that in response to increasing nutrient limitations, plants intensify transpiration to facilitate the uptake of stoichiometric elements from the soil (*32*). Although our results indicate an increase in transpiration, especially at high latitudes, this is probably the result of increasing atmospheric demand rather than nutrient demand. Many studies have suggested that global ecosystems have been widely fertilized by atmospheric N and P deposition and anthropogenic nutrient enrichment (*33*, *34*), but their effectiveness at enhancing ecosystem CO_2 uptake is generally believed to be lower than the negative impacts (*35*). Nevertheless, with so little known about the amount of N and P equilibrium across global ecosystems, it is not affirmative yet to conclude that oligotrophication may be altering coupled C and water cycles.

Conclusions

Focusing on the widespread assertions that plant-to-ecosystem WUE has increased because of the rising C_a, we examined the combined effects of rising C_a, T_a, and VPD on WUE_{eco} over global biomes. We observed an overall significant increase in WUE_{eco} throughout 1982–2016, with a substantial contribution from the period 1982–2000; thereafter, increasing WUE_{eco} has evidently stalled, indicating saturation. The T_a rise–induced increases in VPD diminished WUE_{eco} by suppressing ecosystem gross photosynthesis. At the same time, the apparent saturation in WUE_{eco} was also influenced by increased ET, thus challenging the currently prevailing view that g_s decline reduces transpiration and thus increases WUE_{eco}. Existing climate data and climate projections indicate a likely sustained WUE_{eco} “saturation” into the future because of a durable VPD increase (supplementary text S5 and fig. S22). With other biogeochemical elemental constraints starting to emerge, it remains to be seen whether WUE_{eco} deviates from this course. Furthermore, the saturation of WUE_{eco} does not appear to be the result of changes in vegetation regrowth and land cover, nor in nutrient constraints on photosynthesis due to N and P changes or their disequilibrium. This study emphasizes that human reliance on nature-based climate sinks to achieve C neutrality may be undermined by the adverse effects of climate warming.

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SUPPLEMENTARY MATERIALS

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Materials and Methods
Supplementary Text S1 to S5
Figs. S1 to S22
Tables S1 to S3
References (*36*–*83*)

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Global water use efficiency saturation due to increased vapor pressure deficit

Fei Li, Jingfeng Xiao, Jiquan Chen, Ashley Ballantyne, Ke Jin, Bing Li, Michael Abraha, and Ranjeet John

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Editor's summary

How have plants managed the trade#off between carbon gain and water loss in a world of increasing atmospheric carbon dioxide concentrations and rising temperatures? Li *et al*. showed that plant water use efficiency, the ratio between the net assimilation of carbon through photosynthesis and the stomatal conductance of transpiration, increased from 1982 to 2000, but then remained constant from 2001 to 2016. The authors interpret this as being the result of increases in the vapor pressure and intensifying evapotranspiration. Their results illustrate one more way in which the adverse effects of climate warming make it more difficult to achieve carbon neutrality. —H. Jesse Smith

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