

Global variation in vegetation carbon use efficiency inferred from eddy covariance observations

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Terrestrial ecosystems have been serving as a strong carbon sink that offsets one-quarter of anthropogenic CO₂ emissions. Carbon use efficiency (CUE), the percentage of photosynthesized carbon that is available for biomass production and other secondary carbon products, is one factor determining the carbon sink size. The global variation in CUE remains unclear, however, as recent reports disagree over the responses of CUE to temperature, dryness, forest types and stand age, and there are limited direct observations to constrain the related uncertainty. Here, we propose to infer CUE from spatially distributed observations of land–atmosphere CO₂ exchange from global eddy covariance sites based on the degree of ecosystem respiration–photosynthesis coupling. Across 2,737 site-years, CUE derived from eddy covariance observations is 0.43 ± 0.12 , consistent with previous inventory-based estimates (0.47 ± 0.12 , $n = 301$) but with a better representation of spatial–temporal variation in CUE. We find that CUE consistently decreases with temperature, precipitation, light availability and stand age, with a substantial difference in the baseline CUE among biomes. Importantly, CUE of deciduous forests is typically 15% higher than that of evergreen forests, suggesting that over the long-term deciduous forests are more efficient in using photosynthate. Our study advances the understanding of the global variation in CUE and provides insights to guide best practices of forest conservation, management and restoration for carbon sequestration.

Terrestrial ecosystems serve as a land carbon sink that offsets roughly a quarter of the anthropogenically CO₂ emissions¹. Enhancing the land carbon sink through forest conservation and restoration are regarded as the most cost-effective solutions for climate change mitigation^{2–4}, as protected old-growth trees and newly planted trees can remove CO₂ from the air and fix it into biomass in their lifetime. Many global and regional initiatives, such as reducing emissions from deforestation and degradation (REDD+)⁵ and the Trillion Tree Campaign⁶, are

leveraging the carbon fixation ability of trees to slow down climate change. However, successful implementations of forest conservation and restoration initiatives for carbon sequestration, and more broadly the estimation of the land carbon sink, require knowledge on how efficient different types of vegetation fix and store carbon.

Ecological studies have historically used the concept of carbon use efficiency (CUE) to describe the efficiency of vegetation to convert fixed carbon in potential storage. Trees take up carbon through

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leaf photosynthesis (gross primary productivity (GPP)) and lose a portion of the fixed carbon owing to autotrophic respiration (R_a). The net amount of gross productivity, also referred as the net primary productivity ($\text{NPP} = \text{GPP} - R_a$), is then used for biomass production and other secondary products (soluble organic compounds and biogenic volatile organic compounds), and its ratio to GPP is defined as CUE^7 . Recent studies have updated CUE to biomass production efficiency (BPE), which strictly refers to the ratio of biomass production ($\text{BP} = \text{GPP} - R_a$ —other secondary carbon products) and GPP, although at the annual scale CUE and BPE vary similarly considering that BP is the major fraction of NPP⁸. Given the same rate of photosynthetic assimilation, a higher CUE or BPE often indicates faster accumulation of biomass. Previous studies have suggested that global CUE converges to a constant around 0.47 with little variation (± 0.04 ; mean $\pm$ s.d., $n = 12$)⁹, although this notion has been challenged recently¹⁰, as regional and global syntheses have reported that CUE or BPE varies considerably due to physical (climate and soil fertility)^{8,11}, biological (biome type and stand age)^{7,12–14} and management^{15,16} factors. While these studies reveal substantial variation in CUE, they differ in the inferred responses of CUE to temperature^{11,17–19}, dryness^{11,20,21} and biome types^{7,8,12,15}, leading to conflicting interpretations of the global variation in CUE.

This lack of understanding of CUE variation hinders our ability to predict the land carbon sink^{20–23} and calls into question whether current conservation and reforestation practices are optimal for mitigating climate change. Part of the difficulty stems from the scarcity of direct CUE observations, as globally we only have ~300 CUE records to represent its variation so far^{11,15}, mostly because of the difficulties related to continuous measurements of NPP or R_a . In this study, we propose to fill the knowledge gap by leveraging distributed and high-frequency carbon flux observations of the land surface from a global network of eddy covariance towers. On the basis of the strong coupling between plant photosynthesis and respiration and recent theoretical advances in estimating R_a (ref. 14), we develop a method to estimate CUE for >2,700 site-years of observations across diverse biomes and climates worldwide (Methods). Specifically, our method assumes that the rate of change in ecosystem respiration relative to photosynthesis during growing seasons contains information on CUE (Supplementary Fig. 1). We used independent estimates of CUE and BPE from inventory or biometric measurements (all referred to as CUE_{IN})^{11,15}, site measured NPP, BP^{11,15} and heterotrophic respiration²⁴, and the basal area increment (BAI) of trees estimated from the international tree-ring data bank (ITRDB)²⁵ to validate the CUE inferred from eddy covariance observations (CUE_{EC}). The newly derived CUE_{EC} dataset enables us to examine the variation in CUE and its dependence on biotic and abiotic factors. Using CUE_{EC} , we further map the spatial variability of global CUE, which is a critical element in guiding best practices of forest conservation and restoration for effective and efficient offset of CO_2 emissions.

Results

Vegetation CUE derived from eddy covariance observations

Across biomes and years, the CUE derived from eddy covariance observations (CUE_{EC}) was 0.43 ± 0.12 (mean $\pm$ s.d.), comparable to the CUE and BPE estimated on the basis of inventory data (CUE_{IN}), which was 0.47 ± 0.12 (Fig. 1a). When comparing CUE_{EC} and CUE_{IN} across nine sites that have both records, we found that the two metrics were similar at seven sites, aligning closely along the 1:1 line (Fig. 1b). CUE_{EC} was available for both forest biomes ($n = 1,365$) and non-forest biomes ($n = 1,372$). The CUE_{EC} of forest biomes was 0.41 ± 0.11 , significantly lower ($P < 0.01$; one-way analysis of variance (ANOVA)) than the CUE_{EC} of 0.45 ± 0.12 for non-forest biomes (Fig. 1a). This was consistent with CUE_{IN} , which also showed a significantly ($P < 0.01$) lower CUE_{IN} for forests (0.46 ± 0.12) than for non-forests (0.53 ± 0.15). Among the non-forest biomes, which include grasslands (GRA), wetlands (WET), shrublands (SH), savannas (SAV) and croplands (CRO), SAV had significantly lower ($P < 0.01$) CUE_{EC} ($\text{CUE}_{\text{EC}} = 0.32 \pm 0.12$) than other non-forest biomes ($\text{CUE}_{\text{EC}} = 0.46 \pm 0.11$).

Among forest biomes, we noticed that the CUE_{EC} of deciduous broadleaf forests (DBF) was 0.46 ± 0.12 , significantly higher ($P < 0.01$) than other forest types, such as evergreen needleleaf forests (ENF; $\text{CUE}_{\text{EC}} = 0.39 \pm 0.10$) and evergreen broadleaf forests (EBF; $\text{CUE}_{\text{EC}} = 0.32 \pm 0.12$). In total, CUE_{EC} of DBF was 15% greater than that of evergreen forests. Across all biomes, CUE_{EC} of DBF was among the largest, trailing slightly behind those of CRO ($\text{CUE}_{\text{EC}} = 0.50 \pm 0.09$). Inventory data also showed a relatively higher CUE_{IN} of DBF ($\text{CUE}_{\text{IN}} = 0.49 \pm 0.13$) than other forest types ($\text{CUE}_{\text{IN}} = 0.45 \pm 0.11$), although the difference was not statistically significant, unlike the difference in CUE_{EC} .

We further used an independent metric—paired basal area increment (pBAI) of deciduous trees and evergreen trees at the same site—as a proxy for the relative difference in CUE between DBF and ENF ('Quantify relative CUE from pBAI' in the Methods). A pBAI > 1 indicates that the CUE of DBF is greater than that of ENF. Despite the wide range of pBAI estimates, especially for young stands, the average of pBAI was consistently > 1 across all stand ages, further confirming that the CUE of DBF is greater than that of ENF. Across all stand ages, pBAI averaged to 1.09, suggesting that the CUE of DBF for stem was 9% greater than ENF, which was consistent with the relative difference in CUE_{EC} between DBF and ENF.

The drivers of variation in vegetation CUE

Using the newly derived CUE_{EC} estimates, we applied a linear mixed effect (LME) model to quantify the impacts of various biotic and abiotic factors on CUE (Methods). We found that CUE decreased significantly ($P < 0.01$) with mean annual air temperature (MAT) and insignificantly ($P > 0.01$) with mean annual precipitation (MAP) and mean annual photosynthetically active radiation (PAR). CUE also decreased with stand age ($P = 0.57$), although its impact was not significant (Fig. 2a–e). One important contributor to CUE variability is the inherent difference in baseline CUE associated with each biome, revealing that CRO, DBF and GRA exhibit greater CUE compared to other plant functional types (PFTs) (Fig. 2e). In particular, the baseline CUE of DBF was 0.10 and 0.08 higher than that of EBF and ENF, respectively, accounting for almost all the observed differences in CUE between DBF and other forest types (Fig. 2e).

Understanding autotrophic respiration through CUE

The newly derived CUE_{EC} allows the calculation of NPP from GPP and further enables us to partition the ecosystem respiration (R_{eco}) into R_a and heterotrophic respiration (R_h) at eddy covariance sites. We found that for all PFTs, areas sampled by eddy covariance sites act as carbon sinks, with GPP exceeding R_{eco} by 10–50% on average (Fig. 3a). Upon partitioning R_{eco} into R_a and R_h components, our analysis revealed that R_h was typically smaller than R_a at eddy covariance sites. On site-year average, R_h was about $39 \pm 10\%$ (mean $\pm$ 1 s.d.), $31 \pm 11\%$, $45 \pm 10\%$, $41 \pm 10\%$, $45 \pm 11\%$, $32 \pm 12\%$, $44 \pm 10\%$, $45 \pm 11\%$ and $50 \pm 9\%$ of R_{eco} for ENF, EBF, DBF, mixed forests (MF), SH, SAV, GRA, WET and CRO, respectively. The estimated NPP and R_h were also validated against independent observations and showed reasonable accuracy (Supplementary Fig. 2).

We also examined the relationship between CUE and the key parameters determining R_a (ref. 14) (Methods), including the coefficient of growth respiration (g_r ; unitless), the fraction of live biomass turned into non-respiratory biomass per unit time (τ ; unitless) and the temperature sensitivity of maintenance respiration (E_a (eV)). These parameters were concurrently derived alongside CUE using our method (Methods). We found that CUE was negatively related to g_r , while g_r was constrained in a narrow range from 0.2 to 0.22. With a 0.01 increase in g_r , CUE decreased by 0.15. Meanwhile, τ , a factor determining how fast live biomass turns into non-respiratory materials (sapwood to hardwood), was positively related to CUE. The parameter τ predominantly falls within the range of 0.7 to 0.9 across various PFTs. Swift turnover, indicated by a higher τ , suggests a reduced respiratory cost to maintain live biomass, leading to a corresponding increase in CUE. Finally, we observed that the average site-year E_a was 0.28 ± 0.14 eV.

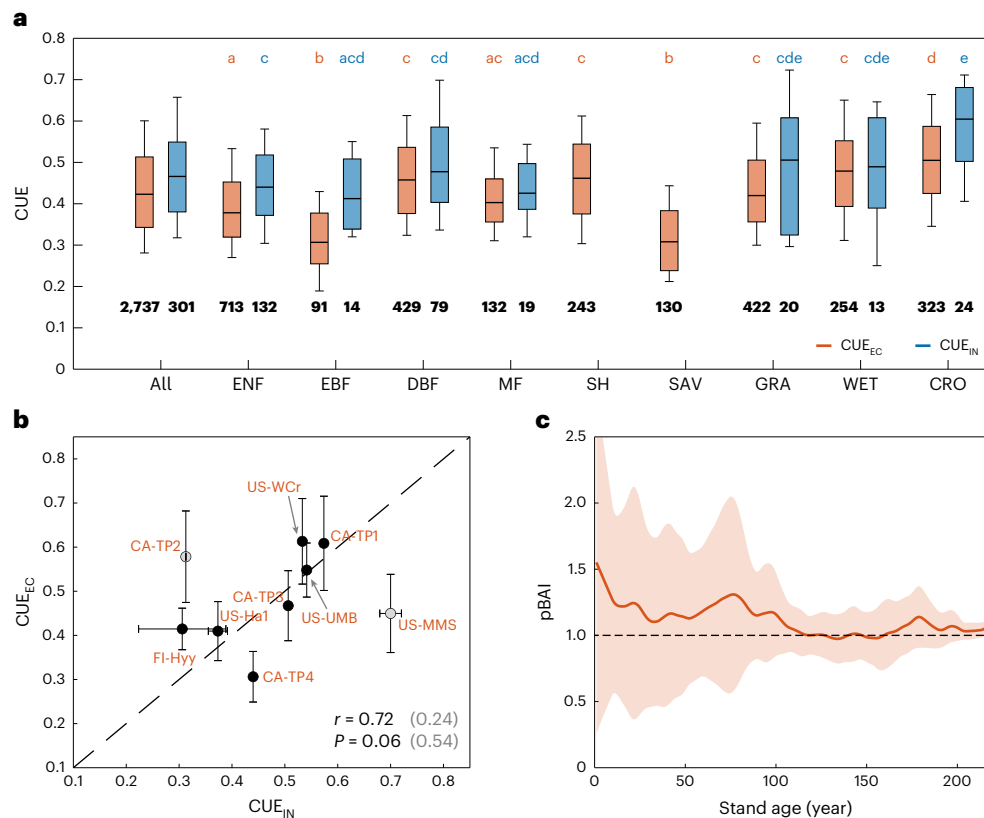


Fig. 1 | CUE derived from eddy covariance observations. a, CUE of different PFTs, which include EBF, ENF, DBF, MF, SH, SAV, GRA, WET and CRO. CUE_{EC} represents the CUE derived from eddy covariance observations; CUE_{IN} represents the CUE derived from inventory data. The letters over each bar indicate whether the groups are significantly different ($P < 0.01$; one-way ANOVA). The number under each bar means the number of samples. In the boxplot, the centre line represents the median, the circle within the box indicates the mean, the limits of the box indicate the 25th and 75th percentiles and the whiskers represent the 10th and 90th percentiles. **b**, Comparison of CUE_{EC} and CUE_{IN} at nine sites: Harvard Forest (US-Ha1, DBF), Morgan Monroe State Forest (US-MMS, DBF), University of Michigan Biological Station (US-UMB, DBF), Willow Creek (US-WCr, DBF), Turkey Point TP02 (CA-TP1, ENF), Turkey Point TP89 (CA-TP2, ENF), Turkey Point TP74 (CA-TP3, ENF), Turkey Point TP39 (CA-TP4, ENF) and Hyytiälä (FI-Hyy, ENF); the dark dots indicate the seven sites where CUE_{EC} agrees with CUE_{IN} , the light dots indicate the two sites where CUE_{EC} is different from CUE_{IN} . The r and P values indicate the correlation between CUE_{EC} and CUE_{IN} excluding the two outlier sites, while the value in brackets indicate the correlation between CUE_{EC} and CUE_{IN} including the two outlier sites. The error bars represent 1 s.d. of the CUE_{EC} and CUE_{IN} for each site. **c**, The paired basal area increment (pBAI) of DBF and ENF (Methods). pBAI is the ratio of the BAI of deciduous trees and evergreen trees at the same locations. The shaded area indicates 1 s.d. of the pBAI values under each stand age. The pBAI is indicative of the relative advantage of DBF to ENF in terms of carbon use for stem growth.

When E_a was < 0.50 eV (93% of the cases), there was a negative relationship between E_a and CUE; however, the negative relationship disappeared when E_a was > 0.50 eV. This indicates that in most site-years when maintenance respiration is more responsive to temperature (greater E_a), more carbon is probably lost through maintenance respiration, thereby reducing CUE.

The global distribution of vegetation CUE

We generated a global map of CUE by using a random forest model trained by CUE_{EC} (Methods). Our estimates of CUE ranged from 0.3 to 0.6, with a clear latitudinal gradient—increasing from the tropics to high latitudes (Fig. 4a). For $> 50\%$ of the global vegetated land surface, CUE converged in a relatively small range between 0.4 and 0.5. Meanwhile, the CUE derived from an ensemble of dynamic global vegetation models (DGVMs) exhibited a similar latitudinal gradient, although with a broader distribution, ranging from 0.3 to 0.7 (Fig. 4c and Supplementary Fig. 3). Notably, the CUE estimated from DGVMs showed substantial spread across models (Fig. 4d and Supplementary Fig. 6), with an average uncertainty of 0.15 (1 s.d. of DGVMs CUE) and the largest uncertainty of 0.21 in the high latitudes. Meanwhile, the uncertainty from CUE estimated from the random forest was spatially homogeneous and generally < 0.10 (Fig. 4d).

Discussion

In this study, we leveraged a global network of eddy covariance sites to estimate CUE and revealed that CUE averaged 0.43 ± 0.12 across 2,737 site-years. We then analysed the biotic and abiotic factors responsible for the global variation in CUE. Among these factors, PFTs emerged as the pivotal contributor to CUE variability, with deciduous broad-leaf forests exhibiting notably higher CUE compared to other forest ecosystems. Meanwhile, non-forest biomes have greater CUE than forest biomes. We found consistently negative impacts of temperature, radiation, rainfall and stand age on CUE. On the basis of the CUE we obtained from eddy covariance data, we further partitioned ecosystem respiration into heterotrophic and autotrophic components, and estimated the global pattern of CUE. Our study provides crucial insight into the global variation in vegetation CUE, which can greatly support our estimates of the land carbon sink and its optimization through land management for climate change mitigation.

Differences in CUE between PFTs

Previous studies have examined whether and how CUE varies by PFT. While some found no discernible distinction in CUE among PFTs¹⁵, others identified substantial differences¹⁰. However, these studies have not reached a consensus regarding the specific effect of PFTs on CUE.

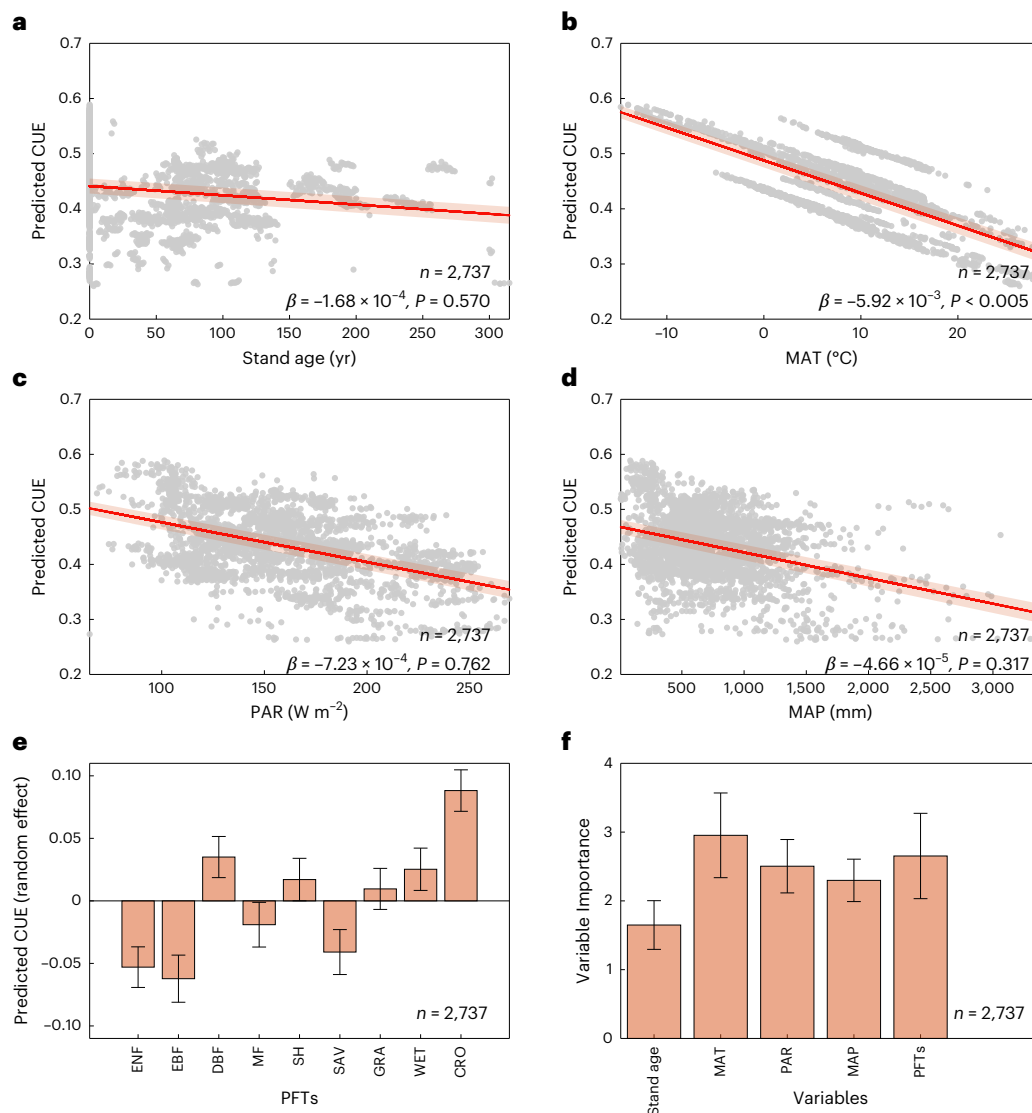


Fig. 2 | The responses of CUE to abiotic and biotic factors. a–e, The biotic factors include stand age (a) and plant functional types (PFTs) (e). **b–d,** The abiotic factors include mean annual air temperature (MAT; $^{\circ}\text{C}$) (b), mean annual photosynthetically active radiation (PAR; W m^{-2}) (c) and mean annual precipitation (MAP; mm year^{-1}) (d). **e, f,** The effect of PFTs on CUE (e) and the relative importance of the abiotic and biotic factors in determining CUE using

a random forest approach (f). The shaded areas in a–d represent the 95% confidence interval of the CUE responses to explanatory factors in the LME, while the error bars in e represent 1 s.d. of the random effects for each PFT in LME. The error bars in f represent 1 s.d. of the variable importance obtained by bootstrapping CUE_{EC} 1,000 times in the random forest.

For instance, temperate deciduous forests have been reported to have either greater CUE^{7,10} or lower CUE¹² than boreal forests. Importantly, our findings indicate that DBF exhibits a significantly ($P < 0.01$) higher CUE than other forest ecosystem types.

From a physiological perspective, the higher CUE was jointly determined by lower g_R and higher τ (Supplementary Fig. 4). The lower g_R means that the carbon cost of DBF building new tissues and components is less than other forests. This difference may manifest in the form of a lower leaf mass per area in DBF compared to other forest ecosystems^{26,27}. Meanwhile, higher τ indicates that there is less live biomass to incur maintenance respiration for DBF than for other biomes.

Our study also reported significantly ($P < 0.01$) higher CUE for non-forests than for forests, except the low CUE of the C_4 grass-dominated savanna ecosystems. The generally higher CUE of non-forests is probably caused by the low carbon stocks and fast turnover rate of their live biomass (Supplementary Fig. 4) and thus less maintenance respiration. CRO has the highest CUE, reflecting the selection of productive varieties for efficient biomass accumulation (crop yield) and better

management^{15,28}. Consistent with our results, a study using an emergent constraint approach to estimate CUE also reported greater CUE (0.55) for CRO than forests¹². Interestingly, we found that SAV demonstrates significantly ($P < 0.01$) lower CUE than other herbaceous species (Fig. 1a), potentially reflecting the high energy and carbon costs of C_4 photosynthesis pathway compared to the more prevalent C_3 pathway in temperate grasslands. Some leaf-level studies indicated that C_4 plants show higher dark respiration rates than C_3 plants²⁹, indicating a higher respiratory need for C_4 and therefore a lower CUE. This high demand of respiration of C_4 vegetation is also indicated by the great g_R values of savanna ecosystems (Supplementary Fig. 4). Meanwhile, we also hypothesize that the warm and dry conditions associated with the growth of C_4 grasses^{30,31} may suppress photosynthesis and enhance respiration, potentially resulting in a lower CUE for savanna ecosystems compared to other ecosystems.

Climate, soil and stand age impacts on CUE

Other than PFTs, we found that CUE is also impacted by climate (temperature, precipitation and light) and stand age. CUE derived from

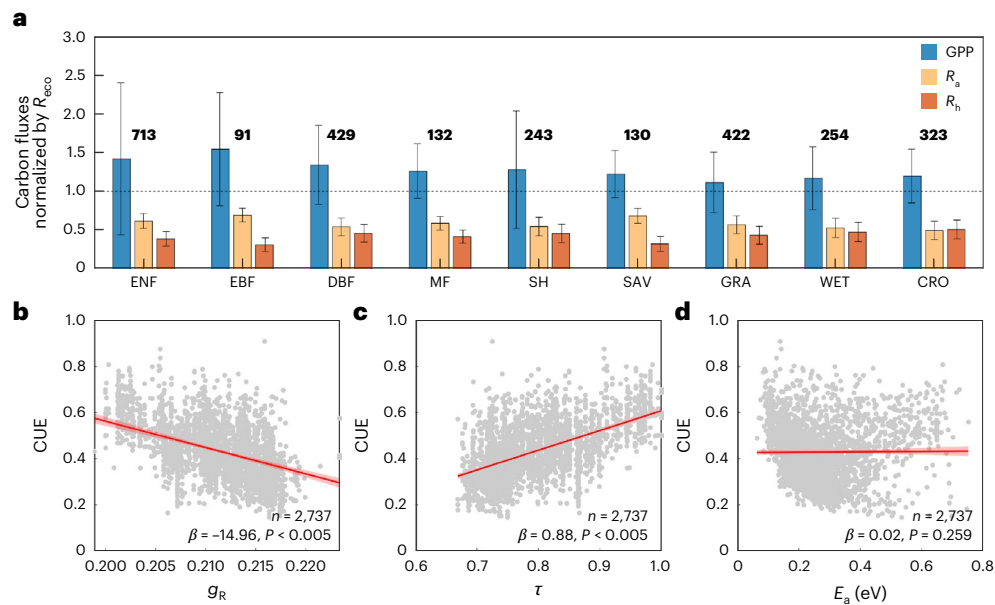


Fig. 3 | Using CUE to improve the understanding of respiration components and processes across flux sites. **a**, Partitioning ecosystem respiration (R_{eco}) into autotrophic respiration (R_a) and heterotrophic respiration (R_h). The panel presents annual GPP, R_a and R_h normalized by R_{eco} . The raw unit for carbon fluxes is $\text{g m}^{-2} \text{year}^{-1}$. The number above each group of bars indicates the number of site-years for that PFTs. The error bars represent 1 s.d. of the variables, calculated from the values of all site-years within each PFT. **b–d**, The relationships

between CUE and the key parameters of R_a , including the coefficient of growth respiration (g_R ; unitless) (**b**), the fraction of live biomass turned into non-respiratory biomass per unit time (τ ; unitless) (**c**) and the temperature sensitivity of the maintenance respiration (E_a (eV)) (**d**). The shaded areas indicate 1 s.d. of the fitting by bootstrapping CUE, g_R , τ and E_a 1,000 times according to their uncertainties.

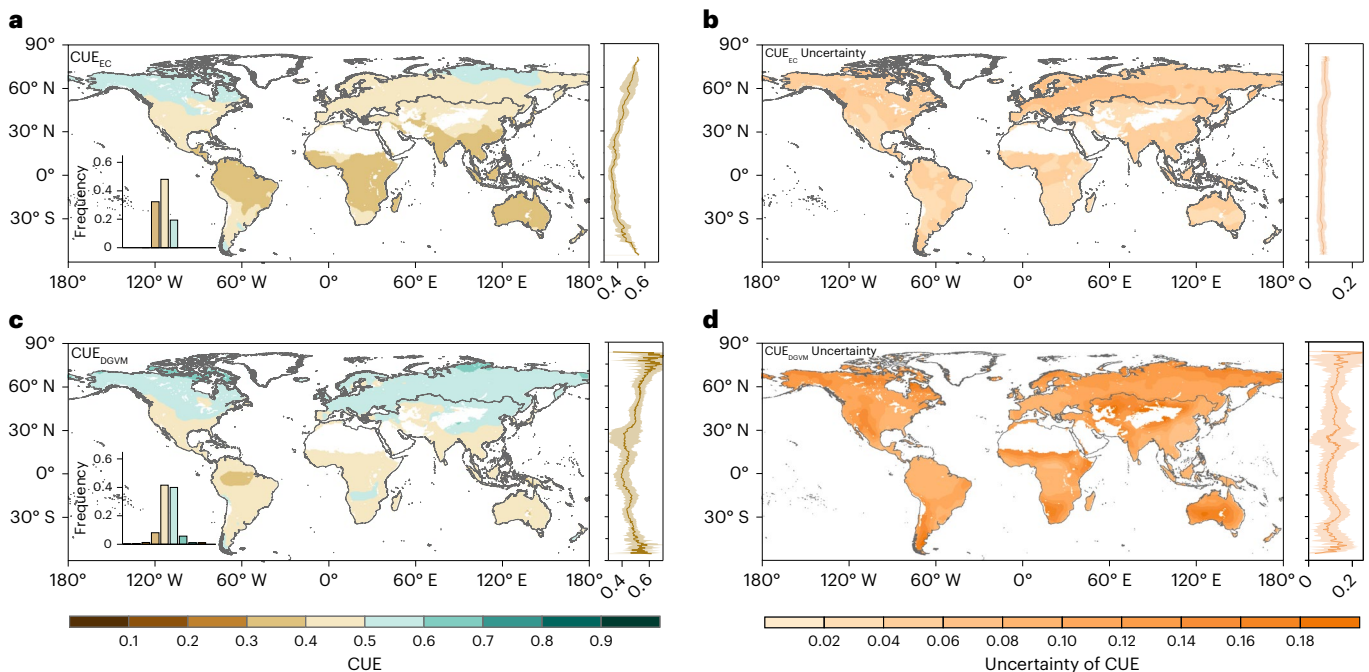


Fig. 4 | The global distribution of CUE and its uncertainty. **a–d**, The global mean CUE estimated by a random forest model trained on CUE_{FC} (**a**) and its associated uncertainty (**c**); the global mean CUE (**b**) and its uncertainty (**d**), calculated from the CUE estimates from an ensemble of DGVMs in the TRENDY v.9 project. The

uncertainty of CUE in **c** is defined as 1 s.d. of 1,000 random forest runs, with a bootstrapped CUE value in each run. The uncertainty of CUE in **d** is defined as 1 s.d. of the CUE estimated from DGVMs.

eddy covariance exhibited a linear decline with stand age, although this trend was not statistically significant ($P = 0.57$). This finding aligns with outcomes reported in earlier research studies^{7,11}. However, we noted that a linear model might not be the most suitable way to

describe the CUE–stand age relationship, since our estimated CUE generally increased with stand age up to ~30–50 years and then gradually decreased after the peak (Fig. 2a). A few studies have noted this nonlinearity in the CUE–stand age relationship^{11,13,32}. Considering that

GPP is not as sensitive to stand age as NPP³³, we hypothesize that the nonlinear association between CUE and stand age suggests an initial rise in NPP with increasing stand age followed by a subsequent decline as in Odum's ecological theory. In fact, this pattern has previously been documented for the primary tree species in the continental USA³⁴.

Previous studies using survey data have reported a positive effect of soil N content on CUE^{8,19}, as nutrient limitation may hinder photosynthesis and biomass production or demand stronger metabolic activities (respiration) for nutrient acquisition. In our attribution analysis (Fig. 2), we did not include soil N as an explanatory factor, as the soil N extracted from Soilgrids for eddy covariance sites demonstrated large biases when validated against the observed soil N (Supplementary Fig. 5) and the statistical performance of our attribution model declined after including soil N (Supplementary Table 1). If we indeed include soil N in our attribution analysis (Supplementary Fig. 6), a positive effect of soil N on CUE_{EC} was detected, consistent with the previous understanding. The increase of CUE with soil N also seems nonlinear, with CUE steeply increasing with soil N under low nitrogen conditions and plateauing when soil N is >0.02 gN kg⁻¹ (Supplementary Fig. 6f).

The negative impacts of climate variables on CUE collectively signify that under warmer, wetter and brighter conditions, a greater portion of photosynthate is lost through R_a (Fig. 2). Increasing temperatures are expected to enhance R_a , whereas their effect on GPP can be either positive or negative. If there is a decline in GPP, or if the rise in R_a outpaces that of GPP, it is plausible that rising temperatures could result in a decrease in CUE¹⁷. It is worth noting that the response of CUE to temperature we observed differs from those reported in a recent synthesis¹¹. We speculate that this difference may arise from three potential factors as follows.

- (1) The previous synthesis omitted PFTs as an explanatory variable. Given that PFTs are influenced by climate variations and have an important role in CUE dynamics, the absence of PFTs could potentially alter the CUE–MAT relationship. For example, we attributed the low CUE in the boreal zone to the presence of ENF, which has a lower CUE baseline than temperate DBF (Fig. 2f). However, if ENF is not accounted for in our attribution analysis, the low CUE in the boreal zone may be attributed to low temperature, thus resulting in a positive CUE–MAT relationship.
- (2) The shift of CUE–MAT relationship with MAT. We analysed the univariate regressions of CUE_{IN} and CUE_{EC} against MAT and found that both CUE_{IN} and CUE_{EC} exhibit a change in their relationship with MAT around 10 °C (Supplementary Fig. 7). Specifically, when MAT is <10 °C, CUE_{IN} increases with MAT, and CUE_{EC} only slightly decreases with MAT. However, when MAT is >10 °C, both CUE_{IN} and CUE_{EC} decrease rapidly with MAT. The shift indicates that the positive effect of MAT on CUE_{IN} reported in the previous synthesis may primarily arise from the CUE records obtained under low temperatures. The shift in CUE–MAT relationship around 10 °C, identified by both CUE_{IN} and CUE_{EC}, merits further examination (Supplementary Fig. 7).
- (3) Thermal acclimation of respiration. Experimental evidence has suggested that thermal acclimation—the declines of base respiration rate or the temperature sensitivity of respiration with the increase of growth temperature—could impact CUE^{35,36}. Although the exact effect of growth temperature on CUE is still subject to debate, it is conceivable that CUE may increase with MAT if GPP increases with growth temperature while the increase of R_a is mitigated by thermal acclimation³⁷. This seems to be consistent with our point (2) above where the increase of CUE with temperature is noted predominantly within the low temperature range. Additionally, we found that E_a (the temperature sensitivity of maintenance respiration) decreases with MAT (Supplementary Fig. 7c), providing further evidence for the existence of temperature acclimation of respiration across global eddy covariance sites.

Water availability directly impacts GPP, as water deficits lead to the downregulation of stomatal openness³⁸ and light use efficiency³⁹. However, the decrease in GPP may not translate into a decrease in NPP or CUE during droughts²⁰. In fact, forests are likely to experience a decrease in biomass residency time (leaf shedding and high tree mortality rate) and then a decrease in R_a , ultimately leading to a CUE increase during droughts²⁰. This mechanism offers a plausible explanation for the negative relationship observed between CUE and precipitation (Fig. 2) and is in line with the notably lower τ values found in the case of wet EBF compared to other forest types (Supplementary Fig. 4).

The influence of light on CUE has received less attention. Nonetheless, the synthesis study we mentioned¹¹ did find a positive correlation between latitude (equivalent to a negative effect of light availability) and CUE. One plausible mechanism is that leaves tend to incur higher construction costs in regions with greater light intensity⁴⁰, which can result in higher g_R and consequently lower CUE. In alignment with this mechanism, our investigation revealed that EBF and SAV in low-latitude regions exhibit significantly higher g_R values ($P < 0.01$) compared to the global average (Supplementary Fig. 4).

Interpretation of CUE derived from eddy covariance

Our method of deriving CUE assumes that there is a strong coupling between R_{eco} and GPP (Supplementary Fig. 1), and within a short period of similar temperature in the growing season, variations in R_{eco} are predominantly influenced by changes in R_a . This hypothesis is based on a series of studies suggesting a temporal mismatch in the variation of R_a and R_h (refs. 41–43), owing to the difference in the substrates and their decomposition rates (for example, Q_{10}). Specifically, R_a uses recent photosynthetic assimilates and is tightly coupled to GPP, while R_h draws substrates from various sources, including plant residues or soil organic matter, which typically change more slowly than photosynthesis. Therefore, changes in R_a (ΔR_a) are more likely driven by changes in GPP (ΔGPP) whereas changes in R_h (ΔR_h) are more likely driven by Q_{10} and temperature⁴¹, supporting the assumption underlying our method. However, we acknowledge a key caveat in our assumption: certain R_h fluxes, such as rhizomicrobial respiration or priming effect (exudes from roots that increases substrate availability for R_h), also use recent photosynthetic assimilates⁴⁴. These rapid changing R_h fluxes could lead to an overestimation of R_a and an underestimation of NPP and CUE (Methods). Nevertheless, the actual magnitudes of rhizomicrobial respiration and priming effect remain largely unknown across ecosystems. On the basis of our validation against in situ biometric observations (Supplementary Fig. 2), we suspect that the underestimation of CUE induced by these factors was minor and not widespread.

Given that we initially determined R_a and then subtracted it from GPP to represent NPP, our NPP estimates encompass not only the carbon available for building biomass but also the carbon used in non-structural and secondary carbon compounds (reserves, root exudates and biogenic volatile organic compound). Those secondary carbon products might use a considerable part of photosynthate^{45,46}. Therefore, our estimate of CUE (NPP/GPP) would be greater than the narrowly defined BPE¹⁰. With the strong dependence of maintenance respiration on temperature¹⁷, it is also anticipated that CUE will exhibit seasonal fluctuation. While our method allows the derivation of seasonal CUE (Supplementary Fig. 8), we did not explore its variation as we lack independent observations to validate seasonal CUE, and the environmental dependences of CUE at the seasonal scale might be different to those at the interannual scale. We, however, have included the seasonality as a part of the uncertainty in the final annual CUE_{EC} estimates ('The workflow to estimate CUE from eddy covariance observations' section in Methods; Supplementary Table 2). Another source of uncertainty in our method, the choice of temperature and time window lengths, was found to have minimal impact on our CUE estimates (Supplementary Fig. 9).

During our validation of CUE_{EC} against CUE_{IN} , we observed good agreement between the two metrics at seven out of the nine sites (Fig. 1b). Nevertheless, at one site (CA-TP2), we observed that CUE_{EC} was considerably greater than CUE_{IN} , and at another site (US-MMS), CUE_{EC} was lower than CUE_{IN} . CA-TP2 is one of the pine plantation sites (CA-TP1, CA-TP2, CA-TP3 and CA-TP4) distributed along a stand age gradient in southern Ontario, Canada. The stand ages for the four sites were 5, 18, 33 and 68 in 2007⁴⁷. Our derived CUE_{EC} for the four sites were 0.61, 0.58, 0.47 and 0.31, respectively, demonstrating a clear negative CUE –stand age relationship. Meanwhile, CUE_{IN} for the four sites were 0.57, 0.31, 0.51, 0.44, with CA-TP2 deviating from the negative CUE –stand age relationship. Given the similar species, climate, topography and soil conditions across the four sites, with stand age being the primary differing factor, we posit that our estimate of CUE_{EC} at CA-TP2 might provide a more accurate reflection of CUE than CUE_{IN} . US-MMS is a diverse deciduous forest (including 29 tree species) in southcentral Indiana, USA⁴⁸. The CUE_{IN} reported there was 0.70 and the CUE_{EC} was 0.45. We noted that the biometric measurements for CUE_{IN} derivation were mostly conducted in plots within 200 m of the tower⁴⁹, while the footprint climatology of the US-MMS tower extending to 500 m in daytime, especially the southwest fetch was under-represented by the plots⁵⁰. Considering the diverse species composition and variable topography of this site, the discrepancy in spatial representativeness between the plots and flux footprint could potentially account for the disparity between CUE_{IN} and CUE_{EC} .

Implications for land carbon sink

Land carbon sink has been increasing proportionally to human emissions of CO_2 and playing a critical role in climate change mitigation. The increase in land carbon sink has been largely attributed to elevated CO_2 (refs. 51,52), changes in other environmental variables⁵³ and natural regrowth after disturbance^{54–56}, meanwhile, the effect of shift in vegetation biomes on carbon uptake has been rarely studied, although large-scale biome shifts have been reported as the expansion of deciduous trees in boreal zones⁵⁷ and savannas⁵⁸. Our study indicates that the shift in biome types would potentially impact land carbon cycle by changing CUE —a synthesis of coupled model intercomparison project phase 5 and phase 6 models suggested that CUE accounts for roughly 15% of the variance in global land carbon storage²³. Moreover, the disparities in CUE among biomes carry great implications for large-scale tree-planting initiatives and forest management strategies. While the restoration of native trees and natural forest regrowth is advocated as the optimal approach for forest restoration^{59,60}, our findings suggest that we could enhance the carbon use and the land carbon sink more effectively by prioritizing native DBF species given a fixed amount of GPP, particularly in regions where deciduous and evergreen trees coexist. To evaluate the effect of CUE on the carbon sink, we considered a hypothetical scenario in which MF and ENF, along with their CUE , were replaced by those of DBF. Using a gridded global GPP and R_{eco} product as the reference⁶¹, we estimated that this scenario would lead to a 0.18 PgC year^{−1} increase in global NPP and a 0.11 PgC year^{−1} increase in the carbon sink. This corresponds to ~10% of annual net emissions from land-use sectors¹.

In summary, our study offers a timely and critical insight into the variability of global CUE . It advances our understanding of the terrestrial carbon cycle by using a new method to derive advanced ecological metrics (for example, CUE) from eddy covariance data. It offers valuable guidance for the implementation of reforestation, afforestation and conservation plans aimed at optimizing the potential of the land carbon sink.

Methods

Theoretical basis to estimate CUE from eddy covariance observations

We used eddy covariance observations of CO_2 flux between ecosystems and the atmosphere provided in the standard FLUXNET2015 dataset⁶²,

as well as the flux data acquired from Ameriflux and ICOS, processed by the FLUXNET2015 pipeline (Supplementary Table 3 and Supplementary Fig. 10a). The pipeline to produce the data includes the quality control of raw flux data and the partitioning of the net CO_2 exchange into GPP and R_{eco} using daytime partitioning method (GPP_DT_REF and Reco_DT_REF) or night-time partitioning method (GPP_NT_REF and Reco_NT_REF). In the main analysis, we used the average of GPP_DT_REF and GPP_NT_REF as the GPP time series and the average of Reco_DT_REF and Reco_NT_REF as the R_{eco} time series. This step is meant to avoid the potential uncertainty incurred by the choice of partitioning method.

According to the definition of CUE , $CUE = (GPP - R_a)/GPP = 1 - R_a/GPP$. Between any two timestamps, we can obtain

$$\Delta R_a = (1 - CUE) \times \Delta GPP \quad (1)$$

in which we assume CUE to be constant between the two timestamps. Meanwhile, we further expanded autotrophic respiration (R_a) to growth respiration (R_G) and maintenance respiration (R_M). Parameter R_G is the cost of producing new biomass (G) and R_M is the cost of maintaining the existing biomass (W_{live}). Therefore, R_G and R_M can be further expanded to the product of their respective respiration coefficients (g_R and m_R) and biomass amounts (G and W_{live})¹⁴, leading to equation (2) below:

$$R_a = R_G + R_M = g_R G + m_R W_{live} \quad (2)$$

Substituting equation (2) into equation (1), the change in R_a between two timestamps can be described as $\Delta R_a = g_R \Delta G + m_R \Delta W_{live}$. The change in new biomass growth (ΔG) is proportional to the change in NPP between two timestamps ($\Delta NPP = \Delta GPP \times CUE$). The changes in live biomass (ΔW_{live}) that needs maintenance are proportional to the accumulated NPP between the two timestamps $\Delta cNPP = \Delta cGPP \times CUE \times (1 - \tau)$, where $cNPP$ and $cGPP$ are the cumulative NPP and GPP from day one of the year, respectively. Parameter τ represents the fraction of live biomass turned to non-respiratory biomass per unit time. Therefore, we can adjust the equation (2) to

$$\Delta R_a = g_R \times CUE \times \Delta GPP + m_R \times CUE \times \Delta cGPP \times (1 - \tau) \quad (3)$$

Note that in equation (3), we assume that all $\Delta GPP \times CUE$ between the two timestamps is used for growth, neglecting the carbon allocated for root exudation or symbiosis of mycorrhizal. This assumption would not affect the estimation of CUE , but may lead to an overestimation of g_R if carbon allocated for non-growth purposes is substantial between the two timestamps.

Since m_R has a strong temperature dependence¹⁷ and changes substantially within a year, to facilitate the comparison between site-years we further include the temperature sensitivity of maintenance respiration (E_a in eV, the Arrhenius activation energy for respiration) into equation (3):

$$\Delta R_a = g_R \times CUE \times \Delta GPP + e^{(-E_a/k_B)(1/T - 1/T_0)} \times m_{R0} \times CUE \times \Delta cGPP \times (1 - \tau) \quad (4)$$

where m_{R0} refers to the baseline m_R of the site-year, T_0 (in K) is the temperature corresponding to m_{R0} , T is the mean temperature of the temperature bin and $k_B = 8.617333262 \times 10^{-5}$ eV K^{−1} is the Boltzmann constant.

Considering the differences in the mechanisms (for example, substrates and decomposition rate) of R_a and R_h , and the consequent differences in the time scales of their changes^{41–43}, we suggest it is feasible to disentangle the signals of ΔR_a and ΔR_h in ΔR_{eco} by meticulously organizing the data by time frames and temperature (Discussion).

Specifically, we used two criteria to organize daily flux data for the derivation of CUE : (1) we grouped flux observations using windows of 5 consecutive days in the growing season and (2) we grouped flux observations by daily mean temperature (the difference in temperature) should be <1 °C and remove the days with rainfall >2 mm day^{−1} to avoid sudden pulses of respiration after rewetting the soil (for example, Birch effect)^{63,64}. The criteria are to ensure there are limited changes in

soil organic matter (most soil organic matter has turnover time longer than a week) and no changes in R_h under similar temperatures, which allow us to assume $\Delta R_a = \Delta R_{eco}$ in these refined data groups.

The workflow to estimate CUE from eddy covariance observations

Following the theoretical basis above, we designed the following workflow to estimate CUE, g_R , τ and E_a for each site-year (Supplementary Fig. 8), using MATLAB (v.2021b) as follows.

Step 1. Organize daily flux data in the growing season into groups of 5 consecutive days. Within each 5-day window, we obtained ΔGPP , ΔR_a and $\Delta cGPP$ between every 2 d. For example, if in a 5-day window the daily GPP are 1.1, 1.2, 1.3, 1.4, 1.5 $g\ m^{-2}\ day^{-1}$, then the ΔGPP between day 5 and day 1 would be $1.5 - 1.1 = 0.4$ and the $\Delta cGPP$ between day 5 and day 1 would be $(1.1 + 1.2 + 1.3 + 1.4 + 1.5) - 1.1 = 5.4$.

For each time window, we got -20 samples of ΔGPP , ΔR_a and $\Delta cGPP$. The growing season was defined as when daily GPP was >20% of the maximum daily GPP of the site-year.

Step 2. Insert the data obtained in step 1 to equations (1) and (3), and estimate CUE, g_R , τ and m_R for each 5-day time window. In this step, since we have 20 samples and 4 unknown parameters, we used the Markov Chain Monte Carlo (MCMC) method⁶⁵ to estimate the optimal values of CUE, g_R , τ and m_R for each 5-day time window. When running MCMC, the prior of variables for CUE, g_R , m_R and τ were set within the ranges of (0, 1), (0.15, 0.3), (0.0, 0.5) and (0.1), respectively.

Step 3. Obtain m_{R0} and T_0 for the site-year, where m_{R0} is the bottom tenth percentile of the m_R values of all 5-day windows in the site-year (from step 2). T_0 is the mean temperature corresponding to m_{R0} . We used the bottom ten percentile to avoid obtaining an extreme m_{R0} value which is not representative of the ecosystem.

Step 4. Obtain g_R and τ for the site-year, where g_R and τ are the average g_R and τ of all 5-day windows (from step 2). The step aligns with the observations that g_R has a small range based on the construction cost of key chemical compounds in plants and should have limited seasonality^{40,66}. There were no previous reports on the seasonality of τ , therefore we assume that it is also a constant for each site-year.

Step 5. Organize daily flux data by temperature and remove the days with precipitation >2 mm. Within each temperature bin (the range of temperature is <1 K), we obtained ΔGPP , ΔR_a and $\Delta cGPP$ between every 2 days. For each temperature bin, we got -20–200 samples of ΔGPP , ΔR_a and $\Delta cGPP$.

Step 6. Insert the data obtained in step 5, the m_{R0} and T_0 obtained in step 3, and the g_R and τ obtained in step 4, to equations (1) and (4), and estimate CUE and E_a for each temperature bin. In this step, since we have 20–200 samples and two unknown parameters, we used MCMC again to estimate the optimal values of CUE and E_a for each bin. When running MCMC, the prior values for CUE and E_a were set within the ranges of (0, 1) and (0.2, 1.5), respectively.

Step 7. Obtain CUE and E_a for the site-year, where CUE and E_a are the average CUE and E_a of all bins from step 6. We removed CUE and E_a estimates from those bins where the estimates were similar to the priors in MCMC, meaning CUE and E_a were not properly constrained. We also acknowledge that while our method provides seasonality of CUE and E_a , we only examined CUE and other parameters at the annual time scale in this study. In total, we obtained 2,737 site-years of CUE record for our analysis. We also got the average CUE for each site for validation (Supplementary Table 2).

Uncertainty. As we only reported annual average CUE of each site-year or site, the main sources of uncertainty for CUE include: (1) the temporal (seasonal and annual) variation in CUE and (2) the posterior distribution of CUE from MCMC. We used a bootstrapping approach to combine the uncertainties incurred by both sources and aggregated them into one uncertainty value for each site-year or site (Supplementary Table 2). Meanwhile, we tested alternative time and temperature windows in

MCMC analysis and found they have limited impacts on the CUE derived (Supplementary Fig. 9).

Ground observations for validation

To validate the CUE derived from eddy covariance (CUE_{EC}) and the associated carbon fluxes, we used multiple independent datasets for validation, including (1) site CUE and BPE obtained from inventory or biometric methods^{11,15}, (2) site NPP and BP obtained from inventory or biometric methods^{11,15}, (3) the ITRDB²⁵ and (4) site R_h from open-source continuous soil respiration database (COSORE)²⁴ and global soil respiration database (SRDB)⁶⁷.

In dataset (1), we obtained 244 records of CUE and BPE from forest sites¹¹ and 57 records of CUE and BPE from non-forest sites¹⁵. These studies used inventory or biometric methods to estimate NPP and BP, which were further used to estimate CUE and BPE (all referred to as CUE_{IN} in this study). Meanwhile, the GPP measured at those sites were obtained from various types of methods (biometric, eddy covariance and site-parameterized modelling). In most cases, we used GPP measured by biometric methods, if they are available, for the derivation of CUE_{EC} . We found that there were 12 sites with collocated biometric and eddy covariance observations. The validation based on dataset (1) was presented in Fig. 1a,b.

In dataset (2), we investigated the same data source as dataset (1) but only used their NPP and BP records. These values are used to assess the robustness of NPP estimated based on CUE_{EC} . Specifically, after deriving a global map of CUE from CUE_{EC} using machine learning, we estimated NPP at those site-years in dataset (2) by multiplying extrapolated CUE_{EC} and the site measured GPP. Then we compared NPP_{EC} against the measured NPP and BP. The validation based on dataset (2) was presented in Supplementary Fig. 2.

In dataset (3), we acquired 15,890 of tree-ring records from 4,479 sites globally. Since our target to assess the relative growth rate of deciduous trees (DB) and evergreen trees (EV) under the similar climate, we only selected those sites with both DB and EV in proximation. At the end we used 1,095 tree-ring records (Supplementary Fig. 10b). Please see 'Quantify relative CUE from pBAI' section in the Methods on using tree-ring data to derive relative CUE. The validation based on dataset (3) was presented in Fig. 1c.

In dataset (4), we use the R_h observations from the COSORE and the SRDB datasets. The R_h was usually obtained by combing measurements from chamber, isotopic, girdling, trench or root exclusion approaches. For COSORE, we estimated annual R_h by multiplying reported R_h values with the length of year. SRDB provided site-level annual R_h . The validation based on dataset (4) was presented in Supplementary Fig. 2a.

Quantify relative CUE from pBAI

In parallel to CUE, the carbon accumulation rate of individual trees is assessed by another metric—BAI. BAI is indicative of NPP, as NPP allocated to stem, NPP_{stem} , can be estimated by scaling BAI with stem density (number of trees per unit area), wood density and tree height. Similar to CUE, many studies have examined BAI and its associated changes in biomass production with abiotic (temperature⁶⁸ and droughts⁶⁹) and biotic factors (stand age⁷⁰, tree size⁷¹, mortality⁷² and forest types⁷³), however, they often had a regional focus and thus lack global implications. Following these studies, we have

$$NPP_{stem} = BAI \times \text{tree height} \times \text{wood density} \times \text{stem density} \quad (5)$$

Meanwhile, we estimated that the CUE for stem is $CUE_{stem} = NPP_{stem}/GPP$, and assume that the difference in CUE_{stem} is indicative of the difference in total CUE. To compare the relative difference between the CUE of DB and EV trees at the same locations (similar climate and thus hypothetically similar GPP), we have

$$\begin{aligned} CUE_{stem,DB}/CUE_{stem,EV} \\ = BAI_{DB}/BAI_{EV} \times \text{height}_{DB}/\text{height}_{EV} \times \text{density}_{DB}/\text{density}_{EV} \end{aligned} \quad (6)$$

where $\text{height}_{\text{DB}}$ and $\text{height}_{\text{EV}}$ are the height of the DB and EV trees at the same location, and $\text{density}_{\text{DB}}$ and $\text{density}_{\text{EV}}$ are the stem density of the DB and EV trees at the same location. Relying on recent global syntheses of tree height^{74,75} and wood density⁷⁶, we found that on global average, $\text{height}_{\text{DB}}$ is 5% smaller than $\text{height}_{\text{EV}}$, and $\text{density}_{\text{DB}}$ is 5% greater than $\text{density}_{\text{EV}}$. Therefore, we assumed $\text{height}_{\text{DB}}/\text{height}_{\text{EV}} \times \text{density}_{\text{DB}}/\text{density}_{\text{EV}}$ is -1, which reduced the equation (6) to

$$\text{CUE}_{\text{stem_DB}}/\text{CUE}_{\text{stem_EV}} \approx \text{BAI}_{\text{DB}}/\text{BAI}_{\text{EV}} = \text{pBAI} \quad (7)$$

where pBAI means the paired BAI of DB and EN trees at the same locations. To obtain pBAI, we used a clean and high-quality version of tree-ring width data from ITRDB²⁵ and estimated BAI from tree-ring width using the functions in an open R package d1pR. We classified the trees into DB and EV, based on the species information compiled at <https://www1.ncdc.noaa.gov/pub/data/paleo/templates/tree-species-code.txt> (accessed in 2021, now archived at https://github.com/lxswr/CUE_fluxnet/blob/main/tree-species-code.txt). Note that the EV trees are mostly evergreen needleleaf trees in ITRDB while evergreen broadleaf trees in the tropics are under-represented. The pBAI provides an independent examination of the difference in CUE_{stem} between DB and EV.

Ancillary climate, soil and model datasets

For site-level analysis, we used the daily meteorological observations from the eddy covariance datasets. The climate variables we used include air temperature, precipitation and photosynthetic active radiation. The stand age of flux sites is acquired from a previous study⁷⁷ wherever there is a record. For sites lacking stand age data, we sourced the required information from the global forest age dataset (GFAD v.1.1)⁷⁸. The stand age of non-forest biomes is assumed to be 1 in all attribution analyses. We extract the soil total nitrogen content (soil N content) for each flux site from Soilgrids at 250-m resolution⁷⁹.

We further used the TS4.04 version of monthly gridded air temperature, precipitation and solar radiation data at 0.5° provided by the Climate Research Unit⁸⁰, along with the aforementioned GFAD v.1.1 stand age dataset and the soil N content from soilgrids, to estimate global CUE using a random forest model (next section of Methods). All gridded datasets were resampled to 0.5°. The gridded climate data were averaged to annual values, including MAT, MAP and mean annual PAR.

Meanwhile, we studied the CUE estimated by 15 DGVMs participating in the TRENDY v.9 project in our study^{81,82}. For each DGVM, we estimated their CUE as the ratio of mean annual NPP to mean annual GPP from 1980 to 2019 (Supplementary Fig. 3). The simulations of NPP and GPP were conducted under the S3 scenario (considering elevated CO₂, climate change and land-use and land-cover changes).

Linear mixed effect model and random forest model

We used the LME model⁸³ to quantify the sensitivities of CUE to abiotic and biotic factors. The LME model suffers less from correlations of samples from similar groups and can quantify the impacts of grouping as the random effect term. This is especially useful in our study to understand the impact of PFTs on CUE, while obtaining the sensitivity of CUE to continuous variables, such as climate and soil properties. We tested several LME models and selected the one that has the lowest Akaike information criterion and Bayesian information criterion, and considers the major factors found in previous studies (Supplementary Table 1). The final LME model to estimate CUE was based on MAT, MAP, PAR, stand age and PFTs, where PFTs were set as a random effect, and the others were fixed effect. The analysis was conducted using the function `fitlme` in MATLAB.

We then trained a random forest model using the 2,737 records of CUE_{EC} and the in situ variables identified by the LME model as inputs. Subsequently, the random forest model was used to estimate global CUE using gridded MAT, MAP, PAR, stand age, soil N and PFTs. External

validation of the random forest model shows good performance in extrapolating CUE ($R = 0.72$, $\text{RMSE} = 0.08$). We chose the random forest model as it can use both continuous variables (climate) and categorical variables (PFT) as inputs, capture the nonlinear dependence of CUE on some variables and demonstrate stronger statistical performance in predicting CUE compared to LME. The random forest model has been widely used for upscaling in ecology and is often regarded as one of the better-performing models^{84–86}.

Reporting summary

Further information on research design is available in the Nature Portfolio Reporting Summary linked to this article.

Data availability

This study used openly available eddy covariance measurements provided by FLUXNET2015 dataset (<https://fluxnet.fluxdata.org/data/fluxnet2015-dataset/>), Ameriflux (<https://ameriflux.lbl.gov/introducing-the-ameriflux-fluxnet-data-product/>) and ICOS (<https://www.icos-cp.eu/data-products>). We acquired the global tree-ring dataset from ITRDB (<https://www.ncei.noaa.gov/products/paleoclimatology/tree-ring>). We requested and obtained the TRENDY v.9 DGVM simulations from S. Sitch at the University of Exeter. The vegetation CUE for eddy covariance sites, a global CUE map and the code used estimate CUE from eddy covariance observations are available via Zenodo at <https://zenodo.org/records/15188212> (ref. 87). Source data are provided with this paper.

Code availability

The code used to support the findings of this study is publicly available via GitHub at [www.github.com/lxswr/CUE_fluxnet](https://github.com/lxswr/CUE_fluxnet) and via Zenodo at <https://zenodo.org/records/15188212> (ref. 87).

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Author contributions

X. Luo designed the study and carried out the analysis. R.Z. aided in producing figures. X. Luo, H.C., A.C., S.F., T.F.K., N.N., W.S., K.Y. and I.C.P. participated in discussions at various stages. R.Y., H.C., X. Lu and L.Y. aided in data collection. All authors contributed to the interpretation of the results and writing.

Competing interests

The authors declare no competing interests.

Additional information

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obtained the TRENDY v9 DGVM simulations from Prof. Stephen Sitch at the University of Exeter. We will deposit the carbon use efficiency of eddy covariance sites and global carbon use efficiency map at <https://zenodo.org/records/15188212>.

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Research sample	In total we used 2737 site-years of data, depending on the data availability of the open databases. For each year, we used our algorithm to estimate a carbon use efficiency value, therefore the total sample size is 2737. We treated all samples equally, and did not conduct any manipulations or exclusions of the data in the analysis.
Sampling strategy	The sample size is dependent on the availability of data from the open databases. We utilised all the available observations to estimate carbon use efficiency. We indicated the sample size were applicable in the research. For example, we have more observations from evergreen needleleaf forests than shrublands. The sample size for each vegetation type is also dependent on the availability of data.
Data collection	The eddy covariance data were collected at global flux towers and then processed using standard FLUXNET2015 protocol by each flux network (Ameriflux, ICOS). We used the processed data provided by these data portals in our study.
Timing and spatial scale	Our study used the observations from 358 eddy covariance sites distributed globally, covering 9 main land cover types. These sites have varying length of observations (in total 2737 site-years). The earliest observation dated back to 1991 and the most recent observation comes from 2021. For each year, we used daily flux data to derive a carbon use efficiency value, therefore the final values we reported are the carbon use efficiency at the annual time step.
Data exclusions	No data were excluded in the analysis. We used all data from open-access flux database for the analysis.
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