LETTER

Increase in forest water–use efficiency as atmospheric carbon dioxide concentrations rise

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Terrestrial plants remove CO_2 from the atmosphere through photosynthesis, a process that is accompanied by the loss of water vapour from leaves[1]. The ratio of water loss to carbon gain, or water-use efficiency, is a key characteristic of ecosystem function that is central to the global cycles of water, energy and carbon[2]. Here we analyse direct, long-term measurements of whole-ecosystem carbon and water exchange[3]. We find a substantial increase in water-use efficiency in temperate and boreal forests of the Northern Hemisphere over the past two decades. We systematically assess various competing hypotheses to explain this trend, and find that the observed increase is most consistent with a strong CO_2 fertilization effect. The results suggest a partial closure of stomata[1]—small pores on the leaf surface that regulate gas exchange—to maintain a near-constant concentration of CO_2 inside the leaf even under continually increasing atmospheric CO_2 levels. The observed increase in forest water-use efficiency is larger than that predicted by existing theory and 13 terrestrial biosphere models. The increase is associated with trends of increasing ecosystem-level photosynthesis and net carbon uptake, and decreasing evapotranspiration. Our findings suggest a shift in the carbon- and water-based economics of terrestrial vegetation, which may require a reassessment of the role of stomatal control in regulating interactions between forests and climate change, and a re-evaluation of coupled vegetation–climate models.

Plants assimilate atmospheric CO_2 through photosynthesis. The complex organic molecules that result ultimately support most of life on Earth. Acquisition of CO_2 is accompanied by the loss of water vapour through stomata, the small pores on leaf surfaces that regulate the diffusion of these two gases between the leaf and the atmosphere[1,4,5]. The rate of carbon uptake per unit of water lost, referred to as water-use efficiency, integrates a suite of biotic and abiotic factors, and, importantly, quantifies how much water an ecosystem uses relative to carbon gained.

The photosynthetic uptake of CO_2, A, and the loss of water vapour from a leaf to the atmosphere (transpiration, E) can both be described as a conductance g_s multiplied by a concentration difference between the atmosphere and the internal leaf mesophyll:

$$A = g_s(c_a - c_i) \qquad (1)$$

$$E = 1.6 g_s(v_i - v_a) \qquad (2)$$

where g_s is the stomatal conductance to CO_2, c_a and c_i represent the ambient and leaf intercellular mole fractions of CO_2 (respectively), v_a and v_i similarly represent the ambient and leaf intercellular water vapour mole fractions, and 1.6 accounts for the greater diffusivity of water vapour relative to CO_2.

At the leaf level, instantaneous water-use efficiency W quantifies the rate of carbon uptake per unit of water lost ($W = A/E$). Similarly, at the ecosystem scale, bulk canopy water-use efficiency is defined as:

$$W_e = \frac{A_e}{E_e} \qquad (3)$$

To account for the effects of atmospheric evaporative demand, D, an 'inherent' ecosystem-scale water-use efficiency[2] can be calculated as $W_{ei} = W_e D$ (see Methods). Combining W_{ei} with equations (1) and (2) shows that the sensitivity of W_{ei} to c_a depends on how c_i varies with c_a, and:

$$\Delta W_{ei} = \Delta(c_a - C_i)/1.6 \qquad (4)$$

where C_i represents the integrated canopy leaf intercellular mole fraction of CO_2 and Δ is the difference operator.

The biochemistry of photosynthesis indicates that increasing atmospheric CO_2 should lead to an increase in both photosynthetic uptake and water-use efficiency[4]—that is, the 'CO_2 fertilization effect'. This could stimulate carbon uptake and storage by the terrestrial biosphere, and may account for largely unexplained increases in forest growth rates[6–8] and terrestrial carbon uptake[9]. CO_2-enrichment experiments[10], proxy reconstructions[11], and models provide support for an increase in plant resource-use efficiency as CO_2 concentrations increase, but are often inconsistent and inconclusive[10,12–14]. The magnitude of any response to elevated CO_2 in natural forest ecosystems is largely unknown[15,16], leading to debate on the effect of nutrient limitations[17]. This is not surprising, given the difficulties in translating results from isotopic proxies and small-scale manipulative experiments to intact natural ecosystems[10,12].

Here we document and analyse recent trends in the inherent water-use efficiency W_{ei} of forest canopies using direct and continuous long-term measurements of CO_2 and water vapour fluxes. We address a variety of factors as possible drivers of the observed trends, including the potential role of increasing levels of atmospheric CO_2. We focus on seven sites in the midwestern and northeastern United States. The forests represent tree species compositions typical of the region, and are not actively managed. This regional analysis is then compared with data from 14 additional temperate and boreal forest sites (FLUXNET, www.fluxdata.org) more widely distributed across the Northern Hemisphere. We use the half-hourly eddy-covariance flux measurements, and concurrently recorded meteorological data, to calculate W_{ei} as the ratio of canopy carbon assimilation to ecosystem evapotranspiration, adjusted for atmospheric evaporative demand (see Methods).

The regional analysis shows that W_{ei} has increased at each forest site over the measurement period (Fig. 1, Supplementary Table 2). Of the seven regional focus sites, the change was significant ($P < 0.05$) at three sites, whereas at all others the slope was positive but with lower P values. The mean trend (± 1 s.e.) across all seven sites is 1.07 ± 0.3

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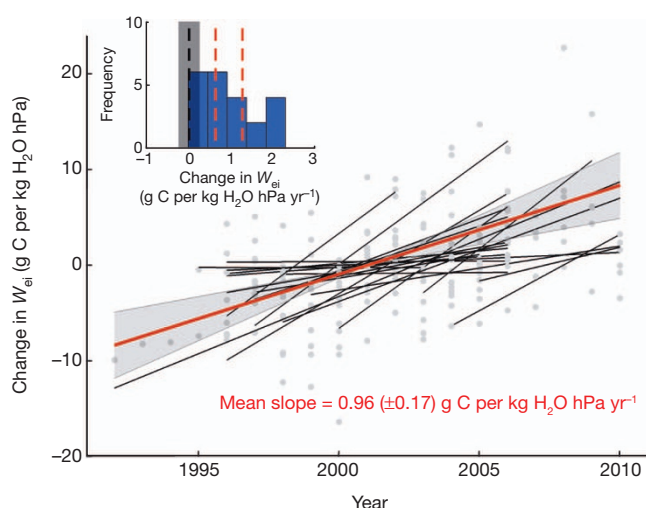
Figure 1 | Long-term change in forest water-use efficiency. The annual change in water use efficiency, ΔW_{ei} (g C per kg H_2O hPa; here, evaporative demand is expressed as vapour-pressure deficit), calculated using daytime fluxes from summer months at all sites. ΔW_{ei} is normalized to mean W_{ei} at each site. The red line represents the mean trend over all sites, extrapolated over the entire measurement period. The grey area highlights trends within one standard deviation about the mean trend. Individual site observations and trends are given as grey dots and black lines respectively. Individual site names, details, statistics and plots are given in the Supplementary Information. The inset shows the distribution of the rate of change in W_{ei} over all sites. Dashed red lines represent bootstrapped 95% confidence intervals for the mean slope. The grey shaded area represents the mean and standard deviation of the slope of increases in W_{ei} simulated by 13 terrestrial biosphere models at four of the US regional sites. See Supplementary Information for more information on the model runs and individual site graphs.

grams of carbon per kilogram of water times a hectopascal per year (g C per kg H_2O hPa yr^{-1}) ($P = 0.011$, Student's t-test), with a joint probability of $P = 0.0016$ (Fisher combined probability). This trend is replicated in the broader FLUXNET data set as well. Eight of these 14 sites show an increase in W_{ei} over the period of record with $P < 0.15$ (Fig. 1), and three of the six remaining sites show increases in W_{ei} with $P < 0.3$ (Supplementary Table 2); for the FLUXNET sites, the joint probability of a significant trend is $P = 1.1 \times 10^{-4}$ (Fisher combined probability). Thus, although the trend is not statistically significant at all individual sites, it is highly significant when multiple sites are considered. For the larger FLUXNET data set, the mean trend is 0.90 ± 0.2 g C per kg H_2O hPa yr^{-1} ($P < 0.001$, t-test), which is not significantly different from the regional analysis sites. Over all sites, deciduous forest sites show a significantly higher ($P = 0.06$, t-test) rate of response (1.4 ± 0.2, $n = 8$) than do evergreen forest sites (0.64 ± 0.3, $n = 10$, mixed forests excluded).

In addition to rising CO_2, a number of other factors, both environmental and biotic, could cause the observed increase in forest water-use efficiency. These include: climate change; nitrogen deposition and accumulation; changes in leaf area, canopy height, surface roughness and the coupling of the canopy to the atmosphere; and long-term instrument drift. We tested each of these competing hypotheses using data from the regional focus sites. To examine whether the increase in W_{ei} can be linked with recent changes in environmental factors affecting plant water use, we stratified the observations for different measurement conditions and tested for trends in climatic variables across all sites (see Supplementary Information sections 6 and 8). This analysis shows that the general trend and magnitude of the increase in W_{ei} is independent of recent changes in environmental factors. The lack of a consistent trend in climatic forcing across all sites (with the exception of vapour pressure deficit, D) further suggests that changes in climatic drivers are not responsible for the consistent increase in W_{ei}.

Similarly, we analysed long-term measurements of leaf area and leaf nitrogen content (where available), together with estimates of surface roughness, and found no significant changes over time (see Supplementary Information sections 9–11). The lack of trends in surface roughness and leaf area, and the lack of a decrease in measured above-canopy wind speeds, suggests that the coupling of the canopy to the atmosphere has remained relatively constant during the measurement period. To minimize instrument biases, strong quality controls are in place at each site[18]. These include *in situ* comparisons with a roving standard instrument, and regular changes of inlet tubes and filters. The variation in magnitude of trends in W_{ei} across sites suggests that local factors (for example, droughts) could result in site-specific trends that are superimposed on the more general response of forests worldwide. Our detailed analysis (see Supplementary Information) suggests that of all the potential drivers of the observed changes in W_{ei}, the only driver that is changing sufficiently and consistently through time at all sites is atmospheric CO_2.

To examine whether the rate of increase in water-use efficiency is consistent with a fertilization effect of elevated atmospheric CO_2, c_a, we combined the flux measurements, observed c_a, and equations (1) to (4), to estimate C_i, the canopy-level equivalent to leaf c_i (see equation (9) in the Methods). This analysis suggests that, if rising CO_2 is the driving factor, then to reproduce the magnitude of the observed trends in W_{ei}, plants would have to partially close their stomata (thereby reducing g_s and hence E) to hold C_i at a relatively constant level (Fig. 2) despite increasing c_a concentrations. By comparison, current theoretical stomatal control models[5,19,20] project a relatively limited enhancement of W_{ei} under elevated c_a. Indeed, we show that 13 state-of-the-art terrestrial biosphere models do not predict long-term trends in W_{ei} (0.02 ± 0.25 g C per kg H_2O hPa yr^{-1}) for forested sites in North America (Fig. 1), in contrast to the observational data presented here. Although the coupling of c_i to c_a is commonly reported to be proportional[14], recent studies report that a near-constant level of c_i under elevated CO_2 is indeed plausible[16].
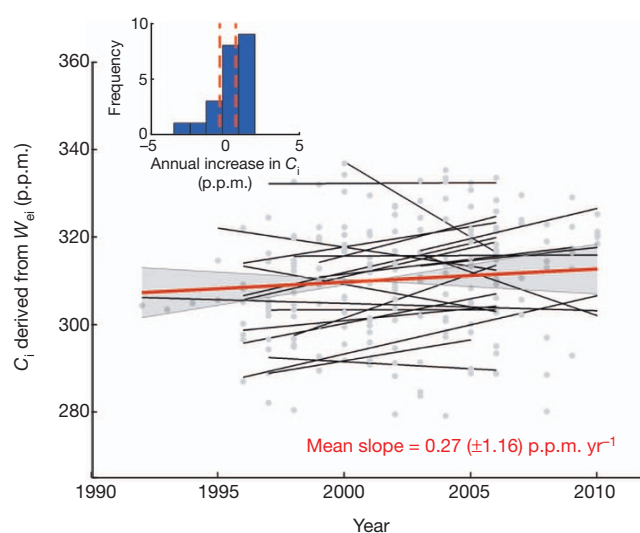
Figure 2 | Canopy-scale leaf intercellular CO_2 concentrations. The derived canopy-scale intercellular CO_2 concentration C_i at all sites. The red line represents the mean trend over all sites, extrapolated over the entire measurement period. The grey area highlights trends within one standard deviation about the mean trend. Individual site observations and trends are given as grey dots and black lines respectively. Individual site names, details, and plots are given in the Supplementary Information. The inset shows the distribution of the rate of change in C_i over all sites. Dashed red lines represent bootstrapped 95% confidence intervals for the mean slope. The distribution of slopes around zero indicates that the observed changes in W_{ei} are consistent with a constant C_i. Site details are given in Supplementary Table 1.

The observed trends in W_{ei} have important consequences for water and carbon cycling in forest ecosystems. The direct tradeoff between water loss and carbon uptake through the stomata—equations (1) and (2)—means that, as water-use efficiency increases, either evapotranspiration (E_e) decreases or gross photosynthetic carbon uptake increases, or both occur simultaneously. Mid-summer forest E_e declined at all but one of the regional US sites. Decreases in E_e are consistent with recent declines in evapotranspiration, and increases in streamflow, at watersheds in the northeastern US[21]. In the global FLUXNET data set, ten of the 14 sites also show a trend of reduced E_e (Supplementary Table 2). Three of the remaining 4 FLUXNET sites that did not demonstrate a decrease in E_e had increased rates of summer photosynthesis, consistent with the overall increase in W_{ei} (Supplementary Table 2) and the water–carbon tradeoff. The mean annual trend in E_e across all sites was $-3.8 \pm 2\,\mathrm{g\,H_2O\,m^{-2}\,h^{-1}\,yr^{-1}}$ ($P = 0.07$, t-test).

Additionally, mid-summer daytime forest net carbon uptake increased during the measurement period for six of the seven regional US sites ($13.1 \pm 5.6\,\mathrm{mg\,C\,m^{-2}\,h^{-1}\,yr^{-1}}$, $P = 0.03$, t-test). At those regional sites with sufficient data to construct annual totals, we observed strong trends in total annual net carbon uptake (Fig. 3). In the FLUXNET analysis, only six of the 14 sites showed trends of increased net carbon uptake over the measurement period, with probabilities ranging between $P = 0.01$ and 0.59 (Supplementary Table 2). The mean trend across all 21 sites was $6.8 \pm 3.6\,\mathrm{mg\,C\,m^{-2}\,h^{-1}\,yr^{-1}}$ ($P = 0.06$, t-test).

To further examine trends in carbon uptake, we carried out a model-data fusion analysis using a parsimonious process-based model (see Supplementary Information section 7). This analysis indicates that only a small fraction of trends in carbon uptake can be explained by changes in climate forcings (temperature, precipitation, humidity, solar radiation) at any site. Previous work attributes a proportion of the net annual increase to a lengthening of the growing season[22]. Our model-data fusion approach, however, shows a large increase in net uptake during the summer months, independent of season length.

The observed increase in water-use efficiency documented here has a range of important implications for ecosystem function, services and feedbacks to the climate system. These include enhanced timber yields[10], improved water availability (which could partially offset the effects of future droughts), and changes in competitive interactions[23]. E_e directly

affects the surface energy balance. Reduced E_e due to higher water-use efficiency[24] could therefore lead to higher air temperatures[25], decreased humidity, and decreased recycling of continental precipitation[26]. This would give rise to increased continental freshwater runoff[26], along with drought in parts of the world that rely on water transpired in other regions[27]. Increases in W_{ei} may account for reports of global increases in photosynthesis[28], forest growth rates[6–8], and carbon uptake[9]. Our analysis suggests that rising atmospheric CO_2 is having a direct and unexpectedly strong influence on ecosystem processes and biosphere–atmosphere interactions in temperate and boreal forests. Understanding how increasing CO_2 induces shifts in terrestrial carbon uptake and water loss and long-term changes in water-use efficiency is of critical importance for improving our ability to project the future evolution of the Earth system.
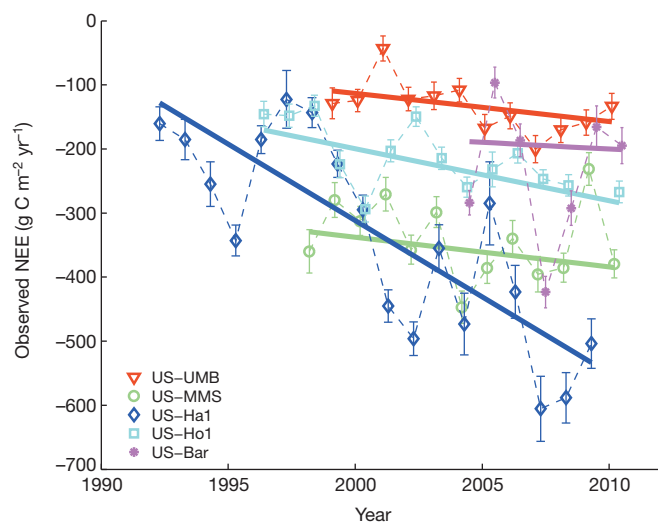
METHODS SUMMARY

Our analysis is based on half-hourly data from 21 flux towers distributed across northern temperate and boreal forest ecosystems. Measurements used include canopy-scale water vapour flux, CO_2 flux, meteorological variables, and estimates of gross primary photosynthesis derived from the CO_2 flux measurements using the eddy covariance technique[3]. We used two distinct data sets, representing both a regional and global focus. The first data set comprised seven unmanaged forested sites in the midwestern and northeastern United States (Supplementary Table 1). The second data set comprised 14 additional forest sites, widely distributed throughout the Northern Hemisphere and subject to various management regimes. The data records ranged in length from 7 to 18 years. We estimated canopy water-use efficiency (W_{ei}) as the ratio of the hourly sums of summer-month daytime gross ecosystem photosynthesis to ecosystem transpiration, adjusted for atmospheric evaporative demand[2]. Trends were estimated using the Mann-Kendall Tau non-parametric trend test with Sen's method, and significance levels on the basis of Mann–Kendall tests.

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Figure 3 | Long-term increase in net ecosystem carbon uptake. The annual net ecosystem carbon uptake (NEE) at five natural forest sites in the northeastern USA. Solid lines represent sen-slope estimates (Methods). Error bars represent the 95% confidence interval, derived by adding uncertainty due to random measurement error and gap-filling uncertainty, using 1,000 bootstrap samples. For two sites included in the regional database there were too many gaps to determine reliable annual sums. Site details are given in Supplementary Table 1.

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Supplementary Information is available in the online version of the paper.

METHODS

We used high-frequency (30 min) measurements of water vapour flux, CO_2 flux, meteorological variables and estimates of gross primary photosynthesis derived from the CO_2 flux measurements. Flux measurements were made at the ecosystem level based on the eddy covariance technique, a method that allows the direct measurement of fluxes of CO_2 and water vapour between Earth's surface and the atmosphere[3]. Two distinct data sets were used, representing both a regional and global focus. The first data set comprises seven unmanaged forested sites in the midwestern and northeastern United States (Supplementary Table 1), suitable for characterizing large-scale regional tendencies. Flux measurements at these sites are all ongoing. The data records we analyse here range in length from seven to 18 years. The second data set (La Thuile FLUXNET 'fair use' database; www.fluxdata. org) consists of a freely available global collection of eddy covariance CO_2 and water vapour flux observations for a variety of ecosystem types. From this database we selected forest sites with closed canopies that had seven years or more of measurements (see criteria below). A description of the seven regional focus sites and the 14 La Thuile sites used in this study can be found in Supplementary Table 1. At all sites, CO_2 and H_2O fluxes were measured using a closed path eddy-covariance system with an LI-6262 gas analyser (changed to LI-7000 at US-MMS in 2004, US-Ha2 in 2004, FI-Sod in 2003, and US-UMB at 2006). Regular tube and filter replacement were performed to ensure high-quality water flux data, along with detailed Ameriflux quality control campaigns[18].

Site selection from the FLUXNET La Thuile data set. We initially considered all freely available data from the 'fair use' La Thuile FLUXNET data set. Of the 153 sites available, we selected the 31 sites that had seven or more years of flux measurements. We focused our analysis on sites that represented temperate and boreal forests. This meant the exclusion of two wetlands, one cropland, one grassland and seven Mediterranean forests. Mediterranean forests are dominated by interannual variability in soil water availability, which complicates the derivation of changes in water-use efficiency driven by atmospheric CO_2. Because water-use efficiency is affected by changes in forest canopy height, we also excluded data from two temperate forests that were recently planted (<25 years old). One eligible forested site (DE-Hai) was excluded owing to errors in water vapour flux estimates that scaled with humidity (La Thuile database curators, personal communication,). This left a total of 14 temperate and boreal forests in the 'fair use' La Thuile data set that met our selection criteria (excluding those that are already in the regional US data set). Note that, in contrast to the seven regional US sites, many of these forests are subject to some level of management.

Flux data processing. Gross ecosystem photosynthesis (GEP) represents the carboxylation rate minus photorespiration in this study. At night, NEE consists of all respiratory processes except photorespiration. Accounting for the temperature sensitivity of this respiration component results in the equivalent respiration during the day which is further subtracted from daytime NEE to derive GEP[29]. There are a variety of approaches to derive GEP[30]. Previous comparisons have shown good agreement between different approaches but recommend the consistent use of a particular approach across sites[30]. Common data processing was performed for all sites. Carbon fluxes were corrected for the storage component and spikes[31]. Data with low turbulent mixing were filtered out using a threshold for friction velocity[29]. GEP for all sites was estimated using the standard FLUXNET on-line flux-partitioning tool (www.bgc-jena.mpg.de/~MDIwork/eddyproc/).

Derivation of canopy-integrated water use efficiency and intercellular CO_2 concentrations. For whole plants or ecosystems, water-use efficiency (W_e) can be calculated in a similar fashion as for leaves, as:

$$W_e = \frac{GEP}{E_e(1 - \phi_W)} \tag{5}$$

where E_e is ecosystem evapotranspiration, and ϕ_w represents the fraction of non-transpiratory water loss.

Transpiration, and thus W_e, are a function of evaporative demand D. 'Inherent' water-use efficiency (W_{ei}) is therefore used when comparing water-use efficiency between species or meteorological conditions[2,32]. At the ecosystem level, W_{ei} can be approximated using eddy-covariance flux measurements[2] (given certain assumptions outlined below), as the ratio between GEP and canopy conductance G_s:

$$W_{ei} = GEP/G_s \tag{6}$$

To do so, both GEP and G_s must first be derived from the measured carbon and water fluxes. GEP was estimated for each site with commonly used flux partitioning algorithms (see above). G_s can be estimated from latent heat measurements given the following assumptions: (1) vapour pressure difference between the leaf and the atmosphere can be approximated by measured atmospheric evaporative demand (D), assuming equal temperatures of leaves and atmosphere, (2) aerodynamic resistance between the canopy and the reference-height for the flux can be neglected, (3) under dry conditions, with no recent precipitation events, measured water vapour fluxes are equivalent to transpiration, giving $\phi_w = 0$ (that is, evaporation contributes minimally). These assumptions allow the definition of the equality $E_e(1 - \phi_w) = G_sD$.

An ecosystem-level representation of water-use efficiency can then be formulated as[2]:

$$W_{ei} = GEP \times D/E_e \tag{7}$$

and

$$W_{ei} = (c_a - C_i)/1.6 \tag{8}$$

where C_i is the canopy integrated concentration of intercellular CO_2, and 1.6 is a physical constant that accounts for the greater diffusivity of water vapour relative to CO_2. We thus calculated W_{ei} directly from flux measurements of water vapour (latent heat flux), meteorological measurements of D, and CO_2 flux-based estimates of GEP, as the ratio of the sum of the filtered fluxes each year. We used hourly or half-hourly measurements for the summer months of June, July and August at each site. Only measured values were used (that is, no gap filled data). Night-time data were excluded, because leaves are photosynthetically inactive at night. During and after rain events, evaporation from wet leaves can contribute largely to measured water fluxes. To focus on stomatal controlled water fluxes, days with rain events, and the day after a rain event, were excluded from the analysis, as interception storage is largely depleted within two days following rain events[33]. Soil evaporation below closed-forest canopies is considered negligible. The W_{ei} values reported here therefore represented mean values for summer daytime hours. See ref. 2 for further details of the derivation and justification of W_{ei}, and an analysis of its spatial variability.

Given the atmospheric CO_2 concentrations (www.esrl.noaa.gov/gmd/), equation (8) can be inverted to estimate C_i. We used the flux-derived W_{ei}, and atmospheric CO_2, to estimate C_i as:

$$C_i = c_a - 1.6W_{ei} \tag{9}$$

It should be noted that the magnitude of W_{ei} at each site could be biased owing to the assumptions applied, and owing to systematic biases in the derived GEP, because it is not a directly measurable flux. Moreover, the available estimates of c_a are regional values and may slightly deviate from local canopy-scale values, thus contributing to potential site-biases. Such biases, however, are not expected to change over long timescales, given that the flux time series at each site is partitioned to GEP using a common algorithm (www.bgc-jena.mpg.de/~MDIwork/eddyproc/). Any biases in W_{ei} or c_a will, however, translate to biases in the magnitude of the derived C_i. This could lead to between-site differences in the mean C_i that are not directly interpretable in an ecological context.

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