Rainfall drives variation in rates of change in intrinsic water use efficiency of tropical forests

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Rates of change in intrinsic water use efficiency ($W$) of trees relative to those in atmospheric [CO$_2$] ($c_a$) have been mostly assessed via short-term studies (e.g., leaf analysis, flux analysis) and/or step increases in $c_a$ (e.g., FACE studies). Here we use compiled data for abundances of carbon isotopes in tree stems to show that on decadal scales, rates of change ($dW/dc_a$) vary with location and rainfall within the global tropics. For the period 1915–1995, and including corrections for mesophyll conductance and photorespiration, $dW/dc_a$ for drier tropical forests (receiving ~1000 mm rainfall) were at least twice that of the wettest (receiving ~4000 mm). The data also empirically confirm theorized roles of tropical forests in changes in atmospheric $^{13}$C/$^{12}$C ratios (the $^{13}$C Suess Effect). Further formal analysis of geographic variation in decade-to-century scale $dW/dc_a$ will be needed to refine current models that predict increases in carbon uptake by forests without hydrological cost.
Rate(s) at which plant processes adjust, acclimate and adapt to rising atmospheric [CO₂] (cₐ), especially processes that govern exchanges of carbon and water with the atmosphere (and their roles in ‘physiological forcing’ of climates²⁻⁴), have profound global implications for policy, practice and predictive models. This significance has been recognised by major research infrastructure (e.g., in free-air carbon enrichment (FACE) studies), decades-long monitoring programs of atmospheric chemistry (e.g.,⁵) and a vast array of modelling studies (e.g. ref. ⁶).

For more than 30 years, theory has suggested increasing cₐ should increase the intrinsic water-use efficiency (W) of plants.¹ There is also an extraordinary volume of empirical research on W (and its components-photosynthetic carbon fixation, A, and stomatal conductance, gₛ) across ecosystems. For temperate and boreal forests, the theory of rising W with cₐ is thus backed by a large body of work (e.g., refs. ⁸⁻¹３), and increases in W of trees are amongst the most common of global responses to rising cₐ, albeit with exceptions. Evidence of increases in W comes from multiple sources including large-scale flux networks⁶⁻⁹, tree ring (or ring proxy) isotope series¹⁰, catchment-scale studies¹¹, model-data fusions¹¹⁻¹³ and hundreds of leaf-scale analyses (e.g.,¹⁴), some based on historic herbarium samples¹⁵. However, and in contrast to the general case that W should rise with cₐ, the long-term rate at which W has been changing has not been rigorously examined across ecosystems or regions or climates.

Many individual studies note that W has seemingly increased more quickly since the 1960s, in concert with the faster rate of increase in cₐ, but formal examinations are largely restricted to leaf-level and relatively short-term studies,⁴⁶¹⁶ (see also ref. ¹¹ for a 28-year study).¹³ C/¹² C ratios of cellulose derived from annual tree rings (or from otherwise age-identified wood) provide a time-integrated measure of W that can be extended to hundreds of years in the case of long-lived trees, and used as an important complement and contrast to shorter-term (often leaf-level) data¹⁷. Such data have been widely used to test models of feedbacks amongst the biosphere, atmosphere and climate. Some of the more significant constraints to its interpretation, such as potential confounding (ontogenic) effects of tree age and size, have recently been characterised¹⁸.

We asked the broad question: what are the rates of change in W of tropical forests? We followed recent suggestions¹⁹ in focusing on isotope series (time series of abundances of stable isotopes of C, as captured in stemwood) as a means of improving our ability to predict responses of forests to global change. Our formal hypotheses were that in the long term, W increases with cₐ, and dW/dt or dW/dcₐ will depend on climate. We used tropical forests to test these hypotheses, since previous theoretical predictions²⁰⁻²¹, and medium-term (<30 years) catchment studies¹¹, have explicitly supported our first hypothesis, albeit over shorter time scales. The significance of our hypotheses was recently demonstrated in a modelling study,²² which suggested that local changes in the rate at which W adjusts to cₐ (physiological forcing) are responsible for the majority of precipitation change above tropical forests. Isotope series data revealed that rainfall is a significant determinant of long-term (80 year) dW/dcₐ, as is nitrogen-fixing capability (legume vs. non-legume).

Analysis of long-term data. We subjected all available long-term isotope series (Data Set 1) to more detailed analysis. Positive relationships of W with cₐ were just as clear when data were aggregated by site (see Table 1; Supplementary Fig. 2). All long-term relationships between cₐ and W were linear and highly significant (Table 1; P < 0.0001), indicating relative invariance in the ratio of intercellular (cᵢ) to cₐ (as W = cᵢ(1 − cᵢ/cₐ)/1.6; see Eq. (3) in the Methods section). Across the tropics, nil canopy increases has increased at different rates in response to increasing cₐ, with fourfold differences amongst sites in dW/dcₐ or dW/dt (Fig. 1a, b). Perhaps surprisingly, mean annual precipitation (MAP) has alone accounted for half of the site-to-site variation in dW/dcₐ (Fig. 1a). When expressed on an annual (time) basis, dW/dt declined by 0.05 μmol mol⁻¹ year⁻¹ for each 1000-mm increase in rainfall (Fig. 2a). In other words, over the course of the last century the W of trees at the driest included site increased by at least 15 μmol mol⁻¹ more than of trees at the wettest. Both dW/dcₐ and dW/dt were even more strongly related to latitude (Fig. 1b, 2b), and were greatest for systems distinguished by a distinct dry season (see also ref. 3⁹). The ratio of MAP to potential evapotranspiration (PET) was also significantly related to dW/dcₐ (see Supplementary Fig. 3a), again explaining ~50% of the variation. Mean annual temperature was not related to dW/dcₐ (Supplementary Fig. 3b).

When we followed Keeling et al. in adopting a more comprehensive approach to calculating W, and included potential effects of mesophyll conductance and photosynthesis on isotope discrimination, there was little change in relationships of dW/dcₐ to MAP, MAP/PET and latitude (Fig. 3a–c). Similarly, we modelled impacts of potential changes in the ratio A/cₐ (where A is net photosynthesis) with increasing cₐ on the relationship of dW/dcₐ to MAP and latitude, in order to test if observed relationships with rainfall might be due to other influences over the past 100 or so years. As one limit, we assumed that A/cₐ remains constant (i.e., A increases in proportion to cₐ). As the other, we assumed that A remains constant regardless of any rise in cₐ. If MAP had no effect on the sensitivity of A to cₐ, then patterns shown in Figs. 1 and 2 are little changed (Fig. 3a–c). If A changed in proportion to cₐ at the lowest rainfall, but became increasingly insensitive to cₐ as rainfall increased (and was constant at the highest rainfall), then relationships were much weakened (Fig. 3i–k). Finally, if the sensitivity of A to cₐ increased with rainfall, then relationships strengthened (Fig. 3e–g). While arguments can be made for all scenarios, the extreme case shown in Fig. 3i–k is highly unlikely, and recent evidence from tropical forests¹¹ suggests the scenario in Fig. 3a–c is most likely.

Growth of individual species responded variably to rising cₐ (Supplementary Table 1), although the magnitude of responses depended on both the period of measurement and site/climate (see also Supplementary Fig. 1b). Most species showed no distinct growth response to rising cₐ, in contrast to positive responses of
Table 1 Significant bivariate relationships between inherent water-use efficiency (W umol mol⁻¹) and atmospheric [CO₂] (cₐ ppm) for canopy-dominant trees in tropical biomes (minimum period = 1915-1995)

| Country, rainfall, legume status | No. of species | No. of trees sampled | Data source | Equation | R² | P-value |
|---------------------------------|----------------|----------------------|-------------|----------|----|---------|
| Ethiopia, 1170 mm, non-legume    | 1              | 5                    | Wils et al.²⁴ | W = -18.4 + 0.38cₐ | 0.91 | 0.000 |
| Thailand, 1500 mm, non-legume   | 2              | 27                   | Nock et al.²⁷ | W = -78.9 + 0.42cₐ | 0.99 | 0.000 |
| Thailand, 1470 mm, legume       | 1              | 82                   | van der Sleen et al.²³ | W = 1.8 + 0.28cₐ | 0.51 | 0.000 |
|                                 |                |                      |             | W = -640 + 92ln(cₐ) | 0.50 | 0.000 |
|                                 |                |                      |             | W = 17 + 0.19cₐ + 0.0001cₐ² | 0.51 | 0.000 |
|                                 |                |                      |             | W = 0.34cₐ⁻⁰.⁹⁷ | 0.50 | 0.000 |
| Thailand, 1470 mm, non-legume   | 3              | 179                  | van der Sleen et al.²³ | W = 3.7 + 0.23cₐ | 0.32 | 0.000 |
|                                 |                |                      |             | W = -390 + 81ln(cₐ) | 0.33 | 0.000 |
|                                 |                |                      |             | W = -154 + 1.2cₐ - 0.001cₐ² | 0.33 | 0.000 |
|                                 |                |                      |             | W = 0.28cₐ⁻⁰.⁹⁶ | 0.31 | 0.000 |
| Peru, 2400 mm, non-legume       | 1              | 1                   | Ballantyne et al.²⁵ | W = -34 + 0.32cₐ | 0.79 | 0.000 |
| Indonesia, 2200 mm, non-legume  | 1              | 16                  | Schollaen et al.²⁸ | W = 8.9 + 0.20cₐ | 0.72 | 0.000 |
| Borneo, 2870 mm, non-legume     | 2              | 2                   | Loader et al.²⁶ | W = 2.2 + 0.18cₐ | 0.77 | 0.000 |
| Borneo, 3000 mm, non-legume     | 2              | 2                   | Loader et al.²⁶ | W = -4.4 + 0.18cₐ | 0.72 | 0.000 |
| Brazil, 3000 mm, non-legume     | 2              | 53                  | Hietz et al.²⁹ | W = -22.6 + 0.3cₐ | 0.98 | 0.000 |
| Cameroon, 4000 mm, legume       | 3              | 268                 | van der Sleen et al.²³ | W = 13.8 + 0.20cₐ | 0.24 | 0.000 |
|                                 |                |                      |             | W = -302 + 66ln(cₐ) | 0.25 | 0.000 |
|                                 |                |                      |             | W = -354 + 4.3cₐ - 0.003cₐ² | 0.29 | 0.000 |
|                                 |                |                      |             | W = 0.57cₐ⁻⁰.⁸⁵ | 0.24 | 0.000 |
|                                 |                |                      |             | W = 36.3 + 0.11cₐ² | 0.19 | 0.000 |
|                                 |                |                      |             | W = -130 + 35ln(cₐ) | 0.19 | 0.000 |
|                                 |                |                      |             | W = -35 + 0.5cₐ - 0.001cₐ² | 0.19 | 0.000 |
|                                 |                |                      |             | W = 4.3cₐ⁻⁰.⁴⁸ | 0.16 | 0.000 |
| Cameroon, 4000 mm, non-legume   | 1              | 94                  | van der Sleen et al.²³ | W = 13.8 + 0.20cₐ | 0.24 | 0.000 |

Relationships are shown for each site and study. The data were pooled (i.e., across species) for each site according to their nitrogen-fixing status (non-legume or legume).

Fig. 1 Rainfall and latitude influences on change in W per unit cₐ. a The relationship of dW/dcₐ (change in intrinsic water-use efficiency (W) per unit atmospheric [CO₂] (cₐ); as derived from tree rings) to mean annual precipitation. b Relationship of dW/dcₐ to absolute latitude. The data are site averages of long-term isotope series (each spanning at least the period 1915-1995) for tropical biomes. Points marked in red in both (a) and (b) are the data for legumes. For both (a) and (b), data sources are: (a) Wils et al.²⁴, (b) Nock et al.²⁷, (c) van der Sleen et al.²³, (d) Ballantyne et al.²⁵, (e) Hietz et al.²⁹, (f) Schollaen et al.²⁸, (g) Loader et al.²⁶

W (Supplementary Table 1). We also examined other possible influences on W. Clear patterns of decreasing dW/dcₐ (Fig. 1) or dW/dt (Fig. 2) with increasing rainfall, are the opposite of what might be expected if tree growth, rather than cₐ, were driving changes in W (see ref. 18).

The novel approach and related sampling adopted by van der Sleen et al.²³ accounts for potential bias due to effects of ontogenic development on W. Nonetheless, the van der Sleen et al.²³ data integrate well with all other available data for the tropics (e.g., Figs. 1–3), including data from single-tree studies.

Nutrient availability is another, frequently suggested, non-climatic constraint to tree responses to rising cₐ. The van der Sleen et al. data²³ contained both legumes and non-legumes, which we have partitioned accordingly. Legumes (Supplementary Fig. 4) maintained significantly greater W than non-legumes, over the full period for which records were obtained (a difference of
7–8 μmol mol⁻¹), in agreement with a recent synthesis of leaf-level data. In all analyses shown in Figs. 1–3, and Supplementary Figs. 2 and 3, data for legumes are identified separately.

Discussion
Collectively, the data compiled here represent tens of thousands of individual measurements of abundance of stable isotopes of carbon in wood samples from a broad range of climates and tree species. Represented ecosystems include monsoonal conifer forests in the Ethiopian highlands (Juniperus), Congo basin rainforests in Cameroon (Daniellia, Terminalia and Brachystegia), lowland dipterocarp rainforests in Indonesia and in Borneo (Tectona, Shorea and Eusideroxylon) and savannas and forests of Thailand (Melia, Toona and Chukrasia) and Brazil (Swietenia, Cedrela and Sweetia). The data show that long-term rates of change in W for trees from tropical biomes (Supplementary Table 1; range 0.10–0.43 μmol mol⁻¹ year⁻¹) are broadly comparable with trees from boreal (0.22 μmol mol⁻¹ year⁻¹), semiarid (0.17 μmol mol⁻¹ year⁻¹) and temperate (0.28 μmol mol⁻¹ year⁻¹) forests in North America,9 and Europe.12

Keeling et al.5 recently calculated that to account for the changing relative abundances of ¹³C vs. ¹²C in atmospheric CO₂ (the ¹³C-Suess effect), there must have been a ~20% increase in W across the globe over the 40 years period 1975–2015, and that a significant proportion of the increase must have been due to tropical forests. The data compiled here provide an empirical confirmation of that calculation for tropical forests (Supplementary Table 1). As far as we can ascertain, our analysis is also the first evidence of rainfall-driven and systematic variation in long-term rates of change in water-use efficiency for any global forest biome. Current models of global patterns in W do not account for this variation (e.g., ref. 6).

Shorter term, more recent studies are an interesting contrast to the long-term patterns that are the focus here. For example, trees used by Nock et al.27 spanned generally shorter time periods (88 years) than other long-term isotope series (see Figs. 1–3), and their data are somewhat of an outlier. Greater DW/dC₄ (Fig. 1a, b), and greater DW/dt recorded by Nock et al.27, is at least partially due to faster rates-of-increase in C₄ in recent decades. Other shorter-term (mostly post 1960) isotope series for the tropics (see Supplementary Table 1, Supplementary Fig. 1 and refs. 30–38), as well as leaf-level studies strongly support long-term patterns (including the influence of rainfall; see ref. 41 for a summary of effects of rainfall on W within individual studies of both ring-forming and ringless trees).

 Obviously, rainfall alone does not define water availability to trees. In the tropics especially, seasonal distributions of rainfall and evaporative demand ensure that soil water storage plays a major role in year-round water availability, which in turn is reflected in seasonal variation in photosynthetic productivity of tropical forests. Broadly speaking, tropical regions with pronounced dry seasons (typically savanna systems) can also be distinguished by seasonal changes in leaf area and transpiration from regions that have more uniform rainfall. Nonetheless, rainfall is a strong predictor of DW/dC₄ across long-term studies (e.g., Fig. 1), as well as within shorter-term and individual studies of tropical forests.

Donohue et al.42 used modelling and FACE data to argue that rates of carbon fixation have broadly increased with C₄. They also showed that disturbance plays a significant role in the reliability of modelled predictions of vegetation responses to C₄. Our analysis supports a conclusion that rates of carbon fixation have continued to rise with C₄ in tropical forests, irrespective of water availability. Disturbances (e.g., fires, floods, hurricanes) are frequently associated with major changes in nutrient and water availability. Evidence (Supplementary Fig. 4) of significant influence of nitrogen fixation on W (but not on DW/dC₄), as well as the enhanced abundance of legumes after disturbance, points to the need for a stronger focus on regenerating forest ecosystems as a means of disentangling more proximal (e.g., nutrient availability) and distal (e.g., disturbance) influences on DW/dC₄.

As reviewed a decade ago, the significance of tropical forests to global carbon and hydrological cycles can scarcely be overstated. That significance has prompted many calls for increased research, for example into the notoriously unknown acclimation responses of plant physiology to rising C₄.21,44 Large year-to-year variation in climatic conditions, phenology and disturbance can easily render tenuous any conclusions based on shorter-term experimentation and observation, as well as models built on such foundations. Long-term rates of change in W shown here, based on integration of climatic and atmospheric information in tree stems, remain one of the best available means of validating and

**Fig. 2** Rainfall and latitude influences on change in W per unit time. The relationship of DW/dt (change in intrinsic water-use efficiency (W) per year; as derived from tree rings) and mean annual precipitation (a), and absolute latitude (b). The data are site averages of long-term isotope series (each spanning at least the period 1915–1995) for tropical biomes. Points marked in red in both (a) and (b) are legumes. For both (a) and (b), data sources are: (a) Wils et al.24, (b) Nock et al.27, (c) van der Sleen et al.23, (d) Ballantyne et al.25, (e) Hietz et al.29, (f) Schollaen et al.28, (g) Loader et al.26.
Fig. 3 Modelled effects of physiology on rates of change in W. Effects of methods for computing intrinsic water-use efficiency (W), and modelled sensitivity to mean annual precipitation (MAP) of the A/c\textsubscript{a} response to c\textsubscript{a} (where A is net photosynthesis and c\textsubscript{a} is atmospheric [CO\textsubscript{2}]) for relationships of dW/dc\textsubscript{a} (change in W per unit c\textsubscript{a}) to: MAP, the ratio of MAP to potential evapotranspiration, absolute latitude and mean annual temperature (MAT). a–d W includes terms to account for mesophyll conductance and photorespiration. e–h as for a–d but A/c\textsubscript{a} response to c\textsubscript{a} increases with MAP. (i–l) as for a–d but A/c\textsubscript{a} response to c\textsubscript{a} decreases as MAP increases. The data are site averages from sources as described in Figs. 1 and 2. See the Methods section for further detail.
improving models for the tropics. Recorded \(dW/\Delta c\) (and \(dW/dt\)) will also help guide efforts to predict future changes in \(W\), at least for the tropical biome, over coming decades. We endorse the call\(^{18,41}\) for greatly increased availability of isotope series data (as collated here) for tropical forests owing to its scientific significance. However, we immediately recognise that developing such an increased availability of data (and being able to reliably apply statistical approaches such as meta-analysis) will likely take many years, if not decades.

A key unknown in the broad field of global climate change is how quickly forests adjust/acclimate/adapt to changing atmospheric and climatic conditions. Evidence here for the tropics suggests that while \(W\) has increased with \(c\), differences in water availability at any given site determined large shifts/variation in the rate of change (\(dW/dc\)). This helps constrain thinking and models directed towards resolving drivers of changing rainfall in the tropics (e.g., ref. \(22\)), and elsewhere. For the tropics, recent evidence\(^{42–47}\) also suggests a slowing of growth and weakening of the tropical forest sink for carbon. At some point, carbon uptake by forests can no longer increase without consequence increases in availability of water and nutrients. Analysis of water limitation 150 years\(^{51}\).

\[\text{eq.1} \]

\[c_i/c_a = (\Delta - a)/(b - a) \]

\[\text{eq.2} \]

\[c_i/c_a = (\Delta - a)/(b - a) A(c_i)/\left(\Delta/c_a + f_1/c_i\right)/(b - a) \]

\[\text{eq.3} \]

\[A/g_c = c_i \cdot (1 - c_i/c_a)/1.6 \]

Data availability All data used in results are available from the first author, as extracted from primary sources or as provided by original authors.

Code availability Code used in calculations of model estimates of rates of change is the property of T.N.B. and is available on request (tnbuckley@ucdavis.edu).

Received: 16 November 2018 Accepted: 30 July 2019 Published online: 14 August 2019
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Acknowledgements

We thank the Australian Research Council and the National Science Foundation (Award #1557906) for financial assistance. This work was supported by the USDA National Institute of Food and Agriculture, Hatch project 1016439. Mana Gharun is thanked for her help in extracting climatic data.

Author contributions

All authors contributed to the conceptualisation of the study, to discussions about the data analysis, to writing of the paper, and to preparation of the presentation materials. T.N.B. conceived and prepared the models. M.A.A. prepared the draft paper. All authors contributed equally to editing drafts of the paper.
Additional information
Supplementary Information accompanies this paper at https://doi.org/10.1038/s41467-019-11679-8.

Competing interests: The authors declare no competing interests.

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Peer review information: Nature Communications thanks Yuting Yang and other anonymous reviewer(s) for their contribution to the peer review of this work.

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