Title
Linking plant functional trait plasticity and the large increase in forest water use efficiency

Permalink
https://escholarship.org/uc/item/7xw1c898

Journal
Journal of Geophysical Research: Biogeosciences, 122(9)

ISSN
2169-8953

Authors
Mastrotheodoros, T
Pappas, C
Molnar, P
et al.

Publication Date
2017-09-01

DOI
10.1002/2017JG003890

Peer reviewed
Linking plant functional trait plasticity and the large increase in forest water use efficiency

Theodorus Mastrotheodoros1, Christoforos Pappas2, Peter Molnar1, Paolo Burlando1, Trevor F. Keenan3, Pierre Gentine4, Christopher M. Gough5, and Simone Fatichi1

1Institute of Environmental Engineering, ETH Zurich, Zurich, Switzerland, 2Département de Géographie and Centre d’études nordiques, Université de Montréal, Montréal, Québec, Canada, 3Climate and Ecosystem Sciences Division, Lawrence Berkeley National Lab, Berkeley, California, USA, 4Earth Institute, Department of Earth and Environmental Engineering, Columbia University, New York, New York, USA, 5Department of Biology, Virginia Commonwealth University, Richmond, Virginia, USA

Abstract Elevated atmospheric CO2 concentrations are expected to enhance photosynthesis and reduce stomatal conductance, thus increasing plant water use efficiency. A recent study based on eddy covariance flux observations from Northern Hemisphere forests showed a large increase in inherent water use efficiency (IWUE). Here we used an updated version of the same data set and robust uncertainty quantification to revisit these contemporary IWUE trends. We tested the hypothesis that the observed IWUE increase could be attributed to interannual trends in plant functional traits, potentially triggered by environmental change. We found that IWUE increased by ~1.3% yr⁻¹, which is less than previously reported but still larger than theoretical expectations. Numerical simulations with the Tethys-Chloris ecosystem model using temporally static plant functional traits cannot explain this increase. Simulations with plant functional trait plasticity, i.e., temporal changes in model parameters such as specific leaf area and maximum Rubisco capacity, match the observed trends in IWUE. Our results show that trends in plant functional traits, equal to 1.0% yr⁻¹, can explain the observed IWUE trends. Thus, at decadal or longer time scales, trait plasticity could potentially influence forest water, carbon, and energy fluxes with profound implications for both the monitoring of temporal changes in plant functional traits and their representation in Earth system models.

1. Introduction

During the last two decades, the atmospheric CO2 concentration ([CO2]) has been increasing at a rate of 2 ppm yr⁻¹, corresponding to ~0.5% yr⁻¹ [Franey et al., 2013]. The effects of increasing [CO2] on plant physiology at the leaf scale are well documented: at elevated [CO2], stomatal conductance tends to be lower than in ambient [CO2] in most plant species, and photosynthesis rates increase for C3 plants in the absence of other limiting factors [Wullschleger et al., 2002b; Long et al., 2004; Ainsworth and Rogers, 2007].

Plants tend to regulate stomatal aperture and photosynthesis so that the ratio between intercellular and atmospheric [CO2] (Ci/Ca) remains relatively constant [Morison, 1985; Drake et al., 1997; Saurer et al., 2004; Ainsworth and Long, 2005; Katul et al., 2010; Peñuelas et al., 2011; Leonardi et al., 2012]. This implies that intrinsic water use efficiency (iWUE, the ratio between carbon assimilation and stomatal conductance; Text S1 in the supporting information, [Beer et al., 2009]) should scale linearly with [CO2], thus increasing at ~0.5% yr⁻¹ in the last 20 years (Text S1). By analogy, ecosystem inherent water use efficiency (IWUE, the ecosystem-scale version of iWUE; see Text S1) should also scale with atmospheric [CO2] if ecosystem Ci/Ca is constant [Medlyn and De Kauwe, 2013] and the canopy is well coupled with the atmosphere [Beer et al., 2009; De Kauwe et al., 2013]. The rate of increase in IWUE with constant Ci/Ca is called hereafter the “expected” rate of increase.

Elevated [CO2] affects plant functioning through various physiological mechanisms that go beyond the leaf scale [Wullschleger et al., 2002a; Ainsworth and Long, 2005; Gedney et al., 2006; Leakey et al., 2009; Cao et al., 2010]. Upscaling leaf-level responses to increased [CO2] at the ecosystem-level remains challenging [Field et al., 1995; Nelson et al., 2004; Leuzinger et al., 2011; Koutavas, 2013; Way et al., 2015; Fatichi et al., 2016a; Knauer et al., 2017], and accounting for interactions between environmental covariates and vegetation dynamics is even more complex [Huang et al., 2007; Leonardi et al., 2012]. Remote sensing observations provide spatial patterns of water use efficiency (WUE) trends; global trends vary on the order of −0.3 to
+0.2% yr\(^{-1}\) over the last 15 years [Tang et al., 2014; Huang et al., 2015; Xue et al., 2015]. Estimates based on the isotope content of tree rings suggest that IWUE increased by 0.1% yr\(^{-1}\) between 1850 and 2000 [Leonardi et al., 2012], 0.1–0.3% yr\(^{-1}\) over the last century [Saurer et al., 2004; Peñuelas et al., 2011; van der Sleen et al., 2014; Frank et al., 2015], and more rapidly (up to 0.7% yr\(^{-1}\)) during the last 40 years [Maseyk et al., 2011; Silva and Anand, 2013]. A recent study combined tree ring, eddy covariance, and atmospheric observations and reported an overall increase of 0.4% yr\(^{-1}\) between 1900 and 2010 [Dekker et al., 2016]. Model analyses also report IWUE increases on the order of 0.2–0.3% yr\(^{-1}\) for the 21st century [Ito and Inatomi, 2012; Huang et al., 2015].

Trends in IWUE can also be estimated using eddy covariance observations of carbon, water, and energy fluxes between the land surface and the atmosphere [Keenan et al., 2013; Zhou et al., 2015]. However, these data sets are restricted to relatively short periods and are subjected to measurement and methodological uncertainties. Gross ecosystem production (GEP) is not a direct observation [Reichstein et al., 2005], and it might be overestimated due to the eddy covariance flux partitioning algorithms [Wohlfahrt and Gu, 2015; Wehr et al., 2016]. Transpiration is also not directly measured but is inferred from latent heat estimates which are uncertain because of the lack of energy budget closure [Leuning et al., 2012] and relatively frequent data gaps. Latent heat includes not only transpiration but also other evaporation fluxes, and partitioning between canopy interception, soil evaporation, and transpiration is also uncertain [Miralles et al., 2015; Van Dijk et al., 2015; Fatichi and Pappas, 2017]. Despite these limitations, eddy covariance observations have provided important insights into IWUE trends. Using eddy covariance observations, Keenan et al. [2013] detected an unexpectedly large increase (2.3% yr\(^{-1}\)) in contemporary IWUE across forest sites in the Northern Hemisphere. This increase is more than five times larger than expected from assumptions of constant \(C_3\)-\(C_4\) from Free-Air Carbon dioxide Enrichment experiments (FACE) and from laboratory experiments [Medlyn and De Kauwe, 2013]. The authors found that this increase is consistent with a strong CO\(_2\) fertilization effect, suggesting that stomata partially close to maintain a near-constant \(C_i\). An open question remains, however, as to what mechanisms explain this larger-than-expected IWUE increase.

Environmental changes, such as for example, the increasing atmospheric [CO\(_2\)], are potential drivers of plasticity in plant functional traits that link plant physiology and the carbon cycle [Franks et al., 2007; Valladares et al., 2007; Nicotra et al., 2010; Galmès et al., 2014; Aubin et al., 2016]. A recent study by Knauer et al. [2017] tested with numerical simulations whether an increase in the stomatal conductance sensitivity to [CO\(_2\)] would be a plausible explanation for the observed IWUE increase. To reproduce the IWUE trends showed by Keenan et al. [2013], the authors imposed a $-2.1\% \text{yr}^{-1}$ trend on the model parameter linking stomatal conductance and net assimilation and found that the simulated trends in evapotranspiration and gross ecosystem productivity are incompatible with both local- and global-scale observed trends in evapotranspiration, discharge, and atmospheric [CO\(_2\)] seasonal amplitude. Thus, they concluded that variables beyond [CO\(_2\)] might have triggered the observed changes in IWUE and that IWUE trends of such magnitude are not a large-scale phenomenon. Other studies have investigated the interactions between WUE and meteorological forcing, such as wind [Schymanski and Or, 2015] or solar radiation [McAusland et al., 2016]. Studies across Europe and the U.S. found that ecosystem IWUE is also sensitive to the vapor pressure deficit (VPD) [Frank et al., 2015; Novick et al., 2015], while low soil moisture availability may offset the positive effect of increasing CO\(_2\) in the IWUE [De Kauwe et al., 2013].

Instead of linking changes in meteorological variables to trends in WUE, some researchers attributed the observed WUE increase to complex interactions between different climate covariates [Leonardi et al., 2012] or to a possible occurrence of synergistic effects of several factors beyond changes in climate variables [Huang et al., 2007]. Possible explanations of the observed increase in WUE also include long-term metabolic shifts [Ehlers et al., 2015] or changes in stomatal density, mesophyll conductance or biochemical and molecular processes, all of which could be driven by plasticity in plant functional traits [Moore et al., 1999; Sun et al., 2014; Franks et al., 2015; de Boer et al., 2016; Flexas et al., 2016; Lawson and McElwain, 2016].

Here we revised the trend estimates of IWUE for the same sites used by Keenan et al. [2013], using an updated data set and extending the period of analysis to the most recent years whenever possible. Subsequently, we tested by means of model simulations the hypothesis that plant trait plasticity—driven by environmental changes and reflected in trends in plant functional traits including, but not limited to, the sensitivity of stomatal conductance to [CO\(_2\)]—could explain the observed increase in IWUE at the ecosystem scale.
2. Materials and Methods

2.1. Data Set

We analyzed eddy covariance data from 20 forest sites in the Northern Hemisphere (Figure S1 and Table S1 in the supporting information) [Granier et al., 2000; Schmid et al., 2000; Goldstein et al., 2000; Berbigier et al., 2004; Aubinet et al., 2002; Hadley and Schedlbauer, 2002; Dolman et al., 2002; Suni et al., 2003; Carrara et al., 2003; Hollinger et al., 2004; Cook et al., 2004; Curtis et al., 2005; Davidson et al., 2006; Grünwald and Bernhofer, 2007; Jenkins et al., 2007; Thum et al., 2007; Urbanski et al., 2007; Dunn et al., 2007; Pilegaard et al., 2011; Gough et al., 2013]. Eddy covariance observations from the freely available gap-filled “Fluxnet 2015” database (http://fluxnet.fluxdata.org/data/fluxnet2015-dataset; release July 2016, Tier 1, more details in Text S2) were used when available and Ameriflux or CarboEurope databases were used for the remaining sites (Table S1).

We excluded all negative values in evapotranspiration, gross ecosystem productivity, and vapor pressure deficit (ET, GEP, and VPD, respectively) before computing IWUE. Gaps in meteorological variables used as model input (e.g., air temperature, relative humidity, wind speed, VPD, and shortwave radiation) were filled linearly or with the mean for that specific hour and day of the year. Data from the European Centre for Medium-Range Weather Forecasts ERA-Interim data set (http://apps.ecmwf.int/datasets/data/interim-full-daily/levtype=sfc/) or information from local rain gauges were used to replace missing values in precipitation time series or for sites where long-term “Fluxnet” precipitation considerably deviates from climatological precipitation. Following the approach of Keenan et al. [2013], we computed the IWUE only for summer months (June–August) and daytime (shortwave radiation > 100 W m$^{-2}$). Rainy days (defined as days with daily precipitation larger than 1 mm) and 1 day after every rainy day were excluded from the analysis to minimize the influence of ground evaporation and evaporation from canopy interception. Although our analysis focuses on summer months, we used only continuous years without any long gaps (roughly longer than a month), because model simulations are conducted continuously and not only during the summer months. The resulting data set includes 20 sites with a median duration of 13 years.

2.2. Inherent Water Use Efficiency

WUE characterizes the ecosystem balance between assimilated carbon and transpired water and is commonly used to describe ecosystem functioning. Linking the water and carbon cycles, WUE provides insights into water resource availability and land surface-atmosphere feedback [e.g., Lemordant et al., 2016; Medlyn et al., 2017]. WUE can be expressed in various ways based on how the water and carbon fluxes are defined and according to the spatial (leaf, plant, or ecosystem) and temporal scales (instantaneous or averaged over a period). Either evapotranspiration or transpiration and net or gross ecosystem production can be used for computing WUE [Ito and Inatomi, 2012; Huang et al., 2015]. Additional variations of these basic WUE definitions include the intrinsic water use efficiency (IWUE) [Beer et al., 2009; Battipaglia et al., 2013; Frank et al., 2015], the underlying water use efficiency [Zhou et al., 2015], and the inherent water use efficiency (IWUE) [Beer et al., 2009; Vickers et al., 2012; Keenan et al., 2013]. Here we used the ecosystem-scale IWUE, because it scales roughly proportionally to $C_a$ under the assumption of a constant $C_i/C_o$ (Text S1):

\[
\text{IWUE} = \frac{\text{GEP}}{\text{ET}} \cdot \frac{\text{VPD}}{\text{ET}}
\]

where IWUE is in mgC g$^{-1}$ H$_2$O hPa, ET is in gH$_2$O m$^{-2}$ h$^{-1}$, GEP is in mgC m$^{-2}$ h$^{-1}$, and VPD is in hPa.

For the calculation of IWUE, we used the average over the summer period of the daytime hourly ET, GEP, and VPD values. Thus, we obtain a single mean IWUE value per year and site, which is much less sensitive to very small or large ET and GEP values at the hourly scale.

2.3. Trend Estimation and Uncertainty

Linear regression and the nonparametric Theil-Sen [Sen, 1968] estimator were applied to quantify the slopes of observed and simulated IWUE, GEP, and ET. The dependent variables are annual IWUE, GEP, or ET, and the independent variable is the corresponding year of the time series. The two methods gave slopes that are highly correlated (Figure S2). Thus, in the following, we only report results for the linear regression slopes, unless otherwise specified. Based on the normality assumption that residuals follow the Gaussian distribution, we applied t-statistics to the estimator of the slope coefficient to obtain the 95% confidence intervals of the
linear slope. Uncertainties in the IWUE slope at individual sites are large (Table S2); yet we expected that a combination of 20 sites would result in a robust estimation of the median and mean slope of the ensemble.

To quantify the uncertainties of the slope computed for the ensemble and verify its statistical robustness, we assumed that for each location the slope could be described by a uniform distribution bounded by the 95% confidence interval of the linear regression slope estimate. While a normal distribution would be a closer approximation of the slope uncertainty at each site, we adopted the most conservative assumption of a uniform distribution in order to indirectly account for other uncertainties such as the lack of surface energy budget closure in the eddy covariance measurements [Foken, 2008; Leuning et al., 2012; Wohlfahrt and Gu, 2015]. For each site, a random value was selected from the corresponding uniform distribution for each of the three variables (i.e., slope of IWUE, GEP, and ET) using a Monte Carlo sampling. In total, 10,000 values were sampled for each location and the corresponding mean and median slopes of the ensemble were computed at each time. With this procedure, we were able to quantify the overall uncertainty of the ensemble mean and median slope. In the following, we mostly refer to median rather than mean values, since the median is a better indicator for small data sets, in being less sensitive to outliers [Kenney and Keeping, 1962].

Time series duration varies across sites and further complicates the analysis. Ideally, a common period should be used for all sites, but given data availability, this would lead to a very small data set. Considering that longer records are more reliable in the slope estimation and given the relatively large variability in time series length between the sites (from 6 to 19 years), we repeated our analysis weighting the slopes by the time series length.

2.4. Numerical Experiments

We used the state-of-the-art mechanistic ecosystem model Tethys-Chloris (T&C), which simulates the main components of the hydrological and carbon cycle [Fatichi et al., 2012]. It resolves the mass and energy budgets at the land surface and describes physiological processes including photosynthesis, phenology, carbon allocation, and tissue turnover. A detailed model description is provided in Text S3, with emphasis on the components of interest in this study [Rutter et al., 1971, 1975; Farquhar et al., 1980; Leuning, 1990, 1995; Sellers, 1997; Brodribb and Holbrook, 2003; Krinner et al., 2005; Bonan et al., 2011]. The model has been extensively validated at various sites worldwide [e.g., Fatichi et al., 2012, 2016b; Fatichi and Ivanov, 2014; Paschalis et al., 2015; Pappas et al., 2016].

For each of the examined sites, T&C simulations were conducted with static, site-specific parameterizations, which were tested to satisfactorily reproduce the energy and carbon fluxes and vegetation phenology through a manual calibration procedure (“base simulations”; Tables S3 and S8). Considering that VPD is rising along with [CO2] [Brzostek et al., 2014; Rigden and Salvucci, 2017] and that this may have profound impact on ecosystem functioning [Novick et al., 2016], we computed the linear trend of temperature and relative humidity based on annual mean values (Table S4). We removed these trends from the hourly time series and repeated the simulations with the same parameterizations in order to assess the effect of trends in VPD on ecosystem response.

Subsequently, we ran the model using time-variable plant functional traits; i.e., we assumed that the parameters are not static and reflect temporal changes in plant functional traits and forest structure. For each time step, ET was calculated as the sum of transpiration and evaporation from the ground and intercepted water. GEP was calculated as gross assimilation, i.e., the sum of net assimilation and leaf maintenance respiration. Subsequently, we followed exactly the same approach we used for the observed data. For each year, we computed an annual mean value over summer, daytime nonrainy days for GEP, ET, and VPD and we calculated the annual mean IWUE before computing the slopes by the time series length.

After an initial screening of nine T&C vegetation parameters (Table S5), the following five most sensitive parameters for estimating IWUE were chosen (Table 1): empirical parameter linking stomatal aperture and net assimilation in the Leuning model of stomatal conductance ($\alpha$, [Leuning, 1995]), top-of-the-canopy maximum Rubisco capacity at 25°C ($V_{\text{max}}$), canopy nitrogen decay coefficient ($K_{\text{nib}}$), specific leaf area ($S_{\text{LA}}$), and maximum leaf-to-root biomass ratio (Ltr). The latter affects model performance only when its value is reached, acting as an upper threshold. The selected parameters represent biochemical ($\alpha$, and $V_{\text{max}}$) and structural ($S_{\text{LA}}$ and Ltr) properties of the vegetation or a combination of the two ($K_{\text{nib}}$). Text S3 provides a list of the equations in which these parameters are involved.
After evaluating single-parameter perturbations, we also conducted the analysis by concurrently perturbing two parameters in each run (10 combinations) in order to account for parameter interactions [e.g., Saltelli and Annoni, 2010; Pappas et al., 2013]. For each parameter, the value adopted in the base simulation (which corresponds to site-specific model calibration over the entire period) was assigned to the center of the time series and a linear trend was imposed according to a given slope expressed as percent change per year (% yr\(^{-1}\)). The sign of the slope was chosen for each parameter so that IWUE was enhanced (see Figure S3). It is worth emphasizing that the selected parameters are representative of the ecosystem scale. Thus, trends in vegetation parameters might be partly driven by changes in forest demography (e.g., species composition, forest structure, or both, as has happened, for example, in the US-Ha1 and US-UMB [Urbanski et al., 2007; Hardiman et al., 2013]) rather than an actual trend in the plant-level functional trait itself.

For two sites (US-UMB and NL-Loo, the latter not shown) we tested several rates of parameter change in the range of 0.5–3% yr\(^{-1}\) and examined the relationship between trends in IWUE and the hypothesized trends in plant functional traits by keeping the model setup and all other parameters identical to the base simulations. We found that this relationship is almost linear for all parameters, which is expected for relatively low parameter perturbations (Figure S3). We chose a 1% yr\(^{-1}\) rate of change in the parameters for all the numerical experiments applied over periods of up to 20 years. This value is small enough to ensure that all parameters remain well within the ranges reported in literature but large enough to modify considerably the ecosystem

<table>
<thead>
<tr>
<th>Table 1. Parameters of the T&amp;C Model that Were Modified in the Numerical Experiments</th>
</tr>
</thead>
<tbody>
<tr>
<td>Symbol</td>
</tr>
<tr>
<td>--------</td>
</tr>
<tr>
<td>(a_1)</td>
</tr>
<tr>
<td>(K_{nit})</td>
</tr>
<tr>
<td>(V_{max})</td>
</tr>
<tr>
<td>(S_{LA})</td>
</tr>
<tr>
<td>LtR</td>
</tr>
</tbody>
</table>

Figure 1. Observed (green) and simulated (purple and red) annual time series of (a) inherent water use efficiency (IWUE), (b) gross ecosystem production (GEP), and (c) evapotranspiration (ET) at the US-UMB site (details in Table S1). The purple represents the base simulations, and the red shows the numerical experiment which best approximates each variable’s slope for this site, i.e., \([+V_{max} - a_1]\) for IWUE, \([-a_1 + K_{nit}]\) for GEP, and \([-a_1]\) for ET. Linear least squares fitting is shown with continuous lines.
response, given the expected influence of plant trait variability in ecosystem carbon and water dynamics [Wang et al., 2012; Pappas et al., 2016].

3. Results

Figure 1 shows example time series of IWUE, GEP, and ET from observations and numerical experiments for the US-UMB site. Observations suggest that IWUE of the 20 sites increased on average by 1.3% yr$^{-1}$ (equivalent to 1% ppm yr$^{-1}$), due to the combination of increasing GEP (0.6% yr$^{-1}$) and decreasing ET (0.3% yr$^{-1}$) (Figure 2 and Tables S2 and S6). Median slopes weighted by the time series length were of smaller magnitude, but they preserved the general pattern; in this case IWUE increased by 1.0% yr$^{-1}$ (Table S7). Despite the large uncertainties of the single-site slopes, the ensemble median slope of IWUE exceeded the expectations (0.5% yr$^{-1}$) with a probability of 95% (Figure 3).

Using static vegetation parameters (base simulations), the modeled IWUE increased by 0.9% yr$^{-1}$, GEP increased by 0.2% yr$^{-1}$, and ET also increased by 0.2% yr$^{-1}$ (Figure 2 and Table S6). Weighted median slopes differ only slightly among sites, with a simulated trend in IWUE of 0.7% yr$^{-1}$ (Table S7). Simulations with detrended temperature and relative humidity show a 0.4% yr$^{-1}$ increase in IWUE (which corresponds closely to the theoretical expectations), while median GEP and ET trends only slightly differ from the base simulations (Figure 3 and Table S2).

The observed IWUE trend is best reproduced by simulations with increased $V_{\text{max}}$ or decreased $a_1$ alone or together with other parameters (Figure 2 and Tables S6 and S7). In order to assess the performance of each numerical experiment regarding both IWUE and its components (GEP and ET), we computed the Euclidean distance between simulated and observed median slopes of IWUE, GEP, and ET. When all three parameters are considered together, a change in $a_1$ describes best the observed trends. Decreasing $a_1$ (alone or together with decreasing $K_{\text{nit}}$ or increasing $S_{\text{LA}}$ or LtR) by 1% yr$^{-1}$ led to an increase in IWUE similar to
the observed trend, mainly improving the simulated trend of ET (Figure 2 and Tables S6 and S7). Overall, differences in reproducing the observed trends among these combinations are rather small, suggesting that they can be considered practically equivalent.

The comparison of observed IWUE slopes between sites reveals different patterns across different vegetation types. Evergreen forests (10 sites) show almost no increase in IWUE ($0.1\%\, yr^{-1}$), while in broadleaf deciduous forests (eight sites) IWUE increased by $3.0\%\, yr^{-1}$ (Figure S4).

4. Discussion

4.1. Observed Trends in IWUE

We found a median increase in IWUE of $1.3\%\, yr^{-1}$ across 20 Northern Hemisphere forest sites in the last two decades. This increase more than doubles the expected increase under the assumption of a constant $C_a/C_i$, but is considerably lower than what Keenan et al. [2013] reported for the same sites ($2.3\%\, yr^{-1}$).

The difference in IWUE trends found in our study compared to Keenan et al. [2013] is mostly due to recent differences in ET trends arising from the inclusion of site years not available at the time of the previous analysis. Recent droughts (e.g., in 2010 and 2012 in Europe and the U.S., respectively) may have contributed to the strong decreasing ET trend found by Keenan et al. [2013] through soil moisture limitations. Indeed, the positive trend in ET seems to be interrupted in recent years [Jung et al., 2010], but it remains unclear if this was an effect of climate variability or rather a sign of a geographical reorganization of ET. Thus, ET trends are uncertain and the inclusion of additional data as well as shifting the analysis to more recent years may change the results (Text S4).

The trends in IWUE were lower when we computed the median increase weighted by the time series length of each site. This is mainly because of reduced ET slopes, while GEP was less dependent on the time series length (Tables S6 and S7). The sensitivity of the slope of ET (and therefore IWUE) on the time series length further verifies that the inclusion of 30% more data in our study potentially improves the robustness of the slope estimation. It further depicts the uncertainties in latent heat observations, as indicated by the lack of energy balance closure [Foken, 2008; Leuning et al., 2012]. It could also be the manifestation of feedback between the surface energy budget and the atmospheric boundary layer, where reduction in latent heat increases atmospheric evaporative demand (higher temperature and VPD) or maintains higher soil moisture, therefore preventing a persistent negative trend in latent heat [Lemordant et al., 2016]. The preprocessing of eddy covariance data in the different Fluxnet products is also not identical (Figure S5); while GEP slopes are similar in the two studies, ET slopes diverge considerably (Figure 3), which can partly explain the discrepancies with previous results.

The confidence in the magnitude of the trend in IWUE for any single site is particularly low (Table S2), testifying that strong conclusions cannot be drawn from a single site or only few sites. However, combining 20 sites increases the robustness of the analysis. We verified the statistical robustness of the median change in IWUE using a Monte Carlo analysis with a very conservative assumption on the uncertainty in the single site slopes.
This analysis showed that the probability that IWUE increases more than the expected (0.5% yr\(^{-1}\)) is larger than 95% (Figure 3). In other words, despite the large site-to-site variability in IWUE slopes, it is very unlikely that the overall trend in IWUE can be explained by theoretical expectations of a constant \(C_r C_p\) at the ecosystem scale.

In the deciduous forests the IWUE increase was larger (Figure S4), in agreement with some previous studies [Keenan et al., 2013; Saurer et al., 2014; Liu et al., 2015]. This may be due to the fact that the stomata of conifers are less responsive to environmental stimuli, such as [CO\(_2\)] [Medlyn et al., 2001; Brodribb and McAdam, 2013; Tor-ngern et al., 2015], or because of increases in LAI that compensate for the decreased stomatal conductance. A comparison between the Duke and the ORNL sites in the U.S. shows the same pattern; IWUE increases more in the deciduous forest mostly because of the negative ET trend [De Kauwe et al., 2013]. However, a tree ring analysis at three FACE sites showed similar IWUE increase in evergreen and deciduous but for different physiological reasons [Battipaglia et al., 2013], while a recent study showed that IWUE of conifers responds to increasing [CO\(_2\)] more than that of broadleaves [Frank et al., 2015].

### 4.2. Plasticity in Plant Functional Traits

Model results show that plasticity in ecosystem-scale physiological and structural traits could explain the observed increase in IWUE. A 1% yr\(^{-1}\) change in one or two key vegetation parameters combined with changes in relative humidity and temperature is sufficient to explain a 2.6 times larger change in IWUE when compared to theoretical expectations and other modeling results [Medlyn and De Kauwe, 2013]. We emphasize that model parameters are representative of the ecosystem scale. This means that a trend in \(S_{LA}, a_1\), or \(V_{\text{max}}\) may not necessarily imply a trend in this parameter for a given species but might be the effect of a change in stand demography, as for example previously documented for the US-Ha1 site [Urbanski et al., 2007] and other ecosystems [Knapp et al., 2012; Hardiman et al., 2013]. While this is unlikely to occur concurrently in all sites, it may partially drive the median trend in IWUE. This has also direct consequences for the interpretation of \(C_r C_p\) and IWUE inferred from tree ring studies, which may not necessarily reflect the trend in IWUE if ecosystem traits are changing because of a shift in forest demographic distribution or composition. Indeed, several of the ecosystems studied here might still be in a growing state and have not yet reached an equilibrium (Table S1). It is also possible that changes in ecosystem functioning arise as a result of very subtle changes in species composition [Knapp et al., 2012].

Many models estimate generally lower WUE increase than the theoretically expected (0.5% yr\(^{-1}\)) [Inatomi, 2012; Keenan et al., 2013; Dekker et al., 2016]. However, the T&C model, even using static parameters, predicts an increase of 0.9% yr\(^{-1}\) in IWUE, which is larger than the expected, while simulating a constant \(C_r C_p\) (Figure S6). This result is independent of changes in the growing season length, but it is related to trends in climate variables, because simulations without trends in temperature and relative humidity show a median increase of 0.4% yr\(^{-1}\) roughly following the expectations. Hydrometeorological variability shapes ecosystem functioning [Pappas et al., 2017] and changes in local meteorological drivers (such as VPD; Figure 3 and Table S2) and the occurrence of favorable weather conditions are indeed capable of modifying long-term ecosystem response as shown by both observations and models [Fatichi and Ivanov, 2014; Paschalis et al., 2015; Forkel et al., 2016; Zscheischler et al., 2016].

We found that the perturbations of \(V_{\text{max}}\) and \(a_1\) (by +1% yr\(^{-1}\) and −1% yr\(^{-1}\), respectively) best simulate the observed IWUE trend. The physiological acclimation of decreasing \(a_1\) (the parameter which connects stomatal aperture and net assimilation rate) could concurrently explain the observed IWUE, GEP, and ET trends, although with lower GEP trends, compared to observations. When pairing \(a_1\) with other parameters, the most effective in terms of performance was the combination with increasing maximum leaf-to-root ratio (LtR) or specific leaf area (\(S_{LA}\)) and with decreasing canopy nitrogen decay coefficient (\(K_{\text{nit}}\)).

The parameter \(a_1\) is the most influential for the IWUE trend, which is not surprising because \(a_1\) represents the sensitivity of stomatal conductance (\(g_s\)) to assimilation rate and environmental drivers ([CO\(_2\)] and VPD) in the Leuning model of stomatal conductance which is implemented in T&C [Leuning, 1995; Leuning et al., 1995; Fatichi and Leuzinger, 2013]. Indeed, \(a_1\) directly affects diffusivity in our experiments; imposing a negative slope in \(a_1\) leads to an increase by +1% yr\(^{-1}\) in \(C_r C_p\), while in all other experiments \(C_r C_p\) was roughly constant (Figure S6). While this result is partially expected, it reinforces the concept that the representation and parameterization of the “closure equation” in the photosynthesis-stomatal model is a cornerstone of model behavior in a changing climate [Damour et al., 2010; Medlyn et al., 2015; Paschalis et al., 2016].
Given the importance of the $a_1$ parameter, assessing the magnitude of its plasticity is pivotal. A recent study, in which the authors followed a similar modeling approach to reproduce the larger IWUE trends originally reported by Keenan et al. [2013], showed that a $-2.1\% \text{yr}^{-1}$ trend in $g_s$ (similar to $a_1$ in our study) would imply (i) unrealistic site-level GEP negative trends, (ii) a decrease in $C_t$ and most importantly (iii) inconsistencies with large-scale trends in evapotranspiration, discharge, and seasonal amplitude of $[\text{CO}_2]$ [Knauer et al., 2017]. However, in all our simulations, both $C_t$ and GEP increase on average (Figure S7 and Tables S6 and S7), in accordance with theoretical expectations and observations [e.g., Ainsworth and Long, 2005], and the most negative ET slopes ($-0.3\% \text{yr}^{-1}$) are considerably smaller in magnitude compared to findings of Knauer et al. [2017] (i.e., $-1\% \text{yr}^{-1}$). Thus, our simulations support the hypothesis that a $1\% \text{yr}^{-1}$ trend in one or more key physiological parameters could be a plausible explanation for the observed trend in IWUE in Northern Hemisphere forests not only at site level but potentially also at larger scales.

The fact that $a_1$ is variable among vegetation types and across temperature and moisture gradients was already explicit in the work of Leuning [1995]. Recent work corroborated that the $g_s$ parameter of an optimal stomatal conductance model [Katul et al., 2010; Medlyn et al., 2011], a parameter closely related to $a_1$, spans a quite large range of values [Lin et al., 2015]. Other studies have also shown that this parameter is not constant [Valentini et al., 1995; Bunce, 2004]. For instance, $g_s$ can be parameterized as a function of soil moisture content [Medlyn et al., 2011]; this parameterization can improve the results of models based on stomatal optimality theory [Manzoni et al., 2011]. Other support comes from studies showing some plasticity in maximum stomatal conductance and leaf epidermal area with changes in $[\text{CO}_2]$, mostly occurring through a decrease in stomatal density, which can be directly translated in a decrease in $a_1$ [de Boer et al., 2011, 2012, 2016; Lammertsma et al., 2011]. While such plasticity is well acknowledged for geological time scales [Franks et al., 2013], it has been also demonstrated for decadal trends [Lammertsma et al., 2011], even though the latter finding is rather uncertain [Reid et al., 2003; Miglietta et al., 2011]. Two studies from the Duke FACE site further support this hypothesis: a study in a loblolly pine plantation [Domec et al., 2009] showed that increased $[\text{CO}_2]$ decreased the sensitivity of stomatal conductance to VPD, while a similar result was also found for Liquidambar styraciflua [Ward et al., 2013]. Overall, while at the ecosystem and decadal scale we cannot bring specific evidence beyond model simulations, we suggest that it is reasonable to hypothesize that $a_1$ is adapting to environmental changes, such as increasing $[\text{CO}_2]$.

Previous research has also shown that $V_{\text{max}}$ is not constant but acclimates to $[\text{CO}_2]$, temperature, or soil moisture availability [Sage, 1994; Kattge and Knorr, 2007; Zhou et al., 2016]. Across 12 FACE experiments, $V_{\text{max}}$ generally decreased in time [Ainsworth and Long, 2005], as happened, for instance, in the Oak Ridge FACE experiment, where photosynthesis was downregulated ($V_{\text{max}}$ was reduced) because of nutrient limitations [Warren et al., 2015]. However, other FACE experiments also showed that trees growing in elevated $[\text{CO}_2]$ have only a marginal decrease in $V_{\text{max}}$ [Ainsworth and Rogers, 2007]. A modeling study showed that the observed changes in the fluxes at Harvard forest can be explained by increases in $V_{\text{max}}$ [Keenan et al., 2012]. Our results suggest that the increase in $V_{\text{max}}$ increases the ratio between net assimilation and stomatal conductance since $V_{\text{max}}$ has a direct effect on carbon assimilation but only an indirect influence on stomatal conductance. Thus, the net outcome is an enhanced IWUE.

Decreasing $K_{\text{nit}}$ (canopy nitrogen decay coefficient) implies that leaf nitrogen content declines less steeply throughout the canopy profile (i.e., more evenly distributed). In other words, for a given top-of-the-canopy $V_{\text{max}}$, the total canopy nitrogen content is increasing. This can be a result of increasing nitrogen deposition or simply of an increased height or structural rearrangement of the examined forest canopies [Guerrieri et al., 2011; Leonardi et al., 2012]. However, any conclusion about changes in $K_{\text{nit}}$ remains quite speculative.

Elevated $[\text{CO}_2]$ influences allocation [Poorter and Nagel, 2000; Palmroth et al., 2006], but it is unclear in which direction, since confounding factors complicate the observed dynamics. Some studies reported both increasing and decreasing leaf-to-root ratio [Rogers et al., 1996], and others detected limited $[\text{CO}_2]$ effect on root-to-shoot ratio [Morison and Gifford, 1984]. Some researchers found that under increasing $[\text{CO}_2]$ usually more carbon is allocated to roots, although it is difficult to quantify the change relative to foliage biomass since many factors affect root production [Matamala and Schlesinger, 2000, and references therein].

Previous studies have shown that $S_{\text{A}}$ decreases rather than increases under elevated $[\text{CO}_2]$ [Morison and Gifford, 1984; Eamus and Jarvis, 1989; Peñuelas and Matamala, 1990; Maillard et al., 2001; Yin, 2002; Ishizaki et al., 2003;
Ainsworth and Long, 2005; De Kauwe et al., 2014; Medlyn et al., 2015]. However, our hypothesis of increasing $S_{L,A}$ is plausible since other environmental changes could be the potential drivers. Overall, the patterns of change in the physiological parameters we perturbed can be considered realistic. Rapid physiological and structural acclimation to environmental change has occurred in several temperate forests recently [Niinemets, 2007; Granier et al., 2008; Gough et al., 2013; Stuart-Haëntjens et al., 2015]. Our results demonstrate that such acclimation—in combination with changes in VPD and temperature—could explain the observed trend in IWUE.

The fact that even trends of 1% yr$^{-1}$ can be so important demands for more observations not only of the current values of the different plant physiological properties but also of their potential change with time or due to environmental change. Trends in plant functional traits at the ecosystem scale within this magnitude are currently difficult to detect because measurements are usually available as snapshots on individual plants. For many vegetation parameters (such as $V_{\text{max}}$, $S_{L,A}$, and $a_{1}$) even considerable changes at the ecosystem scale would be difficult to detect experimentally due to the large heterogeneity within different canopy levels [Niinemets et al., 2015] or at the interspecies [e.g., Kattge et al., 2011] and intraspecies levels [Albert et al., 2011; Siefert et al., 2015]. Intraspecific trait variability is currently not sufficiently documented for any plant trait [Aubin et al., 2016] hampering the assessment of possible trends at the ecosystem level.

Regardless of the choice of the exact vegetation parameter or parameter combinations, we deem as critical the fact that trends in plant functional traits, which are assumed constant in time in most vegetation models, can potentially modify the ecosystem capacity to metabolize water and carbon under changing environmental conditions. The parameterization of vegetation models should be thus revised, considering that plant trait variability in both space and time can lead to more realistic predictions of the ecosystem response to changing environmental conditions [Pavlick et al., 2013; Scheiter et al., 2013; Fyllas et al., 2014; Sakschewski et al., 2015; Pappas et al., 2016]. We advocate that pioneering observation campaigns including forest demography monitoring and many replicates of plant physiological measurements over decadal periods could quantify the velocity of plant trait plasticity and acclimation to environmental change.

### 4.3. Challenges for the Future

Our numerical experiment shows that trends in vegetation parameters, reflecting plant trait plasticity, and/or changes in forest demography and composition, could explain the higher-than-expected IWUE increase. Tracing plant trait plasticity is challenging. Beyond CO$_2$ fertilization [Huang et al., 2007; Battipaglia et al., 2013; Keenan et al., 2013], droughts can alter forest structure and plant functional traits [Koutavas, 2013; Heres et al., 2014; Camarero et al., 2015; Zhou et al., 2016]. Plant acclimation to rising air temperature [Reichstein et al., 2007; Smith and Dukes, 2013] and to changes in VPD [Novick et al., 2016] can also affect ecosystem functioning. The drivers of plant trait plasticity remain unclear, but it seems unlikely that the changes are merely driven by the increase in [CO$_2$].

Variability among species and plant functional types introduces another source of uncertainty [Pappas et al., 2016], which cannot be sufficiently captured by current approaches. We found that evergreen and deciduous tree species exhibited markedly different rates of change in IWUE, while currently T&C can only partially reproduce this difference (Figures S4, S8, and S9). To model such diverging responses, we need a better description of plant physiological behavior over time. This might be achieved through more mechanistic models of stomatal functioning [Damour et al., 2010] together with trait-based approaches [Fyllas et al., 2009; Pavlick et al., 2013; Sakschewski et al., 2015; Pappas et al., 2016] and potentially stochastic parameterizations that account for biotic and abiotic spatiotemporal heterogeneities [Pappas et al., 2015, 2016; Prentice et al., 2015; Fatichi et al., 2016a]. Temperature- or [CO$_2$]-driven acclimation of photosynthesis and respiration [Buckley, 2008; Lombardozzi et al., 2015; Reich et al., 2016; Smith et al., 2016] is another source of uncertainty, which might also be tackled in future analyses since it is not modeled here, but it is expected to reduce rather than increase IWUE. The lack of an explicit representation of mesophyll conductance by most ecosystem models (including T&C) poses another impediment in the simulation of WUE trends [Sun et al., 2014; Flexas et al., 2016] because a response of mesophyll conductance to increased [CO$_2$] and other environmental variables modifies WUE. Finally, interactions between the nutrient cycles and changes in WUE remain challenging [Rodoglou et al., 1992; Peñuelas et al., 2011; Ito and Inatomi, 2012; Liu et al., 2014; Sauer et al., 2014; Huang et al., 2016; Jennings et al., 2016]. Yet many ecosystem models, including the current version of T&C, do not explicitly simulate nutrient dynamics. Using models that...
explicitly describe nutrient cycles and their interaction with plant growth and performance could likely further improve our understanding of changes in WUE.

Short-term plants’ acclimation can be crucial for the survival of forests under climate change [Aubin et al., 2007], but our current knowledge about plasticity and climate change interactions is limited [Valladares et al., 2007]. Evidence of plasticity is still limited to a few species [e.g., Franks et al., 2007; Galmés et al., 2014], but there is increasing interest in the significance of including trait plasticity in ecological studies [Nicotra et al., 2010; Albert et al., 2011]. Our results suggest that even small changes in plant physiological traits could possibly affect forest functioning at the decadal time scale. Clearly, any attempt to better model the ecosystems’ responses to environmental changes requires detailed long-term monitoring of plant functional traits.

Acknowledgments

This work used eddy covariance data acquired and shared by the FLUXNET community (http://fluxnet.fluxdata.org/, last access 30.08.2016), including these networks: AmeriFlux, AfriFlux, AsiaFlux, CarbonAfrica, CarbonEurope, CarboItaly, CarboMont, ChinaFlux, FluxNet-Canada, GreenGrass, ICOS, KoFlux, LBA, NECC, OzFlux-TERN, TCOS-Siberia, and USCCC. The FLUXNET eddy covariance data processing and harmonization were carried out by the ICOS Ecosystem Thematic Center, AmeriFlux Management Project and Fluxdata project of FLUXNET, with the support of CDIC, and the OzFlux, ChinaFlux, and AsiaFlux offices. Funding for AmeriFlux data resources (http://ameriflux.lbl.gov/, last access 16 March 2017) was provided by the U.S. Department of Energy’s Office of Science. The data sources are listed in Table S1. T.M. and S.F. thank the support of the Stavros Niarchos Foundation and the ETH Zurich Foundation (grant ETH-29-09-2). C.P. acknowledges the support of the Stavros Niarchos Foundation and the ETH Zurich Foundation (grant P2EZP2_162293) through a Swiss ETH Zurich Foundation (grant P2EP3_162033) and the Niarchos Foundation and the ETH S.F. thank the support of the Stavros Niarchos Foundation and the ETH S.F. thank the support of the Stavros Niarchos Foundation and the ETH.

References


Erratum
The originally published version of this article included an incorrect Supporting Information file. This error has been corrected and this version may be considered the authoritative version.