

UC Berkeley

UC Berkeley Previously Published Works

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, Theodoros
Pappas, Christoforos
Molnar, Peter
[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

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

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

Correspondence to: T. Mastrotheodoros, mastrotheodoros@ifu.baug.ethz.ch

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 $\sim 1.3\% \text{ yr}^{-1}$, 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 $1.0\% \text{ yr}^{-1}$, 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.

Keywords: water use efficiency, plant functional trait plasticity, vegetation modeling, CO₂ fertilization, climate change

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 $\sim 0.5\% \text{ yr}^{-1}$ [Francey *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] ($C_i:C_a$) 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 $\sim 0.5\% \text{ yr}^{-1}$ 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 $C_i:C_a$ 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 $C_i:C_a$ 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 $+0.2\% \text{ yr}^{-1}$ 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 $0.1\% \text{ yr}^{-1}$ between 1850 and 2000 [Leonardi et al., 2012], 0.1 – $0.3\% \text{ yr}^{-1}$ 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 $0.7\% \text{ yr}^{-1}$) 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 $0.4\% \text{ yr}^{-1}$ between 1900 and 2010 [Dekker et al., 2016]. Model analyses also report iWUE increases on the order of 0.2 – $0.3\% \text{ yr}^{-1}$ 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 ($2.3\% \text{ yr}^{-1}$) in contemporary IWUE across forest sites in the Northern Hemisphere. This increase is more than five times larger than expected from assumptions of constant $C_i:C_a$, 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; Galmés 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 [CO₂—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.*, 2001; 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 $C_i:C_a$ (Text S1):

$$\text{IWUE} = \frac{\text{GEP}}{\text{ET}} \text{VPD} \quad (1)$$

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

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 (a_1 [Leuning, 1995]), top-of-the-canopy maximum Rubisco capacity at 25°C (V_{max}), canopy nitrogen decay coefficient (K_{nit}), specific leaf area (S_{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 (a_1 and V_{max}) and structural (S_{LA} and LtR) properties of the vegetation or a combination of the two (K_{nit}). Text S3 provides a list of the equations in which these parameters are involved.

Table 1. Parameters of the T&C Model that Were Modified in the Numerical Experiments

| Symbol | Description | Units | Typical Range |
|-----------|---|--|---------------|
| a_1 | Empirical parameter connecting stomatal aperture and net assimilation | [-] | 3–11 |
| K_{nit} | Canopy nitrogen decay coefficient | [-] | 0.1–0.5 |
| V_{max} | Top-of-the-canopy maximum Rubisco capacity at 25°C | [$\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$] | 20–120 |
| S_{LA} | Specific leaf area | [$\text{m}^2 \text{ g}^{-1} \text{ C}$] | 0.006–0.050 |
| LtR | Maximum leaf-to-root biomass ratio | [-] | 0.2–1.5 |

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 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⁻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).

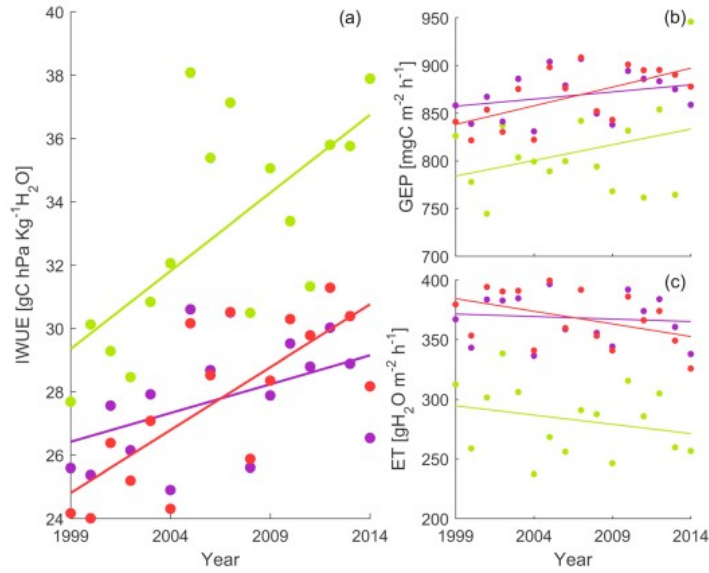


Figure 1. Observed (green) and simulated (purple and red) annual time series of (a) inherent water use efficiency (IWUE), (b) gross ecosystem production (GEP), and (c) evapotranspiration (ET) at the US-UMB site (details in Table S1). The purple represents the base simulations, and the red shows the numerical 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.

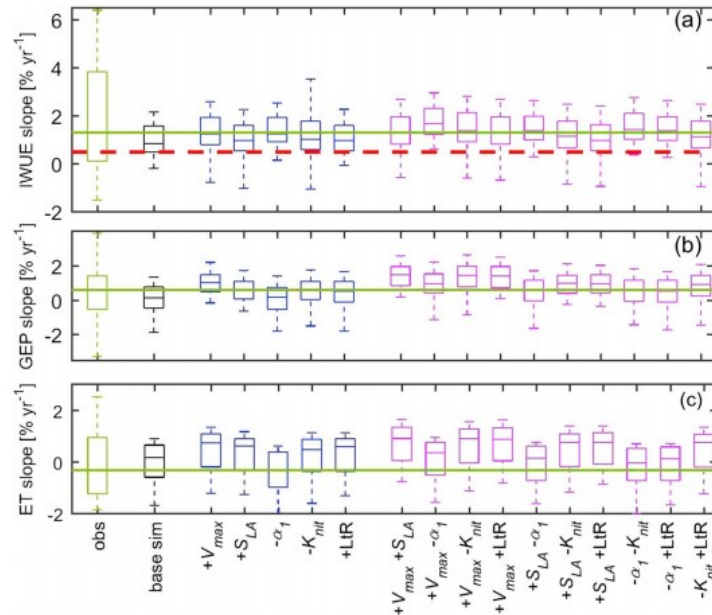


Figure 2. Linear slopes of (a) inherent water use efficiency (IWUE), (b) gross ecosystem production (GEP), and (c) evapotranspiration (ET) for the 20 investigated sites. The box length provides the interquartile range (I_{QR}), the bottom of the box the 25th percentile (first quartile, q_1), the top of the box the 75th percentile (third quartile, q_3), and the horizontal line within the box the median value. The lower whisker corresponds to $q_1 - 1.5I_{QR}$, or to the minimum estimate, and the upper whisker corresponds to $q_3 + 1.5I_{QR}$, or to the maximum estimate. The green represents the observations, the black stands for base simulations, the blue for the experiments in which only one parameter was perturbed, and the magenta for the experiments in which two parameters were perturbed. The red dashed line represents the expected rate of IWUE increase.

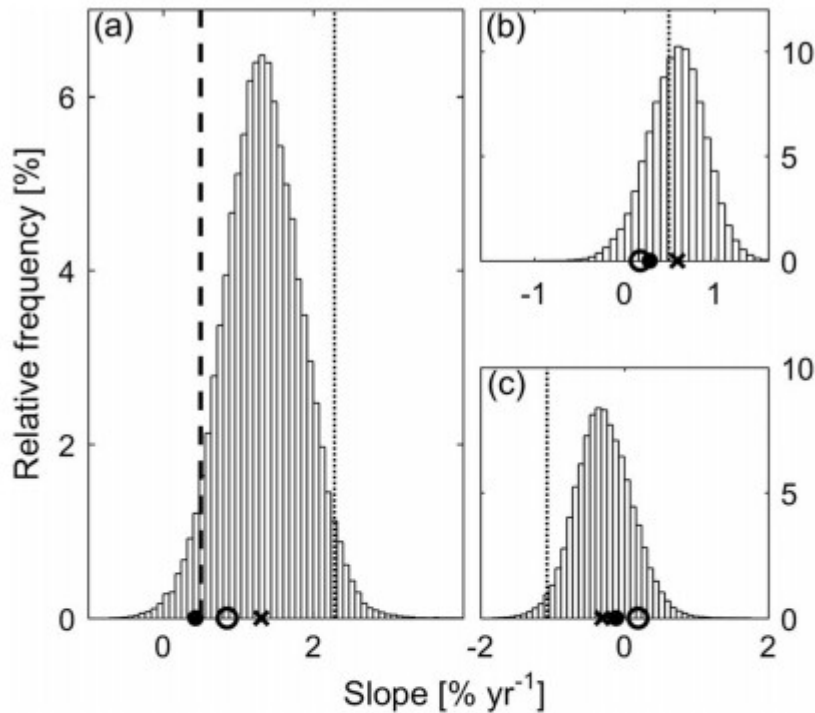


Figure 3. Relative frequency distributions of median slopes in (a) observed inherent water use efficiency (IWUE), (b) gross ecosystem production (GEP), and (c) evapotranspiration (ET). For each site, a slope was selected randomly from the uniform distribution that is bounded by the 95% confidence interval of the estimated linear slope. The histograms show the results of 10,000 Monte Carlo runs. The dotted lines show the median reported by *Keenan et al.* [2013], and the dashed line shows the expected IWUE increase ($0.5\% \text{ yr}^{-1}$). In each subplot we show the median slopes of base T&C simulations (circles), the median slopes of base simulations with detrended temperature and relative humidity (dots), and the numerical experiment which best approximates each variable's slope (crosses), i.e., $[+V_{\max} + \text{LtR}]$ for IWUE, $[-a_1 - K_{\text{nit}}]$ for GEP, and $[-a_1]$ for ET.

Using static vegetation parameters (base simulations), the modeled IWUE increased by $0.9\% \text{ yr}^{-1}$, GEP increased by $0.2\% \text{ yr}^{-1}$, and ET also increased by $0.2\% \text{ yr}^{-1}$ (Figure 2 and Table S6). Weighted median slopes differ only slightly among sites, with a simulated trend in IWUE of $0.7\% \text{ yr}^{-1}$ (Table S7). Simulations with detrended temperature and relative humidity show a $0.4\% \text{ yr}^{-1}$ 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_{\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_{nit} or increasing S_{LA} or LtR) by $1\% \text{ yr}^{-1}$ 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 ($0.1\% \text{ yr}^{-1}$), while in broadleaf deciduous forests (eight sites) IWUE increased by $3.0\% \text{ yr}^{-1}$ (Figure S4).

4 Discussion

4.1 Observed Trends in IWUE

We found a median increase in IWUE of $1.3\% \text{ yr}^{-1}$ 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 $C_i:C_a$ but is considerably lower than what *Keenan et al.* [2013] reported for the same sites ($2.3\% \text{ yr}^{-1}$).

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 ($0.5\% \text{ yr}^{-1}$) 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 $C_i:C_a$ 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 $[\text{CO}_2]$ [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 $[\text{CO}_2]$ 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 $1\% \text{ yr}^{-1}$ 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_{\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 $C_i:C_a$ 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 ($0.5\% \text{ yr}^{-1}$) [Ito and Inatomi, 2012; Keenan *et al.*, 2013; Dekker *et al.*, 2016]. However, the T&C model, even using static parameters, predicts an increase of $0.9\% \text{ yr}^{-1}$ in IWUE, which is larger than the expected, while simulating a constant $C_i:C_a$ (Figure S6). This result is independent of changes in the growing season length, because we restricted our analysis to summer months, but it is related to trends in climate variables, because simulations without trends in temperature and relative humidity show a median increase of $0.4\% \text{ yr}^{-1}$ 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_{\max} and a_1 (by $+1\% \text{ yr}^{-1}$ and $-1\% \text{ yr}^{-1}$, 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_{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 ($[\text{CO}_2]$ 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 a slight reduction in $C_i:C_a$, while in all other experiments $C_i:C_a$ 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_1 (similar to a_1 in our study) would imply (i) unrealistic site-level GEP negative trends, (ii) a decrease in C_i , 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_i 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_1 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_1 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_{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_{max} generally decreased in time [Ainsworth and Long, 2005], as happened, for instance, in the Oak Ridge FACE experiment, where photosynthesis was downregulated (V_{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_{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_{max} [Keenan et al., 2012]. Our results suggest that the increase in V_{max} increases the ratio between net assimilation and stomatal conductance since V_{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_{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_{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_{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_{LA} 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_{LA} 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 $1\% \text{ yr}^{-1}$ 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_{max} , S_{LA} , 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 CO₂ fertilization [Huang *et al.*, 2007; Battipaglia *et al.*, 2013; Keenan *et al.*, 2013], droughts can alter forest structure and plant functional traits [Koutavas, 2013; Hereş *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 [CO₂].

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 [CO₂]-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 [CO₂] and other environmental variables modifies WUE. Finally, interactions between the nutrient cycles and changes in WUE remain challenging [*Radoglou et al.*, 1992; *Peñuelas et al.*, 2011; *Ito and Inatomi*, 2012; *Liu et al.*, 2014; *Saurer 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.*, 2016], 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, CarboAfrica, CarboEuropeIP, 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 CDIAC, 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 14-2). C.P. acknowledges the support of the Stavros Niarchos Foundation and the ETH Zurich Foundation (grant P2EZIP2_162293) through a Swiss National Science Foundation (SNSF) Early Postdoc. Mobility fellowship. T.F.K. acknowledges supported from the Laboratory Directed Research and Development Program of Lawrence Berkeley National Laboratory under U.S. Department of Energy contract DE-

AC02-05CH11231. P.G. acknowledges support from the National Science Foundation CAREER grant (1552304) and Department of Energy Early Career grants.

References

Ainsworth, E. A., and S. P. Long (2005), What have we learned from 15 years of free-air CO₂ enrichment (FACE)? A meta-analytic review of the responses of photosynthesis, canopy properties and plant production to rising CO₂, *New Phytol.*, 165(2), 351- 372, doi:10.1111/j.1469-8137.2004.01224.x.

Ainsworth, E. A., and A. Rogers (2007), The response of photosynthesis and stomatal conductance to rising [CO₂]: Mechanisms and environmental interactions, *Plant Cell Environ.*, 30(3), 258- 270, doi:10.1111/j.1365-3040.2007.01641.x.

Albert, C. H., F. Grassein, F. M. Schurr, G. Vieilledent, and C. Violle (2011), When and how should intraspecific variability be considered in trait-based plant ecology?, *Perspect. Plant Ecol. Evol. Syst.*, 13(3), 217- 225, doi:10.1016/j.ppees.2011.04.003.

Aubin, I., et al. (2016), Traits to stay, traits to move: A review of functional traits to assess sensitivity and adaptive capacity of temperate and boreal trees to climate change, *Environ. Rev.*, 24(2), 164- 186, doi:10.1139/er-2015-0072.

Aubinet, M., B. Heinesch, and B. Longdoz (2002), Estimation of the carbon sequestration by a heterogeneous forest: Night flux corrections, heterogeneity of the site and inter-annual variability, *Global Change Biol.*, 8(11), 1053- 1071, doi:10.1046/j.1365-2486.2002.00529.x.

Battipaglia, G., M. Saurer, P. Cherubini, C. Calfapietra, H. R. Mccarthy, R. J. Norby, and M. Francesca Cotrufo (2013), Elevated CO₂ increases tree-level intrinsic water use efficiency: Insights from carbon and oxygen isotope analyses in tree rings across three forest FACE sites, *New Phytol.*, 197(2), 544- 554, doi:10.1111/nph.12044.

Beer, C., et al. (2009), Temporal and among-site variability of inherent water use efficiency at the ecosystem level, *Global Biogeochem. Cycles*, 23(2), GB2018, doi:10.1029/2008GB003233.

Berbigier, P., J. M. Bonnefond, and P. Mellmann (2001), CO₂ and water vapour fluxes for 2 years above Euroflux forest site, *Agric. For. Meteorol.*, 108(3), 183- 197, doi:10.1016/S0168-1923(01)00240-4.

Bonan, G. B., P. J. Lawrence, K. W. Oleson, S. Levis, M. Jung, M. Reichstein, D. M. Lawrence, and S. C. Swenson (2011), Improving canopy processes in the Community Land Model version 4 (CLM4) using global flux fields empirically inferred from FLUXNET data, *J. Geophys. Res.*, 116, G02014, doi:10.1029/2010JG001593.

- Brodribb, T. J., and N. M. Holbrook (2003), Stomatal closure during leaf dehydration, correlation with other leaf physiological traits, *Plant Physiol.*, 132(4), 2166– 2173, doi:10.1104/pp.103.023879.
- Brodribb, T. J., and S. A. M. McAdam (2013), Unique responsiveness of angiosperm stomata to elevated CO₂ explained by calcium signalling, *PLoS One*, 8(11), e82057, doi:10.1371/journal.pone.0082057.
- Brzostek, E. R., D. Dragoni, H. P. Schmid, A. F. Rahman, D. Sims, C. A. Wayson, D. J. Johnson, and R. P. Phillips (2014), Chronic water stress reduces tree growth and the carbon sink of deciduous hardwood forests, *Global Change Biol.*, 20(8), 2531– 2539, doi:10.1111/gcb.12528.
- Buckley, T. N. (2008), The role of stomatal acclimation in modelling tree adaptation to high CO₂, *J. Exp. Bot.*, 59(7), 1951– 1961, doi:10.1093/jxb/erm234.
- Bunce, J. A. (2004), Carbon dioxide effects on stomatal responses to the environment and water use by crops under field conditions, *Oecologia*, 140(1), 1– 10, doi:10.1007/s00442-003-1401-6.
- Camarero, J. J., A. Gazol, J. C. Tardif, and F. Conciatori (2015), Attributing forest responses to global-change drivers: Limited evidence of a CO₂-fertilization effect in Iberian pine growth, *J. Biogeogr.*, 42(11), 2220– 2233, doi:10.1111/jbi.12590.
- Cao, L., G. Bala, K. Caldeira, R. Nemani, and G. Ban-Weiss (2010), Importance of carbon dioxide physiological forcing to future climate change, *Proc. Natl. Acad. Sci. U.S.A.*, 107(21), 9513– 9518, doi:10.1073/pnas.0913000107.
- Carrara, A., A. S. Kowalski, J. Neiryneck, I. A. Janssens, J. C. Yuste, and R. Ceulemans (2003), Net ecosystem CO₂ exchange of mixed forest in Belgium over 5 years, *Agric. For. Meteorol.*, 119(3–4), 209– 227, doi:10.1016/S0168-1923(03)00120-5.
- Cook, B. D., et al. (2004), Carbon exchange and venting anomalies in an upland deciduous forest in northern Wisconsin, USA, *Agric. For. Meteorol.*, 126(3–4), 271– 295, doi:10.1016/j.agrformet.2004.06.008.
- Curtis, P. S., C. S. Vogel, C. M. Gough, H. P. Schmid, H. B. Su, and B. D. Bovard (2005), Respiratory carbon losses and the carbon-use efficiency of a northern hardwood forest, 1999–2003, *New Phytol.*, 167(2), 437– 456, doi:10.1111/j.1469-8137.2005.01438.x.
- de Boer, H. J., E. I. Lammertsma, F. Wagner-Cremer, D. L. Dilcher, M. J. Wassen, and S. C. Dekker (2011), Climate forcing due to optimization of maximal leaf conductance in subtropical vegetation under rising CO₂, *Proc. Natl. Acad. Sci. U.S.A.*, 108(10), 4041– 4046, doi:10.1073/pnas.1100555108.

de Boer, H. J., M. B. Eppinga, M. J. Wassen, and S. C. Dekker (2012), A critical transition in leaf evolution facilitated the Cretaceous angiosperm revolution, *Nat. Commun.*, 3, 1221, doi:10.1038/ncomms2217.

de Boer, H. J., C. A. Price, F. Wagner-Cremer, S. C. Dekker, P. J. Franks, and E. J. Veneklaas (2016), Optimal allocation of leaf epidermal area for gas exchange, *New Phytol.*, 210(4), 1219– 1228, doi:10.1111/nph.13929.

Damour, G., T. Simonneau, H. Cochard, and L. Urban (2010), An overview of models of stomatal conductance at the leaf level, *Plant Cell Environ.*, 33(9), 1419– 1438, doi:10.1111/j.1365-3040.2010.02181.x.

Davidson, E. A., K. E. Savage, S. E. Trumbore, and W. Borken (2006), Vertical partitioning of CO₂ production within a temperate forest soil, *Global Change Biol.*, 12(6), 944– 956, doi:10.1111/j.1365-2486.2005.01142.x.

Dekker, S. C., M. Groenendijk, B. B. Booth, C. Huntingford, and P. M. Cox (2016), Spatial and temporal variations in plant water-use efficiency inferred from tree-ring, eddy covariance and atmospheric observations, *Earth Syst. Dynam.*, 7(2), 525– 533, doi:10.5194/esd-7-525-2016.

De Kauwe, M. G., et al. (2013), Forest water use and water use efficiency at elevated CO₂: A model-data intercomparison at two contrasting temperate forest FACE sites, *Global Change Biol.*, 19(6), 1759– 1779, doi:10.1111/gcb.12164.

De Kauwe, M. G., et al. (2014), Where does the carbon go? A model-data intercomparison of vegetation carbon allocation and turnover processes at two temperate forest free-air CO₂ enrichment sites, *New Phytol.*, 203(3), 883– 899, doi:10.1111/nph.12847.

Dolman, A. J., E. J. Moors, and J. A. Elbers (2002), The carbon uptake of a mid latitude pine forest growing on sandy soil, *Agric. For. Meteorol.*, 111(3), 157– 170, doi:10.1016/S0168-1923(02)00024-2.

Domec, J. C., S. Palmroth, E. Ward, C. A. Maier, M. Th  r  zien, and R. Oren (2009), Acclimation of leaf hydraulic conductance and stomatal conductance of *Pinus Taeda* (loblolly pine) to long-term growth in elevated CO₂ (free-air CO₂ enrichment) and N-fertilization, *Plant Cell Environ.*, 32(11), 1500– 1512, doi:10.1111/j.1365-3040.2009.02014.x.

Drake, B. G., M. A. Gonzalez-Meler, and S. P. Long (1997), More efficient plants: A consequence of rising atmospheric CO₂?, *Annu. Rev. Plant Physiol. Plant Mol. Biol.*, 48, 609– 639, doi:10.1146/annurev.arplant.48.1.609.

Dunn, A. L., C. C. Barford, S. C. Wofsy, M. L. Goulden, and B. C. Daube (2007), A long-term record of carbon exchange in a boreal black spruce forest: Means, responses to interannual variability, and decadal trends, *Global Change Biol.*, 13(3), 577– 590, doi:10.1111/j.1365-2486.2006.01221.x.

Eamus, D., and P. G. Jarvis (1989), The direct effects of increase in the global atmospheric CO₂ concentration on natural and commercial temperate trees and forests, *Adv. Ecol. Res.*, 34, 1– 55, doi:10.1016/S0065-2504(03)34001-2.

Ehlers, I., A. Augusti, T. R. Betson, M. B. Nilsson, J. D. Marshall, and J. Schleucher (2015), Detecting long-term metabolic shifts using isotopomers: CO₂-driven suppression of photorespiration in C₃ plants over the 20th century, *Proc. Natl. Acad. Sci. U.S.A.*, 112(51), 15,585– 15,590, doi:10.1073/pnas.1504493112.

Farquhar, G. D., S. von Caemmerer, and J. A. Berry (1980), A biochemical model of photosynthetic CO₂ assimilation in leaves of C₃ species, *Planta*, 149(1), 78– 90, doi:10.1007/BF00386231.

Fatichi, S., and V. Y. Ivanov (2014), Interannual variability of evapotranspiration and vegetation productivity, *Water Resour. Res.*, 50(4), 3275– 3294, doi:10.1002/2013WR015044.

Fatichi, S., and S. Leuzinger (2013), Reconciling observations with modeling: The fate of water and carbon allocation in a mature deciduous forest exposed to elevated CO₂, *Agric. For. Meteorol.*, 174–175, 144– 157, doi:10.1016/j.agrformet.2013.02.005.

Fatichi, S., and C. Pappas (2017), Constrained variability of modeled T:ET ratio across biomes, *Geophys. Res. Lett.*, 44(13), 6795– 6803, doi:10.1002/2017GL074041.

Fatichi, S., V. Y. Ivanov, and E. Caporali (2012), A mechanistic ecohydrological model to investigate complex interactions in cold and warm water-controlled environments: 1. Theoretical framework and plot-scale analysis, *J. Adv. Model. Earth Syst.*, 4(2), M05002, doi:10.1029/2011MS000087.

Fatichi, S., S. Leuzinger, A. Paschalis, J. A. Langley, A. Donnellan Barraclough, and M. J. Hovenden (2016a), Partitioning direct and indirect effects reveals the response of water-limited ecosystems to elevated CO₂, *Proc. Natl. Acad. Sci. U.S.A.*, 113(45), 12,757– 12,762, doi:10.1073/pnas.1605036113.

Fatichi, S., C. Pappas, and V. Y. Ivanov (2016b), Modeling plant-water interactions: An ecohydrological overview from the cell to the global scale, *Wiley Interdiscip. Rev. Water*, 3(3), 327– 368, doi:10.1002/wat2.1125.

Field, C. B., R. B. Jackson, and H. A. Mooney (1995), Stomatal responses to increased CO₂: Implications from the plant to the global scale, *Plant Cell Environ.*, 18(10), 1214– 1225, doi:10.1111/j.1365-3040.1995.tb00630.x.

Flexas, J., et al. (2016), Mesophyll conductance to CO₂ and Rubisco as targets for improving intrinsic water use efficiency in C₃ plants, *Plant Cell Environ.*, 39(5), 965– 982, doi:10.1111/pce.12622.

Foken, T. (2008), The energy balance closure problem: An overview, *Ecol. Appl.*, 18(6), 1351– 1367, doi:10.1890/06-0922.1.

Forkel, M., N. Carvalhais, C. Rodenbeck, R. Keeling, M. Heimann, K. Thonicke, S. Zaehle, and M. Reichstein (2016), Enhanced seasonal CO₂ exchange caused by amplified plant productivity in northern ecosystems, *Science*, 351(6274), 696– 699, doi:10.1126/science.aac4971.

Francey, R. J., et al. (2013), Atmospheric verification of anthropogenic CO₂ emission trends, *Nat. Clim. Change*, 3(5), 520– 524, doi:10.1038/nclimate1817.

Frank, D. C., et al. (2015), Water-use efficiency and transpiration across European forests during the Anthropocene, *Nat. Clim. Change*, 5(6), 579– 583, doi:10.1038/nclimate2614.

Franks, P. J., et al. (2013), Sensitivity of plants to changing atmospheric CO₂ concentration: From the geological past to the next century, *New Phytol.*, 197(4), 1077– 1094, doi:10.1111/nph.12104.

Franks, P. J., T. W. Doheny-Adams, Z. J. Britton-Harper, and J. E. Gray (2015), Increasing water-use efficiency directly through genetic manipulation of stomatal density, *New Phytol.*, 207(1), 188– 195, doi:10.1111/nph.13347.

Franks, S. J., S. Sim, and A. E. Weis (2007), Rapid evolution of flowering time by an annual plant in response to a climate fluctuation, *Proc. Natl. Acad. Sci. U.S.A.*, 104(4), 1278– 1282, doi:10.1073/pnas.0608379104.

Fyllas, N. M., et al. (2009), Basin-wide variations in foliar properties of Amazonian forest: Phylogeny, soils and climate, *Biogeosciences*, 6(11), 2677– 2708, doi:10.5194/bgd-6-3707-2009.

Fyllas, N. M., et al. (2014), Analysing Amazonian forest productivity using a new individual and trait-based model (TFS v.1), *Geosci. Model Dev.*, 7(4), 1251– 1269, doi:10.5194/gmd-7-1251-2014.

Galmés, J., P. J. Andralojc, M. V. Kapralov, J. Flexas, A. J. Keys, A. Molins, M. A. J. Parry, and M. À. Conesa (2014), Environmentally driven evolution of Rubisco and improved photosynthesis and growth within the C3 genus *Limonium* (Plumbaginaceae), *New Phytol.*, 203(3), 989– 999, doi:10.1111/nph.12858.

Gedney, N., P. M. Cox, R. A. Betts, O. Boucher, C. Huntingford, and P. A. Stott (2006), Detection of a direct carbon dioxide effect in continental river runoff records, *Nature*, 439(7078), 835– 838, doi:10.1038/nature04504.

Goldstein, A. H., N. E. Hultman, J. M. Fracheboud, M. R. Bauer, J. A. Panek, M. Xu, Y. Qi, A. B. Guenther, and W. Baugh (2000), Effects of climate variability on the carbon dioxide, water, and sensible heat fluxes above a ponderosa pine plantation in the Sierra Nevada (CA), *Agric. For. Meteorol.*, 101(2–3), 113– 129, doi:10.1016/S0168-1923(99)00168-9.

Gough, C. M., B. S. Hardiman, L. E. Nave, G. Bohrer, K. D. Maurer, C. S. Vogel, K. J. Nadelhoffer, and P. S. Curtis (2013), Sustained carbon uptake and

storage following moderate disturbance in a Great Lakes forest, *Ecol. Appl.*, 23(5), 1202– 1215, doi:10.1890/12-1554.1.

Granier, A., et al. (2000), The carbon balance of a young beech forest, *Funct. Ecol.*, 14(3), 312– 325, doi:10.1046/j.1365-2435.2000.00434.x.

Granier, A., N. Bréda, B. Longdoz, P. Gross, and J. Ngao (2008), Ten years of fluxes and stand growth in a young beech forest at Hesse, North-eastern France, *Ann. For. Sci.*, 65(7), 704– 716, doi:10.1051/forest:2008052.

Grünwald, T., and C. Bernhofer (2007), A decade of carbon, water and energy flux measurements of an old spruce forest at the Anchor Station Tharandt, *Tellus B*, 59(3), 387– 396, doi:10.1111/j.1600-0889.2007.00259.x.

Guerrieri, R., M. Mencuccini, L. J. Sheppard, M. Saurer, M. P. Perks, P. Levy, M. A. Sutton, M. Borghetti, and J. Grace (2011), The legacy of enhanced N and S deposition as revealed by the combined analysis of $\delta^{13}\text{C}$, $\delta^{18}\text{O}$ and $\delta^{15}\text{N}$ in tree rings, *Global Change Biol.*, 17(5), 1946– 1962, doi:10.1111/j.1365-2486.2010.02362.x.

Hadley, J. L., and J. L. Schedlbauer (2002), Carbon exchange of an old-growth eastern hemlock (*Tsuga canadensis*) forest in central New England, *Tree Physiol.*, 22(15–16), 1079– 1092, doi:10.1093/treephys/22.15-16.1079.

Hardiman, B. S., C. M. Gough, A. Halperin, K. L. Hofmeister, L. E. Nave, G. Bohrer, and P. S. Curtis (2013), Maintaining high rates of carbon storage in old forests: A mechanism linking canopy structure to forest function, *For. Ecol. Manage.*, 298, 111– 119, doi:10.1016/j.foreco.2013.02.031.

Hereş, A. M., J. Voltas, B. C. López, and J. Martínez-Vilalta (2014), Drought-induced mortality selectively affects Scots pine trees that show limited intrinsic water-use efficiency responsiveness to raising atmospheric CO_2 , *Funct. Plant Biol.*, 41(3), 244– 256, doi:10.1071/FP13067.

Hollinger, D. Y., et al. (2004), Spatial and temporal variability in forest-atmosphere CO_2 exchange, *Global Change Biol.*, 10(10), 1689– 1706, doi:10.1111/j.1365-2486.2004.00847.x.

Huang, J.-G., Y. Bergeron, B. Denneler, F. Berninger, and J. Tardif (2007), Response of forest trees to increased atmospheric CO_2 , *CRC. Crit. Rev. Plant Sci.*, 26(5–6), 265– 283, doi:10.1080/07352680701626978.

Huang, M., S. Piao, Y. Sun, P. Ciais, L. Cheng, J. Mao, B. Poulter, X. Shi, Z. Zeng, and Y. Wang (2015), Change in terrestrial ecosystem water-use efficiency over the last three decades, *Global Change Biol.*, 21(6), 2366– 2378, doi:10.1111/gcb.12873.

Huang, Z., B. Liu, M. Davis, J. Sardans, J. Peñuelas, and S. Billings (2016), Long-term nitrogen deposition linked to reduced water use efficiency in forests with low phosphorus availability, *New Phytol.*, 210(2), 431– 442, doi:10.1111/nph.13785.

Ishizaki, S., K. Hikosaka, and T. Hirose (2003), Increase in leaf mass per area benefits plant growth at elevated CO₂ concentration, *Ann. Bot.*, 91(7), 905–914, doi:10.1093/aob/mcg097.

Ito, A., and M. Inatomi (2012), Water-use efficiency of the terrestrial biosphere: A model analysis focusing on interactions between the global carbon and water cycles, *J. Hydrometeorol.*, 13(2), 681– 694, doi:10.1175/JHM-D-10-05034.1.

Jenkins, J. P., A. D. Richardson, B. H. Braswell, S. V. Ollinger, D. Y. Hollinger, and M. L. Smith (2007), Refining light-use efficiency calculations for a deciduous forest canopy using simultaneous tower-based carbon flux and radiometric measurements, *Agric. For. Meteorol.*, 143(1–2), 64– 79, doi:10.1016/j.agrformet.2006.11.008.

Jennings, K. A., R. Guerrieri, M. A. Vadeboncoeur, and H. Asbjornsen (2016), Response of *Quercus velutina* growth and water use efficiency to climate variability and nitrogen fertilization in a temperate deciduous forest in the northeastern USA, *Tree Physiol.*, 36(4), 428– 443, doi:10.1093/treephys/tpw003.

Jung, M., et al. (2010), Recent decline in the global land evapotranspiration trend due to limited moisture supply, *Nature*, 467(7318), 951– 954, doi:10.1038/nature09396.

Kattge, J., and W. Knorr (2007), Temperature acclimation in a biochemical model of photosynthesis: A reanalysis of data from 36 species, *Plant Cell Environ.*, 30(9), 1176– 1190, doi:10.1111/j.1365-3040.2007.01690.x.

Kattge, J., et al. (2011), TRY—A global database of plant traits, *Global Change Biol.*, 17(9), 2905– 2935, doi:10.1111/j.1365-2486.2011.02451.x.

Katul, G., S. Manzoni, S. Palmroth, and R. Oren (2010), A stomatal optimization theory to describe the effects of atmospheric CO₂ on leaf photosynthesis and transpiration, *Ann. Bot.*, 105(3), 431– 442, doi:10.1093/aob/mcp292.

Keenan, T. F., E. Davidson, A. M. Moffat, W. Munger, and A. D. Richardson (2012), Using model-data fusion to interpret past trends, and quantify uncertainties in future projections, of terrestrial ecosystem carbon cycling, *Global Change Biol.*, 18(8), 2555– 2569, doi:10.1111/j.1365-2486.2012.02684.x.

Keenan, T. F., D. Y. Hollinger, G. Bohrer, D. Dragoni, J. W. Munger, H. P. Schmid, and A. D. Richardson (2013), Increase in forest water-use efficiency as atmospheric carbon dioxide concentrations rise, *Nature*, 499(7458), 324–327, doi:10.1038/nature12291.

Kenney, J. F., and E. S. Keeping (1962), *Mathematics of Statistics*, Part 1, 3rd ed., Princeton, N. J.

- Knapp, A. K., J. M. Briggs, and M. D. Smith (2012), Community stability does not preclude ecosystem sensitivity to chronic resource alteration, *Funct. Ecol.*, 26(6), 1231– 1233, doi:10.1111/j.1365-2435.2012.02053.x.
- Knauer, J., S. Zaehle, M. Reichstein, B. E. Medlyn, M. Forkel, S. Hagemann, and C. Werner (2017), The response of ecosystem water-use efficiency to rising atmospheric CO₂ concentrations: Sensitivity and large-scale biogeochemical implications, *New Phytol.*, 213(4), 1654– 1666, doi:10.1111/nph.14288.
- Koutavas, A. (2013), CO₂ fertilization and enhanced drought resistance in Greek firs from Cephalonia Island, Greece, *Global Change Biol.*, 19(2), 529– 539, doi:10.1111/gcb.12053.
- Krinner, G., N. Viovy, N. de Noblet-Ducoudré, J. Ogée, J. Polcher, P. Friedlingstein, P. Ciais, S. Sitch, and I. C. Prentice (2005), A dynamic global vegetation model for studies of the coupled atmosphere-biosphere system, *Global Biogeochem. Cycles*, 19(1), GB1015, doi:10.1029/2003GB002199.
- Lammertsma, E. I., H. J. de Boer, S. C. Dekker, D. L. Dilcher, A. F. Lotter, and F. Wagner-Cremer (2011), Global CO₂ rise leads to reduced maximum stomatal conductance in Florida vegetation, *Proc. Natl. Acad. Sci. U.S.A.*, 108(10), 4035– 4040, doi:10.1073/pnas.1100371108.
- Lawson, T., and J. C. McElwain (2016), Evolutionary trade-offs in stomatal spacing, *New Phytol.*, 210(4), 1149– 1151, doi:10.1111/nph.13972.
- Leakey, A. D. B., E. A. Ainsworth, C. J. Bernacchi, A. Rogers, S. P. Long, and D. R. Ort (2009), Elevated CO₂ effects on plant carbon, nitrogen, and water relations: Six important lessons from FACE, *J. Exp. Bot.*, 60(10), 2859– 2876, doi:10.1093/jxb/erp096.
- Lemordant, L., P. Gentine, M. Stéfanon, P. Drobinski, and S. Fatichi (2016), Modification of land-atmosphere interactions by CO₂ effects: Implications for summer dryness and heat wave amplitude, *Geophys. Res. Lett.*, 43(19), 10,240– 10,248, doi:10.1002/2016GL069896.
- Leonardi, S., T. Gentilesca, R. Guerrieri, F. Ripullone, F. Magnani, M. Mencuccini, T. V. Noije, and M. Borghetti (2012), Assessing the effects of nitrogen deposition and climate on carbon isotope discrimination and intrinsic water-use efficiency of angiosperm and conifer trees under rising CO₂ conditions, *Global Change Biol.*, 18(9), 2925– 2944, doi:10.1111/j.1365-2486.2012.02757.x.
- Leuning, R. (1990), Modelling stomatal behaviour and photosynthesis of *Eucalyptus grandis*, *Aust. J. Plant Physiol.*, 17(2), 159– 175, doi:10.1071/PP9900159.
- Leuning, R. (1995), A critical appraisal of a combined stomatal-photosynthesis model for C₃ plants, *Plant Cell Environ.*, 18(4), 339– 355, doi:10.1111/j.1365-3040.1995.tb00370.x.

Leuning, R., F. M. Kelliher, D. G. G. de Pury, and E. D. Schulze (1995), Leaf nitrogen, photosynthesis, conductance and transpiration: Scaling from leaves to canopies, *Plant Cell Environ.*, 18(10), 1183- 1200, doi:10.1111/j.1365-3040.1995.tb00628.x.

Leuning, R., E. van Gorsel, W. J. Massman, and P. R. Isaac (2012), Reflections on the surface energy imbalance problem, *Agric. For. Meteorol.*, 156, 65- 74, doi:10.1016/j.agrformet.2011.12.002.

Leuzinger, S., Y. Luo, C. Beier, W. Dieleman, S. Vicca, and C. Körner (2011), Do global change experiments overestimate impacts on terrestrial ecosystems?, *Trends Ecol. Evol.*, 26(5), 236- 241, doi:10.1016/j.tree.2011.02.011.

Lin, Y.-S., et al. (2015), Optimal stomatal behaviour around the world, *Nat. Clim. Change*, 5(5), 459- 464, doi:10.1038/nclimate2550.

Liu, X., W. Wang, G. Xu, X. Zeng, G. Wu, X. Zhang, and D. Qin (2014), Tree growth and intrinsic water-use efficiency of inland riparian forests in northwestern China: Evaluation via $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ analysis of tree rings, *Tree Physiol.*, 34(9), 966- 980, doi:10.1093/treephys/tpu067.

Liu, Y., J. Xiao, W. Ju, Y. Zhou, S. Wang, and X. Wu (2015), Water use efficiency of China's terrestrial ecosystems and responses to drought, *Sci. Rep.*, 5(1), 13,799, doi:10.1038/srep13799.

Lombardozzi, D. L., G. B. Bonan, N. G. Smith, J. S. Dukes, and R. A. Fisher (2015), Temperature acclimation of photosynthesis and respiration: A key uncertainty in the carbon cycle-climate feedback, *Geophys. Res. Lett.*, 42(20), 8624- 8631, doi:10.1002/2015GL065934.

Long, S. P., E. A. Ainsworth, A. Rogers, and D. R. Ort (2004), Rising atmospheric carbon dioxide: Plants FACE the future, *Annu. Rev. Plant Biol.*, 55, 591- 628, doi:10.1146/annurev.arplant.55.031903.141610.

Maillard, P., J. M. Guehl, J. F. Muller, and P. Gross (2001), Interactive effects of elevated CO_2 concentration and nitrogen supply on partitioning of newly fixed ^{13}C and ^{15}N between shoot and roots of pedunculate oak seedlings (*Quercus robur*), *Tree Physiol.*, 21(2-3), 163- 172, doi:10.1093/treephys/21.2-3.163.

Manzoni, S., G. Vico, G. Katul, P. A. Fay, W. Polley, S. Palmroth, and A. Porporato (2011), Optimizing stomatal conductance for maximum carbon gain under water stress: A meta-analysis across plant functional types and climates, *Funct. Ecol.*, 25(3), 456- 467, doi:10.1111/j.1365-2435.2010.01822.x.

Maseyk, K., D. Hemming, A. Angert, S. W. Leavitt, and D. Yakir (2011), Increase in water-use efficiency and underlying processes in pine forests across a precipitation gradient in the dry Mediterranean region over the past 30 years, *Oecologia*, 167(2), 573- 585, doi:10.1007/s00442-011-2010-4.

Matamala, R., and W. H. Schlesinger (2000), Effects of elevated atmospheric CO₂ on fine root production and activity in an intact temperate forest ecosystem, *Global Change Biol.*, 6(8), 967– 979, doi:10.1046/j.1365-2486.2000.00374.x.

McAusland, L., S. Violet-Chabrand, P. Davey, N. R. Baker, O. Brendel, and T. Lawson (2016), Effects of kinetics of light-induced stomatal responses on photosynthesis and water-use efficiency, *New Phytol.*, 211(4), 1209– 1220, doi:10.1111/nph.14000.

Medlyn, B., and M. De Kauwe (2013), Biogeochemistry: Carbon dioxide and water use in forests, *Nature*, 499(7458), 287– 289, doi:10.1038/nature12411.

Medlyn, B. E., et al. (2001), Stomatal conductance of forest species after long-term exposure to elevated CO₂ concentration: A synthesis, *New Phytol.*, 149(2), 247– 264, doi:10.1046/j.1469-8137.2001.00028.x.

Medlyn, B. E., R. A. Duursma, D. Eamus, D. S. Ellsworth, I. C. Prentice, C. V. M. Barton, K. Y. Crous, P. De Angelis, M. Freeman, and L. Wingate (2011), Reconciling the optimal and empirical approaches to modelling stomatal conductance, *Global Change Biol.*, 17(6), 2134– 2144, doi:10.1111/j.1365-2486.2010.02375.x.

Medlyn, B. E., et al. (2015), Using ecosystem experiments to improve vegetation models, *Nat. Clim. Change*, 5(6), 528– 534, doi:10.1038/nclimate2621.

Medlyn, B. E., et al. (2017), How do leaf and ecosystem measures of water-use efficiency compare?, *New Phytol.*, doi:10.1111/nph.14626.

Miglietta, F., A. Peressotti, R. Viola, C. Körner, and J. S. Amthor (2011), Stomatal numbers, leaf and canopy conductance, and the control of transpiration, *Proc. Natl. Acad. Sci. U.S.A.*, 108(28), E275, doi:10.1073/pnas.1105831108.

Miralles, D. G., et al. (2015), The WACMOS-ET project—Part 2: Evaluation of global terrestrial evaporation data sets, *Hydrol. Earth Syst. Sci.*, 20(2), 823– 842, doi:10.5194/hess-20-823-2016.

Moore, B. D., S. H. Cheng, D. Sims, and J. R. Seemann (1999), The biochemical and molecular basis for photosynthetic acclimation to elevated atmospheric CO₂, *Plant Cell Environ.*, 22(6), 567– 582, doi:10.1046/j.1365-3040.1999.00432.x.

Morison, J. I. L. (1985), Sensitivity of stomata and water use efficiency to high CO₂, *Plant Cell Environ.*, 8(6), 467– 474, doi:10.1111/j.1365-3040.1985.tb01682.x.

Morison, J. I. L., and R. M. Gifford (1984), Plant growth and water use with limited water supply in high CO₂ concentrations. II*. Plant dry weight,

partitioning and water use efficiency, *Aust. J. Plant Physiol.*, 11(5), 375- 384, doi:10.1071/PP9840375.

Nelson, J. A., J. A. Morgan, D. R. LeCain, A. R. Mosier, D. G. Milchunas, and B. A. Parton (2004), Elevated CO₂ increases soil moisture and enhances plant water relations in a long-term field study in semi-arid shortgrass steppe of Colorado, *Plant Soil*, 259(1-2), 169- 179, doi:10.1023/B:PLSO.0000020957.83641.62.

Nicotra, A. B., et al. (2010), Plant phenotypic plasticity in a changing climate, *Trends Plant Sci.*, 15(12), 684- 692, doi:10.1016/j.tplants.2010.09.008.

Niinemets, Ü. (2007), Photosynthesis and resource distribution through plant canopies, *Plant Cell Environ.*, 30(9), 1052- 1071, doi:10.1111/j.1365-3040.2007.01683.x.

Niinemets, Ü., T. F. Keenan, and L. Hallik (2015), A worldwide analysis of within-canopy variations in leaf structural, chemical and physiological traits across plant functional types, *New Phytol.*, 205(3), 973- 993, doi:10.1111/nph.13096.

Novick, K. A., A. C. Oishi, E. J. Ward, M. B. S. Siqueira, J.-Y. Juang, and P. C. Stoy (2015), On the difference in the net ecosystem exchange of CO₂ between deciduous and evergreen forests in the southeastern United States, *Global Change Biol.*, 21(2), 827- 842, doi:10.1111/gcb.12723.

Novick, K. A., et al. (2016), The increasing importance of atmospheric demand for ecosystem water and carbon fluxes, *Nat. Clim. Change*, 6(11), 1023- 1027, doi:10.1038/nclimate3114.

Palmroth, S., R. Oren, H. R. McCarthy, K. H. Johnsen, A. C. Finzi, J. R. Butnor, M. G. Ryan, and W. H. Schlesinger (2006), Aboveground sink strength in forests controls the allocation of carbon below ground and its [CO₂]-induced enhancement, *Proc. Natl. Acad. Sci. U.S.A.*, 103(51), 19,362- 19,367, doi:10.1073/pnas.0609492103.

Pappas, C., S. Fatichi, S. Leuzinger, A. Wolf, and P. Burlando (2013), Sensitivity analysis of a process-based ecosystem model: Pinpointing parameterization and structural issues, *J. Geophys. Res. Biogeosci.*, 118, 505- 528, doi:10.1002/jgrg.20035.

Pappas, C., S. Fatichi, S. Rimkus, P. Burlando, and M. O. Huber (2015), The role of local-scale heterogeneities in terrestrial ecosystem modeling, *J. Geophys. Res. Biogeosci.*, 120, 341- 360, doi:10.1002/2014JG002735.

Pappas, C., S. Fatichi, and P. Burlando (2016), Modeling terrestrial carbon and water dynamics across climatic gradients: Does plant trait diversity matter?, *New Phytol.*, 209(1), 137- 151, doi:10.1111/nph.13590.

Pappas, C., M. D. Mahecha, D. C. Frank, F. Babst, and D. Koutsoyiannis (2017), Ecosystem functioning is enveloped by hydrometeorological

variability, *Nat. Ecol. Evol.*, 1(9), 1263– 1270, doi:10.1038/s41559-017-0277-5.

Paschalis, A., S. Fatichi, G. G. Katul, and V. Y. Ivanov (2015), Cross-scale impact of climate temporal variability on ecosystem water and carbon fluxes, *J. Geophys. Res. Biogeosci.*, 120, 1716– 1740, doi:10.1002/2015JG003002.

Paschalis, A., G. G. Katul, S. Fatichi, S. Palmroth, and D. A. Way (2016), On the variability of the ecosystem response to elevated atmospheric CO₂ across spatial and temporal scales at the Duke Forest FACE experiment agricultural and Forest meteorology, *Agric. For. Meteorol.*, 232, 367– 383, doi:10.1016/j.agrformet.2016.09.003.

Pavlick, R., D. T. Drewry, K. Bohn, B. Reu, and A. Kleidon (2013), The Jena Diversity-Dynamic Global Vegetation Model (JeDi-DGVM): A diverse approach to representing terrestrial biogeography and biogeochemistry based on plant functional trade-offs, *Biogeosciences*, 10(6), 4137– 4177, doi:10.5194/bgd-9-4627-2012.

Peñuelas, J., and R. Matamala (1990), Changes in N and S leaf content, stomatal density and specific leaf-area of 14 plant-species during the last 3 centuries of CO₂ increase, *J. Exp. Bot.*, 41(9), 1119– 1124, doi:10.1093/jxb/41.9.1119.

Peñuelas, J., J. G. Canadell, and R. Ogaya (2011), Increased water-use efficiency during the 20th century did not translate into enhanced tree growth, *Global Ecol. Biogeogr.*, 20(4), 597– 608, doi:10.1111/j.1466-8238.2010.00608.x.

Pilegaard, K., A. Ibrom, M. S. Courtney, P. Hummelshøj, and N. O. Jensen (2011), Increasing net CO₂ uptake by a Danish beech forest during the period from 1996 to 2009, *Agric. For. Meteorol.*, 151(7), 934– 946, doi:10.1016/j.agrformet.2011.02.013.

Poorter, H., and O. Nagel (2000), The role of biomass allocation in the growth response of plants to different levels of light, CO₂, nutrients and water: A quantitative review, *Aust. J. Plant Physiol.*, 27(6), 595– 607, doi:10.1071/PP99173.

Prentice, I. C., X. Liang, B. E. Medlyn, and Y.-P. Wang (2015), Reliable, robust and realistic: The three R's of next-generation land-surface modelling, *Atmos. Chem. Phys.*, 15(10), 5987– 6005, doi:10.5194/acp-15-5987-2015.

Radoglou, K. M., P. Aphalo, and P. G. Jarvis (1992), Response of photosynthesis, stomatal conductance and water-use efficiency to elevated CO₂ and nutrient supply in acclimated seedlings of *Phaseolus-vulgaris* L, *Ann. Bot.*, 70(3), 257– 264, doi:10.1093/oxfordjournals.aob.a088467.

Reich, P. B., K. M. Sendall, A. Stefanski, X. Wei, R. L. Rich, and R. A. Montgomery (2016), Boreal and temperate trees show strong acclimation of respiration to warming, *Nature*, 531(7596), 633– 636, doi:10.1038/nature17142.

Reichstein, M., et al. (2005), On the separation of net ecosystem exchange into assimilation and ecosystem respiration: Review and improved algorithm, *Global Change Biol.*, 11(9), 1424- 1439, doi:10.1111/j.1365-2486.2005.001002.x.

Reichstein, M., et al. (2007), Determinants of terrestrial ecosystem carbon balance inferred from European eddy covariance flux sites, *Geophys. Res. Lett.*, 34(1), L01402, doi:10.1029/2006GL027880.

Reid, C. D., H. Maherali, H. B. Johnson, S. D. Smith, S. D. Wullschleger, and R. B. Jackson (2003), On the relationship between stomatal characters and atmospheric CO₂, *Geophys. Res. Lett.*, 30(19), 1983, doi:10.1029/2003GL017775.

Rigden, A. J., and G. D. Salvucci (2017), Stomatal response to humidity and CO₂ implicated in recent decline in US evaporation, *Global Change Biol.*, 23(3), 1140- 1151, doi:10.1111/gcb.13439.

Rogers, H. H., A. P. Stephen, G. B. Runion, and R. J. Mitchell (1996), Root to shoot ratio of crops as influenced by CO₂, *Plant Soil*, 187(2), 229- 248, doi:10.1007/BF00017090.

Rutter, A. A. J., A. J. Morton, and P. C. Robins (1975), A predictive model of rainfall interception in forests 2. Generalization of the model and comparison with observations in some coniferous and hardwood stands, *J. Appl. Ecol.*, 12(1), 367- 380, doi:10.2307/2401739.

Rutter, A. J., K. A. Kershaw, P. C. Robins, and A. J. Morton (1971), A predictive model of rainfall interception in forests. 1. Derivation of the model from observation in a plantation of Corsican pine, *Agric. Meteorol.*, 9(1971-1972), 367- 384, doi:10.1016/0002-1571(71)90034-3.

Sage, R. F. (1994), Acclimation of photosynthesis to increasing atmospheric CO₂: The gas exchange perspective, *Photosynth. Res.*, 39(3), 351- 368, doi:10.1007/BF00014591.

Sakschewski, B., W. von Bloh, A. Boit, A. Rammig, J. Kattge, L. Poorter, J. Peñuelas, and K. Thonicke (2015), Leaf and stem economics spectra drive diversity of functional plant traits in a dynamic global vegetation model, *Global Change Biol.*, 21(7), 2711- 2725, doi:10.1111/gcb.12870.

Saltelli, A., and P. Annoni (2010), How to avoid a perfunctory sensitivity analysis, *Environ. Model. Softw.*, 25(12), 1508- 1517, doi:10.1016/j.envsoft.2010.04.012.

Saurer, M., R. T. W. Siegwolf, and F. H. Schweingruber (2004), Carbon isotope discrimination indicates improving water-use efficiency of trees in northern Eurasia over the last 100 years, *Global Change Biol.*, 10(12), 2109- 2120, doi:10.1111/j.1365-2486.2004.00869.x.

- Saurer, M., et al. (2014), Spatial variability and temporal trends in water-use efficiency of European forests, *Global Change Biol.*, 20(12), 3700– 3712, doi:10.1111/gcb.12717.
- Scheiter, S., L. Langan, and S. I. Higgins (2013), Next-generation dynamic global vegetation models: Learning from community ecology, *New Phytol.*, 198(3), 957– 969, doi:10.1111/nph.12210.
- Schmid, H. P., C. S. B. Grimmond, F. Cropley, B. Offerle, and H. B. Su (2000), Measurements of CO₂ and energy fluxes over a mixed hardwood forest in the mid-western United States, *Agric. For. Meteorol.*, 103(4), 357– 374, doi:10.1016/S0168-1923(00)00140-4.
- Schymanski, S. J., and D. Or (2015), Wind increases leaf water use efficiency, *Plant Cell Environ.*, 39(7), 1448– 1459, doi:10.1111/pce.12700.
- Sellers, P. J. (1997), Modeling the exchanges of energy, water, and carbon between continents and the atmosphere, *Science*, 275(5299), 502– 509, doi:10.1126/science.275.5299.502.
- Sen, P. K. (1968), Estimates of the regression coefficient based on Kendall's tau, *J. Am. Stat. Assoc.*, 63(324), 1379– 1389, doi:10.2307/2285891.
- Siefert, A., et al. (2015), A global meta-analysis of the relative extent of intraspecific trait variation in plant communities, *Ecol. Lett.*, 18(12), 1406– 1419, doi:10.1111/ele.12508.
- Silva, L. C. R., and M. Anand (2013), Probing for the influence of atmospheric CO₂ and climate change on forest ecosystems across biomes, *Global Ecol. Biogeogr.*, 22(1), 83– 92, doi:10.1111/j.1466-8238.2012.00783.x.
- Smith, N. G., and J. S. Dukes (2013), Plant respiration and photosynthesis in global-scale models: Incorporating acclimation to temperature and CO₂, *Global Change Biol.*, 19(1), 45– 63, doi:10.1111/j.1365-2486.2012.02797.x.
- Smith, N. G., S. L. Malyshev, E. Shevliakova, J. Kattge, and J. S. Dukes (2016), Foliar temperature acclimation reduces simulated carbon sensitivity to climate, *Nat. Clim. Change*, 6(4), 407– 411, doi:10.1038/nclimate2878.
- Stuart-Haëntjens, E. J., P. S. Curtis, R. T. Fahey, C. S. Vogel, and C. M. Gough (2015), Net primary production of a temperate deciduous forest exhibits a threshold response to increasing disturbance severity, *Ecology*, 96(9), 2478– 2487, doi:10.1890/14-1810.1.
- Sun, Y., L. Gu, R. E. Dickinson, R. J. Norby, S. G. Pallardy, and F. M. Hoffman (2014), Impact of mesophyll diffusion on estimated global land CO₂ fertilization, *Proc. Natl. Acad. Sci. U.S.A.*, 111(44), 15,774– 15,779, doi:10.1073/pnas.1418075111.
- Suni, T., J. Rinne, A. Reissell, N. Altimir, P. Keronen, Ü. Rannik, M. Dal Maso, M. Kulmala, and T. Vesala (2003), Long-term measurements of surface fluxes above a scots pine forest in Hyytiälä, southern Finland, 1996–2001, *Boreal Environ. Res.*, 8(4), 287– 301.

- Tang, X., et al. (2014), How is water-use efficiency of terrestrial ecosystems distributed and changing on Earth?, *Sci. Rep.*, 4, 7483, doi:10.1038/srep07483.
- Thum, T., T. Aalto, T. Laurila, M. Aurela, P. Kolari, and P. Hari (2007), Parametrization of two photosynthesis models at the canopy scale in a northern boreal Scots pine forest, *Tellus B*, 59(5), 874– 890, doi:10.1111/j.1600-0889.2007.00305.x.
- Tor-ngern, P., R. Oren, E. J. Ward, S. Palmroth, H. R. Mccarthy, and J. C. Domec (2015), Increases in atmospheric CO₂ have little influence on transpiration of a temperate forest canopy, *New Phytol.*, 205(2), 518– 525, doi:10.1111/nph.13148.
- Urbanski, S., C. Barford, S. Wofsy, C. Kucharik, E. Pyle, J. Budney, K. McKain, D. Fitzjarrald, M. Czikowsky, and J. W. Munger (2007), Factors controlling CO₂ exchange on timescales from hourly to decadal at Harvard Forest, *J. Geophys. Res.*, 112, G02020, doi:10.1029/2006JG000293.
- Valentini, R., J. A. Gamon, and C. B. Field (1995), Ecosystem gas exchange in a California grassland: Seasonal patterns and implications for scaling, *Ecology*, 76(6), 1940– 1952, doi:10.2307/1940725.
- Valladares, F., E. Gianoli, and J. M. Gómez (2007), Ecological limits to plant phenotypic plasticity, *New Phytol.*, 176(4), 749– 763, doi:10.1111/j.1469-8137.2007.02275.x.
- van der Sleen, P., P. Groenendijk, M. Vlam, N. P. R. Anten, A. Boom, F. Bongers, T. L. Pons, G. Terburg, and P. A. Zuidema (2014), No growth stimulation of tropical trees by 150 years of CO₂ fertilization but water-use efficiency increased, *Nat. Geosci.*, 8(1), 24– 28, doi:10.1038/ngeo2313.
- Van Dijk, A. I. J. M., et al. (2015), Rainfall interception and the coupled surface water and energy balance, *Agric. For. Meteorol.*, 214–215, 402– 415, doi:10.1016/j.agrformet.2015.09.006.
- Vickers, D., C. K. Thomas, C. Pettijohn, J. G. Martin, and B. E. Law (2012), Five years of carbon fluxes and inherent water-use efficiency at two semi-arid pine forests with different disturbance histories, *Tellus Ser. B Chem. Phys. Meteorol.*, 64(1), 1– 14, doi:10.3402/tellusb.v64i0.17159.
- Wang, Y. P., X. J. Lu, I. J. Wright, Y. J. Dai, P. J. Rayner, and P. B. Reich (2012), Correlations among leaf traits provide a significant constraint on the estimate of global gross primary production, *Geophys. Res. Lett.*, 39(19), L19405, doi:10.1029/2012GL053461.
- Ward, E. J., R. Oren, D. M. Bell, J. S. Clark, H. R. McCarthy, H. S. Kim, and J. C. Domec (2013), The effects of elevated CO₂ and nitrogen fertilization on stomatal conductance estimated from 11 years of scaled sap flux measurements at Duke FACE, *Tree Physiol.*, 33(2), 135– 151, doi:10.1093/treephys/tps118.

- Warren, J. M., A. M. Jensen, B. E. Medlyn, R. J. Norby, and D. T. Tissue (2015), Carbon dioxide stimulation of photosynthesis in *Liquidambar styraciflua* is not sustained during a 12-year field experiment, *AoB Plants*, 7(1), plu074, doi:10.1093/aobpla/plu074.
- Way, D. A., R. Oren, and Y. Kroner (2015), The space-time continuum: The effects of elevated CO₂ and temperature on trees and the importance of scaling, *Plant Cell Environ.*, 38(6), 991– 1007, doi:10.1111/pce.12527.
- Wehr, R., J. W. Munger, J. B. McManus, D. D. Nelson, M. S. Zahniser, E. A. Davidson, S. C. Wofsy, and S. R. Saleska (2016), Seasonality of temperate forest photosynthesis and daytime respiration, *Nature*, 534(7609), 680– 683, doi:10.1038/nature17966.
- Wohlfahrt, G., and L. Gu (2015), The many meanings of gross photosynthesis and their implication for photosynthesis research from leaf to globe, *Plant Cell Environ.*, 38(12), 2500– 2507, doi:10.1111/pce.12569.
- Wullschlegel, S. D., C. A. Gunderson, P. J. Hanson, K. B. Wilson, and R. J. Norby (2002a), Sensitivity of stomatal and canopy conductance to elevated CO₂ concentration—Interacting variables and perspectives of scale, *New Phytol.*, 153(3), 485– 496, doi:10.1046/j.0028-646X.2001.00333.x.
- Wullschlegel, S. D., T. J. Tschaplinski, and R. J. Norby (2002b), Plant water relations at elevated CO₂—Implications for water-limited environments, *Plant Cell Environ.*, 25(2), 319– 331, doi:10.1046/j.1365-3040.2002.00796.x.
- Xue, B.-L., Q. Guo, A. Otto, J. Xiao, S. Tao, and L. Li (2015), Global patterns, trends, and drivers of water use efficiency from 2000 to 2013, *Ecosphere*, 6(10), 174, doi:10.1890/ES14-00416.1.
- Yin, X. (2002), Responses of leaf nitrogen concentration and specific leaf area to atmospheric CO₂ enrichment: A retrospective synthesis across 62 species, *Global Change Biol.*, 8(7), 631– 642, doi:10.1046/j.1365-2486.2002.00497.x.
- Zhou, S., B. Yu, Y. Huang, and G. Wang (2015), Daily underlying water use efficiency for AmeriFlux sites, *J. Geophys. Res. Biogeosci.*, 120, 887– 902, doi:10.1002/2015JG002947.
- Zhou, S. X., B. E. Medlyn, and I. C. Prentice (2016), Long-term water stress leads to acclimation of drought sensitivity of photosynthetic capacity in xeric but not riparian Eucalyptus species, *Ann. Bot.*, 117(1), 133– 144, doi:10.1093/aob/mcv161.
- Zscheischler, J., et al. (2016), Short-term favorable weather conditions are an important control of interannual variability in carbon and water fluxes, *J. Geophys. Res. G Biogeosci.*, 121, 2186– 2198, doi:10.1002/2016JG003503.