Changes in the Shadow: the Shifting Role of Shaded Leaves in Global Carbon and Water Cycles under Climate Change

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Key points:

- Shaded leaves in tropical forests mitigate the adverse warming effect.
- Global GPP from shaded leaves is less susceptible to climate extremes.
- Clumped structure of boreal canopies is an unfavorable attribute to warming-induced GPP increase.

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Abstract

Globally shaded leaves contribute to more than a half of the total increase in GPP (7.6 Pg C) for 1982-2016. During 1982-2016, the fraction of shaded GPP increases by 1.1% (p<0.01) in tropical forests, and decreases by 1.4% (p<0.01) and 1.8% (p<0.01) in evergreen needleleaf and deciduous needleleaf boreal forests, respectively, suggesting an ecological niche of certain canopy structure for ecosystems to achieve maximum GPP. Unlike transpiration from sunlit leaves that has a turning point in the trend in 2003, global transpiration from shaded leaves steadily increased at the rate of 34 km^3 yr^{-1} (p<0.0001) during 1982-2016. Our study, therefore, suggests that shaded leaves have an increasing role in buffering the adverse impact of climate change and extremes. Further studies are still needed to reduce the uncertainties in reported trends arisen from climate forcing data, leaf area index and land cover and land change products.

1. Introduction

In 1982 to 2016, the global land surface air temperature has increased by 0.79°C (GISTEMP, 2017; Hansen, Ruedy, Sato, & Lo, 2010). The warming trend continues with large uncertainties associated to human's commitment to reduce carbon emission (Millar et al., 2017). Global warming with CO_2 fertilization (Drake, Hanson, Lowrey, & Sharp, 2017), regional increase of droughts and heatwaves (Mazdiyasni & AghaKouchak, 2015; Williams, 2014; Y. Zhang et al., 2016) and aerosol emissions (Landry, Partanen, & Matthews, 2017; Lu, Chen, Liu, Miralles, & Wang, 2017) have led to significant impacts on terrestrial ecosystem's structure, function and evolution (Maestre et al., 2016; McCluney et al., 2012; Pecl et al., 2017; Soliveres, Smit, & Maestre, 2015; Vazquez, Gianoli, Morris, & Bozinovic, 2017). Plant photosynthesis and transpiration are primary functions of an ecosystem, and their variations at different spatio-temporal scales are needed to understand the impacts of climate change on terrestrial ecosystems.

Carbon (C) assimilation through photosynthesis is tightly coupled with transpiration through stomata at the leaf level (Wolz, Wertin, Abordo, Wang, & Leakey, 2017). Radiation, ambient air temperature, and transpiration together determine leaf temperature, which in turn affects the leaf photosynthetic capacity through altered carboxylation rate. The sunlit portion of a canopy receives both direct and diffuse radiation, while shaded leaves receive only diffuse radiation for photosynthesis; therefore, the temperature of shaded leaves is usually a few degrees lower than that of sunlit leaves (Spayd, Tarara, Mee, & Ferguson, 2002). Systemic change in leaf temperature can significantly affect the C assimilation and transpiration (Amissah, Mohren, Kyereh, & Poorter, 2015; Martins et al., 2014; Quero, Villar, Maranon, & Zamora, 2006). For example, shading a canopy from the sun was found to be effective for photo-inhibition mitigation and water use efficiency improvement (Alarcon, Ortuno, Nicolas, Navarro, & Torrecillas, 2006; Montanaro, Dichio, & Xiloyannis, 2009; Sofo, Dichio, Montanaro, & Xiloyannis, 2009). Rising temperature leads to increases in stomatal conductance and transpiration, which in turn may result in reduction of leaf temperature (J. Urban, M. Ingwers, M. A. McGuire, & R. O. Teskey, 2017; J. Urban, M. W. Ingwers, M. A. McGuire, & R. O. Teskey, 2017). Due to the complexity of canopy structure (Ashton & Berlyn, 1992; de Casas et al., 2011; Keenan & Niinemets, 2017; Valladares, Laanisto, Niinemets, & Zavala, 2016), it is expected that the same climate change may cause opposite consequences to the shaded and sunlit parts of an ecosystem, depending on the location of biomes and structure of a canopy (Supplementary Information, SI; Figure S1).

Advanced ecosystem models separate the calculation of C assimilation and transpiration for sunlit and shaded leaves (Bonan, Williams, Fisher, & Oleson, 2014; J. M. Chen, Liu, Cihlar, & Goulden, 1999; Dai, Dickinson, & Wang, 2004; Jiang & Ryu, 2016) assuming a canopy is stratified into representative sunlit and shaded leaf groups. For each group, a leaf-level photosynthesis model is used to calculate the coupled C and water fluxes (Ball, Woodrow, & Beny, 1987; Farquhar, Caemmerer, & Berry, 1980). The canopy-level flux is then taken as the total fluxes from sunlit and shaded leaf groups. The separation of C and water fluxes into their sunlit and shaded components enable us to diagnose the nonlinear effects of climate change on global C and water cycles (Bin Chen et al., 2016; J. M. Chen et al., 2012; Mao et al., 2015; Y. Q. Zhang et al., 2016). Stratification of canopy into two or more layers optimizes the modeling of carbon-water coupling for improving fluxes estimation (Luo et al., 2018). For example, a multi-layer model was used to find the optimal canopy structure to achieve maximum crop productivity without change in water use or albedo (Drewry, Kumar, & Long, 2014).

Although a great number of global estimates of the two largest fluxes in terrestrial ecosystems, gross primary production (GPP) and evapotranspiration (ET), are currently available, they do not converge on spatial distributions nor in long-term trends (Anav et al., 2015; Beer et al., 2010; M. Chen et al., 2017; L. He, Chen, Liu, Bélair, & Luo, 2017; L. M. He et al., 2017; Jiang & Ryu, 2016; M. Jung et al., 2010; Martin Jung et al., 2011; Knauer et al., 2017; Mao et al., 2015; Mu, Zhao, & Running, 2011; Zeng et al., 2012; Y. Q. Zhang et al., 2016). So far, no analysis has been conducted on the trends of GPP and ET components for sunlit and shaded leaf groups. Therefore, our analysis could reconcile some of the differences in the existing GPP and ET products. The objective of this study is to investigate the shifting roles of shaded and sunlit components of C and water fluxes under recent climate change. Specifically, we focus on the shaded part of these fluxes that are often considered as less important.

2. Materials and methods

We use a two-leaf model, namely the boreal ecosystem productivity simulator (BEPS) to calculate the coupled GPP and ET components at an hourly time-step (Baozhang Chen, Chen, & Ju, 2007; J. M. Chen et al., 1999; J. M. Chen et al., 2012; L. He et al., 2014; Ju et al., 2006; J. Liu, Chen, Cihlar, & Park, 1997). MERRA-2 (Modern-Era Retrospective Analysis for research and Applications, Version 2) data from GSFC, NASA are used to drive BEPS to simulate GPP and ET in 1981.7-2016.12 (Gelaro et al., 2017). The data have a spatial resolution of 0.625° (longitude) by 0.5° (latitude) and a temporal resolution of one hour. To drive BEPS, relative humidity, wind speed, and air temperature at 2 m above the surface, surface atmosphere pressure and incoming solar shortwave flux, and total precipitation at the surface level are spatially interpolated to the global 36 km EASE-Grid 2.0.

Two global leaf area index (LAI) products are used in this study. The first LAI product is a long-term consistent global LAI product (1981-2016, Version 3) that is retrieved from combined Advanced Very High Resolution Radiometer (AVHRR) and Moderate-resolution imaging spectroradiometer (MODIS) datasets (Liu, Liu, & Chen, 2012). This product is general referred to as GLOBMAP (Zhu et al., 2016). In Version 3, LAI from MODIS (Collection 6) has been corrected for sensor degradation and reprocessed using a new cloud screening algorithm (Y. Liu, Liu, & Chen, 2012). The second LAI product is the Global Inventory Modeling and Mapping Studies (GIMMS) LAI3g that is produced using only AVHRR data (Zhu et al., 2013). The root-mean-square errors (RMSEs) for the two products are 0.81 and 0.68 LAI unit, for GLOBMAP and GIMMS LAI3g, respectively. The LAI data are also re-projected to the 36 km resolution.

In BEPS, the canopy-level photosynthesis (A_{canopy}) is calculated as the sum of photosynthesis of sunlit and shaded leaf groups (J. M. Chen et al., 1999):

$$A_{canopy} = A_{sun} \cdot L_{sun} + A_{sh} \cdot L_{sh} \tag{1}$$

where the subscripts "sun" and "sh" denote the sunlit and shaded components of the photosynthesis (A) and LAI (L). The canopy-level ET is obtained as the sum of Transpiration (T) and Evaporation (E):

$$ET = T_{sun} \cdot L_{sun} + T_{sh} \cdot L_{sh} + E_l + E_g \tag{2}$$

where E_l and E_g are evaporation rates of intercepted water from canopy and ground surface, respectively.

The temperature response function of maximum carboxylation rate (V_{cmax}), the separation of sunlit and shaded LAI, the calculation of radiation and leaf temperature for each leaf group, and more detailed descriptions of the model and data are provided in the SI (Baldocchi, 1994; dePury & Farquhar, 1997; Friedl et al., 2002; L. He, Chen, Pisek, Schaaf, & Strahler, 2012; L. M. He et al., 2016; Matsushita & Tamura, 2002; Matsushita, Xu, Chen, Kameyama, & Tamura, 2004; Medlyn et al., 1999; Monteith, 1965; Norman, 1982; Rienecker et al., 2011; Sellers et al., 1996; Sitch et al., 2008; Wang et al., 2004).

The BEPS simulated GPP is validated against eddy covariance measurements from 124 flux tower sites (FLUXNET2015 Dataset in Tier 1; http://fluxnet.fluxdata.org/) at the site level. Validation suggests that BEPS simulates annual GPP well with a coefficient of determinations (R^2) of 0.81, a RMSE of 347 g C m^{-2} yr^{-1}, and a bias of 172 g C m^{-2} yr^{-1} (Figure S2).

3. Results and discussion

In the following sections, we present trends of GPP and ET components using the Mann-Kendall test for the timeframe of 1982-2016. We report the result based on GLOBMAP LAI product unless otherwise specified. In the following content, we report the averages of GPP and ET estimates along their one standard deviations (mean ± 1 std) in 1982-2016. This one std does not indicate an uncertainty estimate against observations; instead, it provides a relative change in the time series.

3.1 The shift of global and regional GPP from the shaded leaf group

With the GLOBMAP LAI (V3), the BEPS-simulated global GPP increases from 119.1 Pg C in 1982 yr^{-1} to 133.2 Pg C yr^{-1} in 2016 with an average of 124.4±4.3 Pg C yr^{-1} and a trend of 0.38 Pg C yr^{-1} ($p<0.01$) (Figure 1); these estimates are close to recent report with a trend of 0.39 Pg C yr^{-1} (2000-2016) and a global GPP in 129.4 Pg C $year^{-1}$ in 2016 (Y. Zhang et al., 2017). Comparing to simulation using GLOBMAP LAI V2, the annual GPP estimates are consistently larger by 3 Pg C yr^{-1} in 1982-2004, and since 2005, there is a significant growth in GPP driven by the LAI V3 with MODIS sensor degradation corrected (Figure S3). The consistent increase in simulated GPP is due to the removal of cloud-contaminated LAI retrievals that usually have low values. The growth in GPP driven by LAI V3 since 2005 is corresponding to the recent C budget imbalance (Figure S3) that is unexplained by other earth system models (Le Quéré et al., 2017).

The sunlit GPP increases from 69.1 Pg C yr^{-1} in 1982 to 75.6 Pg C yr^{-1} in 2016 with an average of 71.4±3.3 Pg C yr^{-1} and a trend of 0.189 Pg C yr^{-1} ($p<0.01$), while the shaded GPP increases from 50.0 Pg C yr^{-1} to 57.6 Pg C yr^{-1} with an average of 53.0±2.1 Pg C yr^{-1} and a trend of 0.192 Pg C yr^{-1} ($p<0.01$). The fraction of shaded-to-total GPP increases from 42.0% to 43.2% with a trend of 0.02% yr^{-1} ($p<0.01$) during the same time frame. The shaded GPP fractions are slightly larger than the 39% found in a previous study (J. M. Chen et al., 2012). This change is due to an increase of understory LAI in BEPS according to Y. Liu, Liu, Pisek, and Chen (2017). Although the shaded GPP constitutes to less than a half of the total GPP, it contributes to more than a half of the total GPP increase (7.63 of 14.1 Pg C) since 1982, suggesting its increasing role in the global C cycle and budget.

There are considerable divergence among land cover types in terms of the fractions and trends of shaded GPP (Figure 1). Generally, shaded GPP contributes more to total GPP in forest ecosystems because of their large LAI (i. e., 55.2±0.6%, 57.2±0.5%, 55.1±0.98%, and 48.6±0.4% for evergreen needle leaf forest (ENF), evergreen broadleaf forest (EBF), deciduous needleleaf forest (DNF), and deciduous broadleaf forest (DBF), respectively). Whereas, shaded GPP contributes less in the remaining terrestrial ecosystems (i. e., 12.5±0.6%, and 21.4±1.4% for Shrub&Grass and Crops, respectively). In EBF, the fraction of shaded GPP has negligible change, while the shaded fractions in EBF (0.03% yr^{-1}, $p<0.01$), Shrub & Grass (0.05% yr^{-1}, $p<0.01$), and Crops (0.13% yr^{-1}, $p<0.01$) follow increasing trends, and the shaded fractions in boreal forest have decreasing trends (-0.04% yr^{-1}, $p<0.01$, and -0.05% yr^{-1}, $p<0.01$ for ENF and DNF, respectively).

Two major drivers may lead to the shift in the shaded fraction of total GPP (Figure S1). The first is related to climate change. For example, an increase in air temperature near the surface causes an increase in leaf temperature, which may lead to increased or reduced shaded GPP fraction depending on the leaf temperature, i.e., below or above the optimal photosynthesis temperature. In BEPS, a Boltzmann distribution is used to adjust the temperature responses of V_{cmax} and the maximum rate of electron transport (J_{max}) for photosynthesis (Baldocchi, 1994) (Figure S1). Another driver is the change in LAI. When LAI is small (e.g., less than 1.5), the increase of LAI mostly contributes to an increase in sunlit LAI; while most of the increased LAI is shaded when the canopy is dense (Figure S1). Therefore, an increase of LAI may lead to different trends in the shaded GPP fractions. The causes of LAI changes may be CO_2 fertilization and/or nutrient availability. These two drivers may be coupled in an ecosystem. Therefore, we only report the integral changes in the shaded GPP fraction in this letter and leave the quantitative attribution of drivers for subsequent studies.

In tropical rainforests located at Amazon and central Africa, we found declining sunlit GPP trends which were compensated by increasing shaded GPP trends (Figure S4). The decline of sunlit GPP is unlikely due to reduction in LAI since the LAI in these regions is as high as eight. Therefore, climate change (e.g., warming) may be the driver for this decline (Peñuelas et al., 2017). The increases of the shaded GPP trend and its fraction (Figure 2) suggest that the shaded leaf group offsets the decline of sunlit GPP and plays an increasing role in mitigating the adverse warming effect in the tropical area (Brienen et al., 2015). The increase in the shaded GPP fraction also provides a niche for a potential evolution in canopy structure in the tropical forests that have already been observed (Cernusak et al., 2013; Cusack et al., 2016; Feeley, Davies, Perez, Hubbell, & Foster, 2011; Feeley, Hurtado, Saatchi, Silman, & Clark, 2013; Morueta-Holme et al., 2015; Slot & Winter, 2016). In the near future, if climate warming continues, the rainforests will be exposed to air temperatures that are even higher than the optimal temperature for photosynthesis (Cavaleri, Reed, Smith, & Wood, 2015; Peñuelas et al., 2017). Our study suggests that a more clumped canopy structure (with more shaded leaves) is in favor of tropical ecosystem productivity and provides resilience to over-warming in the future. The trend in the fraction of shaded GPP in south Asian tropical forests is insignificant, suggesting that it may also be affected by other drivers (e.g., nitrogen deposition due to agricultural fertilizer use).

In DNF and ENF boreal forests, we found that the trend of sunlit GPP is positive while the trend of shaded GPP is close to neutral (Figure S4), suggesting that climate warming at high latitudes has more effect on sunlit leaves than on shaded leaves. Boreal conifers have adapted to the cold climate with narrow conical tree crowns to shed snow in winter, and their evergreen needles have an advantage in maximizing the growing season length in the cold climate. However, the clumped canopy structure reduces the fraction of leaves exposed to direct sunlight (i. e., sunlit leaves). Under global warming, this cold adaptation of boreal conifer canopies could lose out to deciduous forests that have less clumped canopies to receive more direct sunlight. Our study helps explain the observed northward shift of boreal forests (Boulanger et al., 2017; Girardin et al., 2016; Savage & Vellend, 2015).

The variations of annual global GPP and ET are strongly modulated by El Niño-Southern Oscillation (ENSO) that causes climate extremes (Cavaleri et al., 2017). By separating shaded from sunlit GPP, we found that both absolute and relative variations of shaded GPP are less than that of sunlit GPP (0.83 Pg C, or 1.5% for shaded GPP, and 1.34 Pg C, or 1.9% for sunlit GPP, in terms of one standard deviation, after their linear trends are removed from their time series), suggesting that shaded GPP is less affected by ENSO.

3.2 The accompanied change in shaded ET

There are large discrepancies of the global ET estimates, in terms of their trends and variabilities (Anabalon & Sharma, 2017; Dong & Dai, 2017; Shi, Mao, Thornton, & Huang, 2013; Ukkola & Prentice, 2013; Zeng et al., 2014), the reported trends can also be affected by the starting and ending years (Zeng et al., 2012). Separating the ET components help to identify their different drives under climate change (Y. Q. Zhang et al., 2017) and reconcile the differences among ET products; for example, rising CO_2 improves water use efficiency (WUE) and yields decreasing trend in canopy transpiration (Mao et al., 2015; Y. Q. Zhang et al., 2016), while this decreasing trend may be compensated by the Earth's greening (Zeng et al., 2016). The trivial and divergent trends of global ET products may be attributed to uncertainties in fractions of ET components.

In this study, the global ET simulated by BEPS (Figure 1 and Figure S5) decreases from 64.4×10^3 km^3 yr^{-1} in 1982 to 63.6 $\times10^3$ km^3 yr^{-1} in 2016 with an average of $62.5\pm1.0\times10^3$ km^3 yr^{-1} and an insignificant trend of -0.015×10^3 km^3 yr^{-1} ($p=0.46$). The ET estimates in the first few years may be affected by model spin-up. Our simulation is close to the estimate (63.2×10^3 km^3 yr^{-1} in 1982-2012) by observation-driven Penman-Monteith-Leuning (PML) model (Y. Q. Zhang et al., 2016). Using PML model as reference, our simulation has a R^2 of 0.89, uRMSE of 107 mm yr^{-1}, and bias of -29.9 mm yr^{-1}. While this global trend is insignificant, we found that the trends of ET components are much clear: the global evaporation decreases from 26.9×10^3 km^3 yr^{-1} in 1982 to 24.7×10^3 km^3 yr^{-1} in 2016 with an average of $25.0\pm0.7\times10^3$ km^3 yr^{-1} and a trend of -0.038×10^3 km^3 yr^{-1} ($p<0.01$); the global transpiration increases from 37.4×10^3 km^3 yr^{-1} in 1982 to 38.9×10^3 km^3 yr^{-1} with an average of $37.6\pm0.6\times10^3$ km^3 yr^{-1} and a trend of 0.021×10^3 km^3 yr^{-1} ($p<0.05$). Transpiration accounts for 60.2% of global ET from our simulation, similar to the value (61%) estimated from a compilation of 81 studies (Schlesinger & Jasechko, 2014), the estimate (64%) by Good, Noone, and Bowen (2015), and the estimate (57.2%) by Wei et al. (2017). Should the ratio of transpiration from our simulation have more weight, the estimated global ET trend can be reversed. Our study echoes the result by Y. Q. Zhang et al. (2016), which show opposing trends in E and T. Therefore, we suggest that both the ratio and the trends of ET components are reported in future studies.

Separating global transpiration for the sunlit and shaded leaf groups (T_s and T_{sh}) reveals even more information: the T_s and T_{sh} also show opposite trends (Figure 1). T_s decreases from 22.1×10^3 km^3 yr^{-1} in 1982 to 21.8×10^3 km^3 yr^{-1} in 2016 with an average of $21.6\pm0.4\times10^3$ km^3 yr^{-1} and a trend of -0.015×10^3 km^3 yr^{-1} ($p<0.05$); while the T_{sh} increases from 15.3×10^3 km^3 yr^{-1} in 1982 to 17.2×10^3 km^3 yr^{-1} in 2016 with an average of $16.0\pm0.5\times10^3$ km^3 yr^{-1} and a trend of 0.034×10^3 km^3 yr^{-1} ($p<0.01$). Globally, forests with large LAI values contribute most of the ET. Since sunlit LAI in forests is less sensitive to the Earth's greening, the decreasing trend of T_s may be more attributed to improved WUE due to rising CO_2. Accompanying the growing of shaded GPP, shaded leaves contribute most of the increasing trend in global transpiration; the greening may contribute more than WUE for the increasing T_{sh} trend.

Notably, the significance of T_s trend ($p<0.05$) is less than that of T_{sh} ($p<0.01$). Separating between T_s and T_{sh} enables us to find an important turning point (year 2003) in the time series of T_s as suggested by M. Jung et al. (2010) due to limited soil moisture supply: T_s decreases significantly from 1982 to 2003 (-0.037×10^3 km^3 yr^{-1}, $p<0.01$) and also increases significantly since then (0.065×10^3 km^3 yr^{-1}, $p<0.01$), while T_{sh} has a consistent increasing trend in 1982-2016. Therefore, the turning point, connecting two significant but opposite trends, explains the low significance of T_s trend. The turning point in T_s is also useful to reconcile the global ET trends from different ET products: the sign of ET trend may change depending on the starting and ending years of a specific period in different studies. There is no turning point in T_{sh} due to the same soil moisture supply; possible reasons include (1) transpiration from shaded leaf is less affected by water stress (Barradas, Nicolas, Torrecillas, & Alarcon, 2005; Nicolas et al., 2008; Pepin, Livingston, & Whitehead, 2002), and (2) strong greening trend in LAI has more effect on shaded leaves and overrides the turning point in T_{sh}. Clearly, T_{sh} dominates the increasing trend of the total T. In contrast to GPP, we found that T_{sh} (0.39×10^3 km^3, or 2.5%) has larger inter-annual variations than T_s (0.35×10^3 km^3, or 1.6%) after the linear trend is removed.

The fraction of global transpiration (T divided by ET) increases from 41.0% in 1982 to 44.1% in 2016 with an average of 42.5±1.0% and an increasing trend of 0.07% yr^{-1} ($p<0.01$). The fraction of T_{sh} (T_{sh} divided by T) is similar to the fraction of shaded GPP (Figure 1). The fractions of T_{sh} are 51.4±0.7%, 56.1±1.3%, 52.1±1.0%, 48.0±0.7%, 14.8±0.7%, and 23.6±1.4% for ENF, EBF, DNF, DBF, Shrub&Grass, and Crops, respectively. The change in the trend of the fraction of T_{sh} is insignificant for ENF ($p=0.16$) and DNF ($p=0.86$) in boreal forests (Figure S6). All other land cover types show an increasing trend of T_{sh} (0.09% yr^{-1} and $p<0.01$, 0.04% yr^{-1} and $p<0.01$, 0.06% yr^{-1} and $p<0.01$, and 0.13% yr^{-1} and $p<0.01$ for EBF, DBF, Shrub&Grass, and Crops, respectively). Similar to the increasing trend of the fraction of shaded GPP, our study suggests that T_{sh} also has an increasing role in the global water cycle.

3.3 Uncertainties

Climate reanalysis data are the outputs of an Earth system models that assimilate various archived observations. Global reanalysis data are the best available datasets for this study. Recent validation suggests that MERRA2 datasets have relative small errors comparing to a few other reanalysis datasets (Draper, Reichle, & Koster, 2018; Eyre & Zeng, 2017; Reichle, Draper, et al., 2017; Reichle, Liu, et al., 2017; Simmons et al., 2017). However, further studies are still needed to reduce the uncertainties of trend analysis from forcing data.

The GPP and ET trends may also be affected by different LAI products. In this study, we compared the result based on GLOBMAP LAI to simulation based on GIMMS LAI3g. We found consistent results except at conifer forests (Figures S7-S12). Compared to other land covers, the conifer forests have one extra clumping effect at the shoot level (J. M. Chen, Rich, Gower, Norman, & Plummer, 1997). The clumping above shoot-level is explained in the GLOBMAP using a clumping index map (L. He et al., 2012), while this effect is uncorrected in the LAI3g product yet. Therefore, we found that the ratio of shaded GPP from conifers based on LAI3g is less than that simulated using GLOBMAP. Corresponding, we found that ratios of shaded GPP in ENF and DNF are still in decreasing trends, but the trends are insignificant from LAI3g product.

4. Conclusions

The changing ambient temperature and CO_2 concentration, together with radiation and water and nutrient availability, can greatly alter C and water fluxes in terrestrial ecosystems. Exposed to diffuse radiation only, the shaded part of a canopy has lower temperature than the sunlit part; therefore, shaded and sunlit leaves will have different responses to climate change. We used a two-leaf modeling approach to investigate the changing role of shaded leaves under climate change in terms of photosynthesis and transpiration during 1982-2016. We found that globally shaded leaves contribute 42.6±0.4% of the total gross primary production (GPP) (124.4±4.3 Pg C yr^{-1}). However, shaded GPP and sunlit GPP share a similar increasing trend (0.19 Pg C yr^{-1}, $p < 0.01$); therefore, shaded leaves contribute to half the total GPP increase (7.6 Pg C) during the 35-year period. Due to different dependence of leaf temperature on V_{cmax}, the proportion of shaded GPP increases in tropical forests (0.03% yr^{-1}, $p<0.01$) and decreases in boreal forests (-0.04% yr^{-1} for evergreen needleleaf forests with $p<0.01$ and -0.05% yr^{-1} for deciduous needleleaf forests with $p<0.01$), suggesting a potential shift in canopy structure for ecosystems to achieve maximum GPP. By differentiating transpiration between shaded (T_{sh}) and sunlit leaves (T_s), we identified that T_{sh} has an increasing trend of 0.034×10^3 km^3 yr^{-1} ($p<0.01$), while T_s has a sharp turning point in the trend due to change of moisture supply, with a decreasing trend of -0.037×10^3 km^3 yr^{-1} ($p<0.01$) in 1982-2003, followed by an increasing trend of 0.065×10^3 km^3 yr^{-1} ($p<0.01$) in 2004-2016. According to our simulation, global GPP from shaded leaves is less susceptible to climate warming, compared to their sunlit counterparts. Our study clearly suggests that the shaded leaf group has an increasing role during the last three and a half decades.

The uncertainties from the MERRA2 forcing data, LAI product and land cover and land change products, model parameters and other missing drives that may cause effects in capturing the GPP and ET trends are data source specific, difficult to quantify, and cannot be ruled out.

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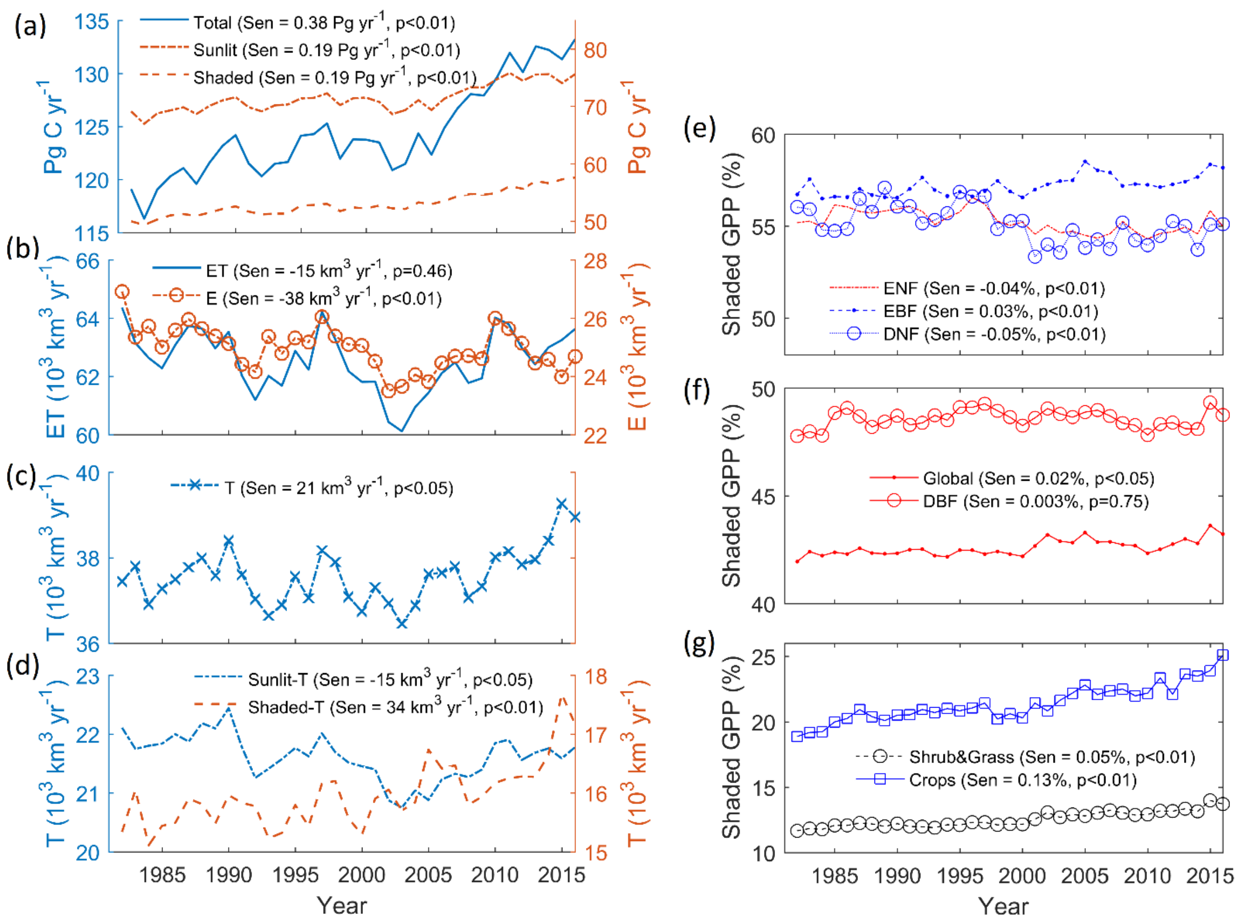

Figure 1. Time series of global gross primary production (GPP) and evapotranspiration (ET) components and the percentages of shaded GPP for different plant function types (ENF: evergreen needle leaf forest; EBF: evergreen broadleaf forest; DNF: deciduous needle leaf forest (DNF); DBF: deciduous broadleaf forest). (a) global total GPP, GPP estimates from the sunlit- and shaded- groups, respectively. (b) and (c) global total ET, evaporation (E), and transpiration (T). (d) transpirations from the sunlit- and shaded- leaf groups. (e) to (f) percentages of shaded GPP for different PFTs. "Sen" indicates Sen's slope in Mann-Kendall test. The simulation is conducted using GLOBMAP LAI product.

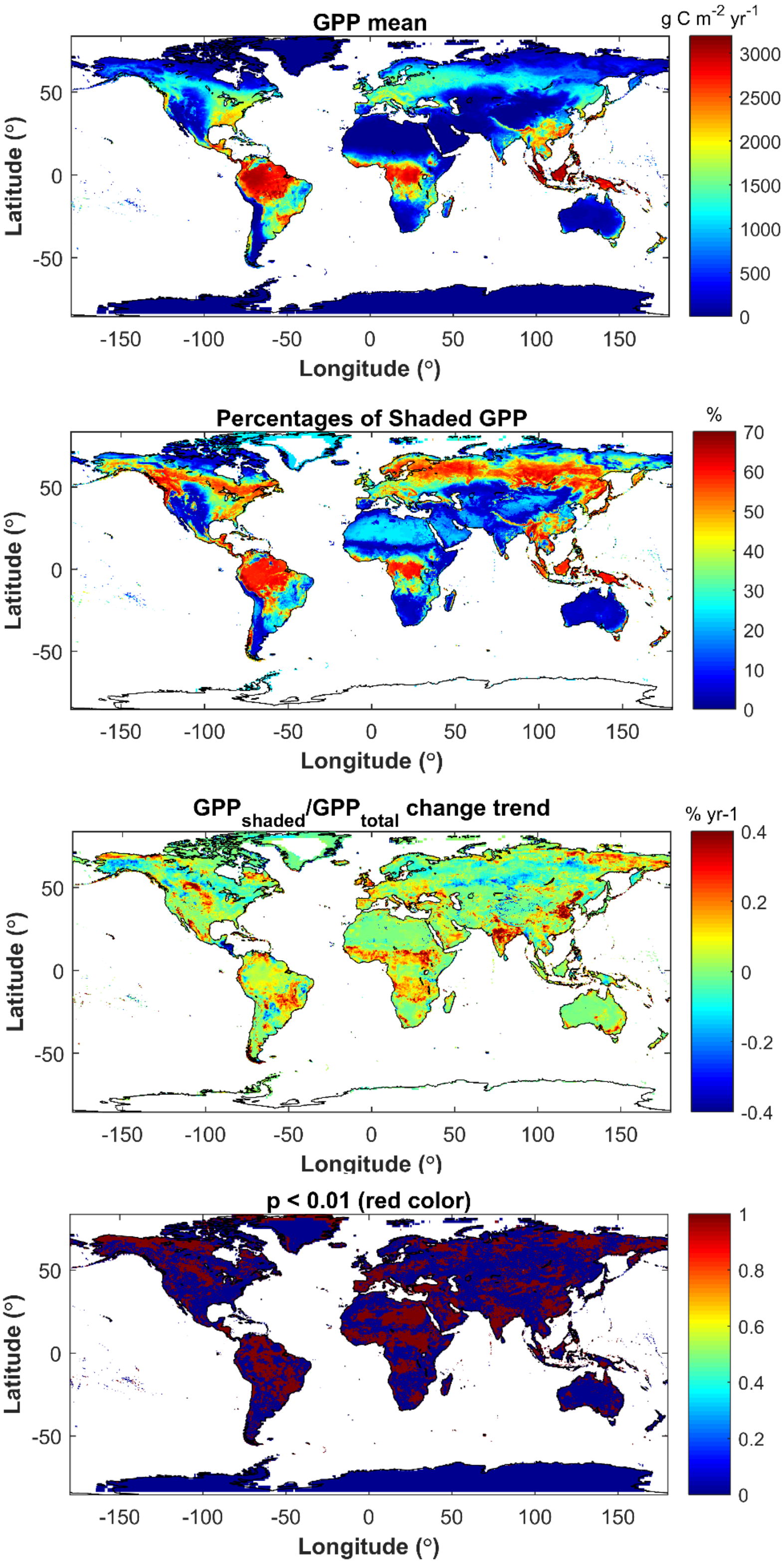

Figure 2. Global distributions of annual GPP averaged in 1982-2016 (upper panel), the percentages of shaded GPP (second panel), and the change trend in the fraction of shaded GPP and its significance (third and bottom panels), where the positive trend indicates that the fraction of shaded GPP is increasing (the third panel). The simulation is conducted using GLOBMAP LAI product.