

Water balance of pine forests: Synthesis of new and published results

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ABSTRACT

The forest hydrologic cycle is expected to have important feedback responses to climate change, impacting processes ranging from local water supply and primary productivity to global water and energy cycles. Here, we analyzed water budgets of pine forests worldwide. We first estimated local water balance of forests dominated by two wide-ranging species: *Pinus taeda* (36 °N) and *Pinus sylvestris* (64 °N). In these stands, growing season evapotranspiration (E_T) was largely insensitive to inter-annual variation of precipitation (P), consistent with the insensitivity of canopy transpiration to P . Extending the analyses to include published data from 117 studies on 27 pine species, we found that pine forests annually use $\sim 66\% \pm 17\%$ (SD) of P as E_T , regardless of climatic regime, leaving a third of P as runoff to downstream aquatic ecosystems and users. However, during the growing season, pine forests used more water as E_T than P in regions where $P \leq 326 \pm 39$ (SE) mm. Forests in regions of low growing season P exist in their current state only where the rooting depth is sufficient to supply trees with water from soil storage in addition to P , and these forests are likely to support only ephemeral streams that dry down during the growing season. Thus, globally, water use by pine forests is adapted to mean annual P , but shows a limited capacity to respond to inter-annual variability in P . Forests with a small buffer of growing season water availability ($P +$ soil water storage - E_T), are likely to be most sensitive to variation in P regimes, changing canopy leaf area, tree density, and species composition depending on the degree, direction and persistence of the change in P .

1. Introduction

Global climate change impacts on precipitation (P) and temperature regimes may alter forest water budgets (Wullschleger and Hanson, 2006). Across the globe, plants greatly affect evapotranspiration (E_T), the total amount of water evaporated from terrestrial ecosystems to the atmosphere, by regulating transpiration (Jasechko et al., 2013). Forest evapotranspiration (E_T) can be divided into four components: canopy transpiration (E_C), transpiration from the understory vegetation, soil evaporation and evaporation of precipitation intercepted by canopy (I_C). Despite a number of studies reporting estimates of these components, E_T partitioning into its sources is still uncertain. For example, canopy wetness may dominate the above-canopy water flux, but the degree to which E_C and I_C contribute to E_T is largely determined by canopy openness and rainfall patterns (Barbour et al., 2005). In closed-

canopy forests, overstory tree transpiration usually dominates E_T since limited energy is available below the canopy to evaporate soil water (Wullschleger et al., 1998). In open-canopy forests, however, large contributions from the subcanopy components have been reported (Unsworth et al., 2004; Barbour et al., 2005).

In the forest hydrologic cycle, incoming P is coarsely partitioned into E_T , outflow and additions to soil water storage. In areas where incoming P includes appreciable amount of snowfall during the non-growing season, melting snow may contribute to recharging soil water in the early part of the growing season (if the soil was not already saturated in the fall), but contributes little to E_C and E_T compared to growing season rainfall. Because E_T determines the amount of P that is available for groundwater recharge and outflow to downstream ecosystems and users, it is critical to understand how the different components of E_T contribute to its magnitude and variability. Because E_C is

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often the major component of E_T , inter-annual variation of E_T reflects the sensitivity of E_C to weather changes, and may differ among forest types at a given location. For instance, annual E_T of a *Pinus taeda* (L.) (loblolly pine) plantation has been shown to be sensitive to variation in P , while such sensitivity was not observed at nearby broadleaved deciduous stands (Phillips and Oren, 2001; Schäfer et al., 2002; Stoy et al., 2006; Oishi et al., 2010; Ford et al., 2011). Similar results have been inferred from water yield studies on intensively managed stands as compared to unmanaged controls (Swank and Douglass, 1974; Komatsu et al., 2008). It is likely that the greater demand for water to support higher E_C of these southern U.S. pine forests, compared to forests in the higher latitudes, makes them more sensitive to variation in water availability. Annual mean P is predicted to increase in high-latitude regions and decrease in some mid-latitude and subtropical dry regions (Stocker et al., 2013). Depending on the sensitivity of E_C , and thus E_T to environmental and climatic changes, variation of P may produce disproportional effects on outflow from forests (Oishi et al., 2010), with further implication for projected impacts on water and energy cycling.

The sensitivity of E_C in pine forests to annual P (Stoy et al., 2006; Ilvesniemi et al., 2010; Ford et al., 2011) reflects a sensitivity at finer temporal scale of leaf area production and loss, and stomatal response to soil moisture and vapor pressure deficit (Oren et al., 1998a,b; Oishi et al., 2010). In years of high growing season P , soil moisture is typically high, and D is low (Oishi et al., 2010). Under such conditions, it is easy for plants to extract soil moisture, and stomatal conductance is high (Oren et al., 1999; Tor-ngern et al., 2017). However, low D and net radiation reduce the driving force for evapotranspiration. In dry years, D is high and soil moisture is low, meaning that high driving force must operate against greater resistance to water uptake from the soil and lower stomatal conductance. As a result, the inter-annual variation in E_C may span a smaller relative range than those of P (Oishi et al., 2010) as long as soil moisture can supply water in addition to the limited precipitation.

Forests dominated by the genus *Pinus* are found over a wide range of environments with contrasting growing season lengths and soil texture. Species within this genus are also commonly and increasingly used in plantations worldwide (Wear and Greis, 2012), due to their high carbon uptake potential (Novick et al., 2015), which can lead to significant alterations in the provisioning of other ecosystem services such as water yield (Jackson et al., 2005). Therefore, investigating variations of water fluxes from *Pinus* spp. forests at annual and growing season scales will provide better information for assessing the likely responses of water flux components to changing precipitation.

The main objective of this study was to investigate the sensitivity of the hydrologic components of pine stands to variation in P , across latitudes, considering both growing season and annual variabilities. We began with an intensive, site-level analyses of forest water balance and its components in two sites representative of the most dominant pine species worldwide: a mid-latitude *Pinus taeda* (L.) (North Carolina, USA) and a high-latitude *Pinus sylvestris* (L.) (Northern Sweden), both growing on sandy soil, for three growing seasons. The site of the latter species included two levels of nutrient availability. Then, we combined the new results from these stands with others from published studies to evaluate the sensitivity of evaporative components to growing season and annual P supplied to global pine forests.

2. Materials and methods

2.1. Site description

The study was conducted in pine forests of contrasting nutrient availability and climate zones (for detailed stand characteristics see Supplementary Material Table S1). The *Pinus taeda* plantation (PT) in North Carolina, USA ($36^{\circ} 20'N$ $79^{\circ} 28'W$) was established in 1965, thinned in 1983, and harvested in 2006. The broadleaf understory was sparse, comprising 2% of stand basal area (Uebelherr, 2008). The soil

was well-drained sand (Johnson et al., 1995) with average bulk density and porosity (in the top 60 cm) of 1500 kg m^{-3} and 0.43, respectively. Long-term (30-year) average annual temperature and total precipitation were 15.4°C and 1189 mm (year 1983–2012; www.ncdc.noaa.gov). The growing season usually covers the months of April to September (Stoy et al., 2006).

The *Pinus sylvestris* (PS) forests in Rosinedal, Sweden ($64^{\circ} 10'N$, $19^{\circ} 45'E$) were regenerated with seed trees in 1920–1925, pre-commercially thinned in 1955 and thinned in 1976 and 1993, respectively. These forests have been used for a long-term fertilization experiment with control and fertilized stands located $\sim 2 \text{ km}$ apart. Fertilizer of $100 \text{ kg N ha}^{-1} \text{ yr}^{-1}$ was applied to the fertilized site from 2006 to 2011 and a reduced rate of $50 \text{ kg N ha}^{-1} \text{ yr}^{-1}$ has been used afterwards (Lim et al., 2015). The understory of both stands is characterized by a field layer of dwarf shrubs and a ground layer of mosses and lichens (Hasselquist et al., 2012; Palmroth et al., 2014). Both stands share similar soil texture of well-drained, deep sandy sediment with bulk density and porosity (in the top 10 cm) of 1230 kg m^{-3} (Giesler et al., 1996) and 0.49 (Lundmark and Jansson, 2009). The 30-year mean annual temperature and precipitation (1981–2010), measured at the Svartberget field station (8 km from the control PS site), were 1.8°C and 614 mm, respectively (Laudon et al., 2013). The growing season months usually range from May to October (Laudon and Ottosson-Löfvenius, 2016). Further information on the sites and stand is provided in Tor-ngern et al. (2017).

2.2. Environmental measurements

In the PT stand, air temperature (T_A , $^{\circ}\text{C}$) and relative humidity (RH, %) (HMP35C probes, Campbell Scientific, Logan, UT, USA), photosynthetically active radiation (PAR, $\mu\text{mol m}^{-2} \text{s}^{-1}$; LI-190, Li-Cor BioSciences, Lincoln, NE, USA), latent heat flux (LE, W m^{-2} ; eddy covariance system CSAT3, Campbell Scientific, Logan, UT, USA and IRGA, LI-7500, Li-Cor, Lincoln, NE, USA) and precipitation (P , mm; TE-525M, Texas Electronics, Dallas, TX, USA) were measured above the forest canopy. More details on the eddy covariance measurements are provided in Manoli et al. (2016). Sap flux measurement was conducted on 24 trees from May 2003 to August 2005 and data were used to estimating canopy transpiration of PT (Tor-ngern et al., 2017). Volumetric soil moisture across the topmost 30 cm layer of the mineral soil ($\theta_{0-30 \text{ cm}}$, $\text{m}^3 \text{ m}^{-3}$) was measured using a 30 cm long probe installed vertically (CS615 Campbell Scientific, Logan, UT, USA) at four locations. All sensors were connected to a data logger (CR23X, Campbell Scientific, Logan, UT, USA) which stored 30-minute mean (and sum in case of P) values from January 2003 to December 2005. Throughfall (P_T , mm) was collected biweekly using 10 rain gauges (Productive Alternatives, Fergus Falls, MN, USA) with a collection diameter of 0.1 m and accuracy of 0.2 mm (Schäfer et al., 2002). Sapwood area (A_S , m^2) was estimated from stem discs taken at breast height from the harvest in 2006. Hemi-surface leaf area index (L) was estimated from monthly measurements (LAI-2000, Li-Cor BioSciences, Lincoln, NE, USA) performed at 20 locations each along two perpendicular transects. We used a factor of 0.5 to convert the hemi-surface L to projected L and a correction factor of 0.59 (Thérézien et al., 2007) to account for foliage clumping (Stenberg, 1996). During the three study years, growing season average L of PT was $1.6 \pm 0.32 \text{ SD}$, similar to the annual mean of 1.76 ± 0.04 .

In Sweden, T_A and RH (HC2-S3 and MP-101A, Rotronic AG, Switzerland) were measured at 1.5 m above ground, below forest canopies, in both PS sites. These data were used to represent those above the canopy because of strong coupling between the canopy and the atmosphere and small gradient of vapor pressure deficit throughout the canopy depth in forests with low L (Ewers et al., 2000). PAR was measured above the unfertilized PS canopy (LI-190SA, Li-Cor Inc., Lincoln, USA). LE was derived from eddy-covariance measurements (R3, Gill Instruments Ltd., Lymington, UK and LI-7200, Li-Cor Inc.,

Lincoln, USA) above the canopies of both PS sites (Jocher et al., 2017), and P was measured with a tipping bucket (ARG100, Campbell Sci, Logan, UT, USA) at the top of the fertilized PS canopy. In each site, six trees were selected for sap flux measurement from July 2011 to October 2013 and data were used to calculate canopy transpiration, with additional trees added in shorter-term campaigns (Tor-ngern et al., 2017). In each of the PS sites, θ was measured using a 5 cm long probe ($\theta_{10-15\text{cm}}$; SM300, Delta-T devices Ltd., Cambridge, UK) installed at a depth of 15 to 20 cm, at one location near the eddy covariance tower, operating continuously from July 2011, and six other locations distributed around the sap-flux trees, taking measurements from June to September 2013. To obtain $\theta_{10-15\text{cm}}$ at the plot level, we employed the relationship between the long- (near tower) and short- (near sap-flux trees) term data during June–September 2013 ($r^2 \geq 0.85$) to adjust values from the continuous measurement. All sensors were connected to a data logger (CR10X, Campbell Scientific, Logan, UT, USA) which stored 30-minute mean values. P_T was manually collected biweekly from nine collectors, with collection area of 0.5 m², each in the PS sites. A_S and L were estimated from allometric equations, with annual production and litterfall for L , derived from six harvest trees in 2011 each in the PS stands (Lim et al., 2015). The average L during the growing season of the study period was 2.5 ± 0.36 and 3.1 ± 0.32 for control and fertilized PS sites, changing little because of longer leaf longevity (> 3 years) than PT (~ 1.5 years).

At all sites, the growing season was delineated beginning the day after daily mean temperature exceeded +5 °C for five consecutive days, and lasted until it dropped below +5 °C for five consecutive days (Mäkelä et al., 2006). Consequently, the average growing season period during three study years was approximately March - November in PT and May - September in PS sites. To facilitate the cross-site comparison, soil moisture was represented by Relative Extractable Water (REW) calculated as (Granier et al., 2000)

$$\text{REW} = \frac{\theta - \theta_m}{\theta_{FC} - \theta_m} \quad (1)$$

where θ_m is minimum volumetric soil water and θ_{FC} is the soil water at field capacity with average value of $0.15 \pm 0.02 \text{ m}^3 \text{ m}^{-3}$ for PS sites, close to the regional estimate of $0.155 \text{ m}^3 \text{ m}^{-3}$ for sandy soil (Kätterer et al., 2006). For PT site, where no measurement of θ_{FC} was available, we used maximum volumetric soil moisture during the study period as θ_{FC} for the REW calculation, after verifying that it was not different from the soil moisture value during periods in winter when soil moisture stabilized between rain events ($p = 0.23$). Vapor pressure deficit (D) was calculated from T_A and RH (Abtew and Melesse, 2013). Daylength-normalized D (D_Z) was calculated as $D_D \cdot (\frac{n}{24})$ where D_D was daytime mean D and n was number of daylight hours (Phillips and Oren, 2001).

2.3. Calculations of water balance components

For each growing season in the study sites, local water balance was used to estimate the size of the residual component (R), reflecting a lack of budget closure (Schäfer et al., 2002) based on the mass balance equation:

$$P = I_C + E_C + E_U + Q + \Delta S + R \quad (2)$$

where P is precipitation, I_C is evaporation from canopy interception, E_C is canopy transpiration, E_U is below-canopy evaporation including evaporation from soil and litter and transpiration from the understory vegetation, Q is drainage below rooting zone (2 m depth in PT; Ewers et al., 2000, and 0.4 m depth in the PS sites; Mellander et al., 2004) and ΔS is the change in soil moisture storage which was measured from 0 to 0.3 m depth ($\theta_{0-30\text{cm}}$) in PT and 0.15 to 0.20 m depth ($\theta_{10-15\text{cm}}$) in the PS stands. All components are in mm per growing season. Overland flow was assumed to be negligible due to flat topography and high

infiltration rate of the soil in these sites (cf. Abrahamson et al., 1998).

The evaporation from canopy interception (I_C) was calculated as the difference between P and throughfall (P_T). To estimate P_T values for the entire growing season, a linear relationship between the biweekly sum of P and P_T was developed for each site to gap-fill the time series after excluding data representing multiple rain events in PT (Uebelherr, 2008), and because measurements were taken during only parts of the growing season in the PS sites (slopes were 0.88 ± 0.02 (SE) for PT and 0.79 ± 0.03 for PS; $r^2 \geq 0.94$, $p < 0.0001$ for the relationships and $p = 0.64$ for the difference between control and fertilized PS sites). Canopy transpiration (E_C) was scaled from the continuous measurement of sapwood-specific sap flux density (J_S) using self-constructed thermal dissipation probes (Granier, 1987), and an estimate of the stand-level sapwood area. Gaps in data existed in some periods, due primarily to temporary power outages. Thus, continuous data were obtained by gap-filling missing values of J_S (ranging 19–36% of total growing season days) with a function dependent on daily average photosynthetically active radiation (PAR) and D_Z . More details on the approach for calculating E_C is described in the Supplementary Material.

Below-canopy evaporation (E_U) was estimated as the difference between eddy-covariance-based latent heat flux (E_T) and canopy transpiration on days without precipitation (thus zero I_C). Below-canopy non-intercepted PAR (Stoy et al., 2006) and soil moisture were considered as two factors that potentially drive E_U . To establish a continuous time series of E_U , we applied a stepwise linear regression to non-growing season data (when daily average $T_A < 5^\circ\text{C}$), representing conditions of negligible canopy transpiration (Mäkelä et al., 2006). We calculated non-intercepted PAR by subtracting total canopy PAR absorption from the above-canopy PAR, where canopy PAR absorption was determined using a radiative transfer model (Schäfer et al., 2003; Kim et al., 2011). Although both variables significantly affected E_U , ($p \leq 0.02$), we selected the model which related E_U to below-canopy non-intercepted PAR only because of the higher explained variations ($p \leq 0.001$; $r^2 = 0.43$ for PT and 0.29 for PS) than the additive model of both below-canopy non-intercepted PAR and REW ($p \leq 0.08$; $r^2 = 0.38$ for PT and 0.26 for PS). We used these relationships to estimate E_U for the growing season as well.

We assessed whether our estimates of E_U , as a fraction of total E_T , are consistent with the L of the understory relative to total stand L at the Swedish site. The fraction of understory L in *P. sylvestris* forests of similar characteristics (latitude, canopy L) range ~15–30% of total stand L (Kulmala et al., 2011), somewhat higher than the annual E_U fraction of E_T ranging 14–20% in our sites. The difference between the typical fractions of understory L and our estimates of E_U -to- E_T ratio may reflect variation among stands, or lower fractional transpiration rates of understory species (due to lower available light) and lower evaporation (due to less precipitation input) as compared to the canopy, although moderate intensity rain events may actually increase water availability to shallow-rooted understory individual without affecting water availability of canopy individuals. We note that even though the response to soil moisture and the reasonable closeness of the understory fractional L and E_T (i.e., E_U) estimates seem reasonable, understory evapotranspiration is the least certain among the hydrologic balance components of our sites. This is due to potential errors from operational challenges in eddy-covariance latent heat flux measurements used in this estimating approach, as well as the use of relationship developed during one set of conditions (non-growing season) for estimating E_U over the entire year.

Stemflow was neglected in our analysis because of its typically small amount in coniferous forests (Delfs, 1967; Viville et al., 1993; Uebelherr, 2008). Drainage (Q) was modeled from a plane at the bottom of rooting zones (Schäfer et al., 2002; Oishi et al., 2010). The model was parameterized using physical properties of sand (Clapp and Hornberger, 1978; Katul et al., 1997). Root profiles were obtained from nearby sites of the same species and soil characteristics (Ewers et al., 2000; Hacke et al., 2000 for PT; Mellander et al., 2004 for PS sites). For

PS sites, we used the averaged soil moisture for modeling drainage because of the similarity of stand characteristics, soil type, precipitation and canopy transpiration between the non-fertilized and fertilized PS sites (Tor-ngern et al., 2017). For acceptable local water balance, the residual component (R) should be small and the sum of all measured and estimated components should not be significantly different from P (Oren et al., 1998a,b).

2.4. Survey data for global pine forests

We searched through Web of Science and SCOPUS database for data on water balance in pine forests. The terms: ‘sap flow’, ‘transpiration’, ‘evapotranspiration’, ‘water balance’, ‘water budget’, ‘hydrologic balance’ and ‘hydrologic budget’ were used in combination with ‘pine’. A total of 27 species from 117 studies (Table S1) was selected for the analyses of I_C , E_C and E_T versus P in mm of growing season and annual sums. For multiple-year studies, we analyzed the average of the quantities. Furthermore, we used throughfall (P_T), calculated as $P - I_C$, as the water input to the soil in the growing season for the analysis of fractions of E_C and the difference between E_T and I_C to total water input to the soil during the growing season.

In addition, we analyzed variations of light and water availability, represented by theoretical maximum photosynthetically active radiation (PAR_{\max}) and precipitation, along the latitudinal gradients based on the survey data. Daily PAR_{\max} was calculated from the solar zenith angle using coordinates as reported in the published studies and atmospheric transmittance of 0.7 (Campbell and Norman, 1998). The annual PAR_{\max} was estimated from the total sum of daily PAR_{\max} . For growing season estimates, we derived a function of growing season length with latitudes using a global distribution of growing season length from the global agro-ecological zones assessment GAEZ v3.0 (online source: <http://www.fao.org/nr/gaez/about-data-portal/agro-climatic-resources/en/#>). Data used to derive the function were obtained by approximating the modes of growing season length for ranges of latitudes and performing a regression analysis (Details are presented in Supplementary Material Fig. S2). The growing season PAR_{\max} was then computed as the sum of daily PAR_{\max} according to the number of growing season days at the corresponding latitude.

2.5. Statistical analyses

All regression analyses were performed in SigmaPlot version 12.0, from Systat Software, Inc., San Jose, CA USA. We used an F -test to compare fitting results on different datasets with the same function (e.g., comparisons of scaling and gapfilling functions between control and fertilized PS sites, Table S3 in Supplementary Material). Mean comparisons of growing season values were done with t -test. Other computations, including calculations of variables and drainage model, were conducted in MATLAB 9.0 R2016a (Natick, Massachusetts: The MathWorks Inc., 2016).

3. Results

3.1. Climatic drivers of inter-annual variability in the hydrologic cycle

The *P. taeda* site (PT) experienced a range of hydrologic conditions during the study period, with a wet growing season (Precipitation (P) = 850 mm) in 2003 and a relatively dry growing season (P = 449 mm) in 2005 (Fig. 1a). Consistent with high P , in 2003 PAR and daylength-normalized vapor pressure deficit (D_Z) were lower than in other years (Fig. 1b). Growing season relative extractable water (REW) was high in 2003 (averaged $\text{REW} = 0.56 \pm 0.08$ (SD) or $\sim 0.45 \pm 0.05 \text{ m}^3 \text{ m}^{-3}$ of $\theta_{0-30\text{cm}}$), moderate in 2004 (averaged $\text{REW} = 0.47 \pm 0.06$ or $\sim 0.32 \pm 0.04 \text{ m}^3 \text{ m}^{-3}$ of $\theta_{0-30\text{cm}}$) and decreased to an average of 0.32 ± 0.14 ($\sim 0.22 \pm 0.04 \text{ m}^3 \text{ m}^{-3}$ of $\theta_{0-30\text{cm}}$) during the 2005 growing season (Fig. 1a). In contrast, growing

season weather was relatively similar among the study years in the *P. sylvestris* (PS) sites with average P and photosynthetically active radiation (PAR) of $400 \pm 30 \text{ mm}$ and $29 \pm 2 \text{ mol m}^{-2} \text{ d}^{-1}$ (Fig. 1c, d). However, D_Z was slightly lower in 2012 relative to other years (Fig. 1d). As expected based on P , REW values were fairly similar among years (Fig. 1c).

Among PT and PS sites, components of the growing season hydrologic budget showed similar responses to variability in P (Fig. 2a, $p \leq 0.0006$, Table 2). While canopy interception (I_C) increased with P , E_U was independent of P ($p = 0.58$), slightly dampening the sensitivity of total evaporation to P . Canopy transpiration (E_C) did not show significant change with the observed values of P ($p = 0.26$). Thus, compared to the variability in P ($\text{CV} = 35\%$) and I_C ($\text{CV} = 37\%$), E_T showed lower inter-annual variability ($\text{CV} = 22\%$). Generally, low variability in E_T resulted in Q increasing with P at a rate of 0.61 mm mm^{-1} . Because growing season change in soil moisture storage (ΔS) was estimated only for the topmost soil layers (0.3 m for PT and 0.15 m for PS sites), while drainage below rooting zone (Q) was calculated at a greater depth representing the root zone (2 m for PT and 0.4 m for PS sites), ΔS could be underestimated, resulting in an overestimation of the residual of the water balance equation (R , see Eq. (2)).

Nevertheless, change in soil moisture storage was small and our component-based estimates of the growing season hydrologic budget achieved good closure, with the lack of closure ranging 1% to 9% of P (Table 1) and not significantly different from zero at either site ($p \geq 0.21$). Because this statistical insignificance may be due to having only three years at each site, we evaluated the closure of the budget with two additional tests: (1) based on the nine site-years combined, mean of residuals will be $1.7 \pm 4.3\%$, with $p = 0.26$ for difference from zero, and (2) the relationship between the sum of all hydrologic budget components across the nine site-years and precipitation (upper line in Fig. 2a) was not significantly different from unity ($p = 0.36$).

During the growing seasons, E_C and E_U were $50 \pm 1\%$ SD and $18 \pm 2\%$ of evapotranspiration (E_T), respectively, while I_C was $32 \pm 5\%$ of E_T , and $22 \pm 2\%$ of P . Overall, E_T was $68 \pm 3\%$ of P , allowing $\sim 30 \pm 3\%$ as Q below the rooting depth. Fig. 2b illustrates the inter-annual variability of hydrologic components within each site. The relative amount of I_C to P was insensitive to changing P ($p = 0.28$). Canopy transpiration was also a constant fraction of E_T , regardless of P regime ($p = 0.19$). Accordingly, the fraction of E_C and E_T to P similarly decreased with increasing P ($p \leq 0.04$). As a result, the fraction of Q to P increased with P ($p = 0.01$). Additionally, we examined the effect of soil moisture (REW) on evaporative components at weekly timescale for these sites. Results showed that E_C and E_T did not vary with REW ($p \geq 0.21$) while that E_U significantly decreased with soil drying ($r^2 = 0.21$, $p < 0.0001$). These results are roughly consistent with the coarser temporal scale results we show, but we note that variation in these quantities at fine temporal scales depend on several factors affecting the components of E_T , including stomatal response to light, temperature, vapor pressure deficit, in addition to soil moisture, which are not directly transferable to seasonal or annual quantities.

3.2. Climatic drivers of spatial variability in the hydrologic cycle

We expanded our analysis to include estimates of water balance components from pine forests worldwide (117 studies on 27 species; Table S1). Specifically, we examined inter-annual variability of the major evaporative components (i.e., I_C , E_C and E_T) with changing precipitation at both annual and growing season timescales.

A synthesis of evaporative components of global pine forests showed differences in their sensitivity to P during growing season compared to annually (Fig. 3, Table 2). Canopy interception (I_C) significantly increased with P (Fig. 3a, d) with 24% and 22% of incoming P contributed to I_C in these pine forests at seasonal and annual timescales, respectively (Table 2). This proportion of P was also in agreement with results from our PS and PT sites (22% of P , Fig. 2, Table 2). In contrast,

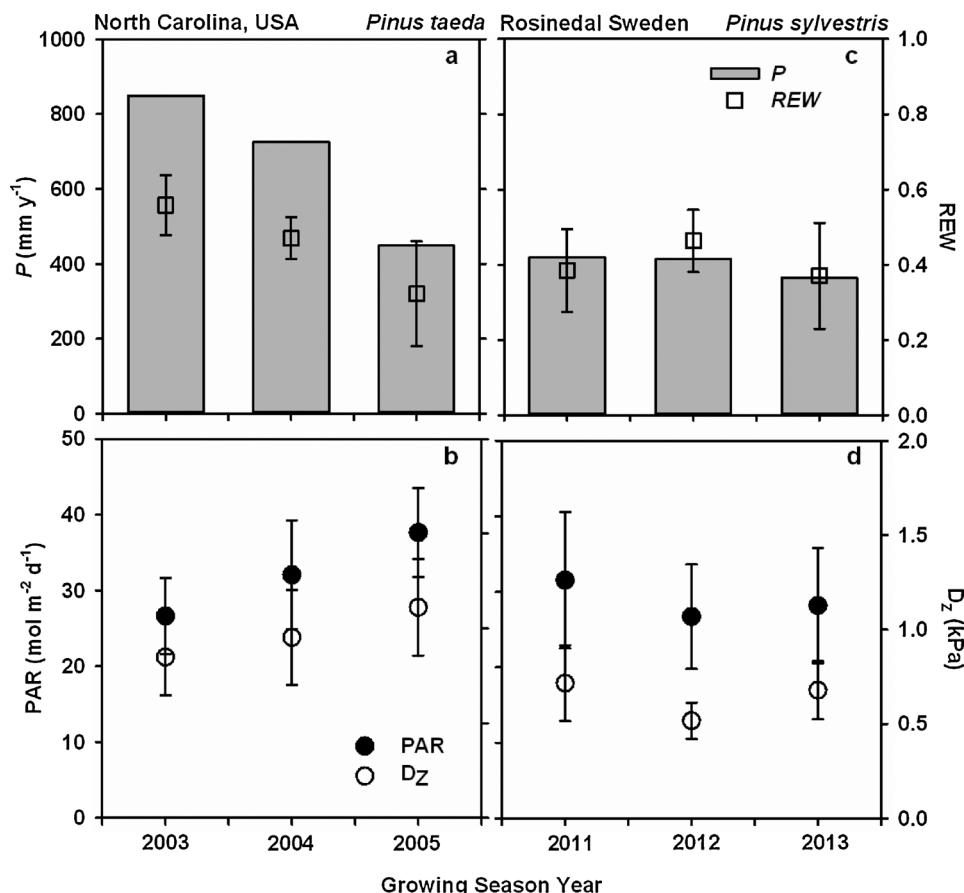


Fig. 1. Weather conditions during the study periods. (a), (c) Soil moisture expressed as Relative Extractable Water (REW, squares) and precipitation (P in mm, bars). (b), (d) Daily sum of photosynthetically active radiation (PAR in $\text{mol m}^{-2} \text{d}^{-1}$, closed circles) and daylength-normalized daytime average vapor pressure deficit (D_Z in kPa, open circles). Data for PAR, D_Z and REW are presented as average values for the growing season days with one standard deviation of the daily estimates shown as error bars.

both E_C and E_T showed different sensitivities to P between annual and seasonal estimates. During growing season, E_C exceeded P in regions with $P \leq 134 \pm 37 \text{ mm}$, but a similar pattern was not observed on the annual timescale (compare Fig. 3b and e), noting that P must also satisfy the water requirements of I_C and E_U . For E_T estimates, pine forests in regions with $P \leq 326 \pm 39 \text{ mm}$ used on average more water than they received during growing season (Fig. 3f), but these forests consistently returned $66\% \pm 17\%$ (SD) of P to the atmosphere annually (Fig. 3c).

Because water cycling in forests is also driven by available energy and leaf area index (L), we attempted to explain the variation of E_C and E_T based on these variables as well, using theoretical maximum PAR (PAR_{max}) as a proxy for energy input. We note that information on L was available for only a subset of sites for which we found data on E_C and/or E_T during growing season and/or annually, and that more data were available for annual than seasonal analyses. We also note that leaf area index and precipitation were not correlated ($p = 0.23$, $n = 76$ for annual values and $p = 0.12$, $n = 36$ for growing season values), and were thus regarded as separate predictors. Using P with either L or PAR_{max} (and an interaction term) in a stepwise regression analysis, we found that L explained the greatest amount of variation in E_C at both time scales (selection based on $p < 0.05$; $r^2 = 0.36$, $n = 27$ for growing season and $r^2 = 0.37$ and $n = 44$ for annual). The final model, however, included P at both time scales, as an additive component for the seasonal E_C ($r^2 = 0.43$) and multiplicative for annual E_C ($r^2 = 0.56$). Moreover, at both time scales, variation in P explained most of that in E_T ($r^2 = 0.53$, $n = 38$ for growing season, and $r^2 = 0.73$ and $n = 84$ for annual E_T), with slight (~2%) decreases of unexplained variation with incorporation of either PAR_{max} or L . Adding annual potential evapotranspiration (PET) as a potential predictor yielded 1% decrease in the explained variation in E_T relative to having P as the only predictor. We note that focusing only on stands of *P. taeda* and *P. sylvestris* produced

results similar to those of all species combined (data not shown).

We further examined ratios of the evaporative fluxes (E_C , E_T) and water inputs (P , throughfall (P_T)) (Fig. 4). The results were consistent with the findings from the site-level analyses in that pine forests are governed by different patterns of water use at seasonal and annual time scales (e.g., Fig. 3). Annually, the fraction of P consumed by forests as E_C decreased with P , but at a slower rate compared to the pattern observed in the growing season (compare Fig. 4a and 4c). The ratios of annual E_C to P did not exceed 1.0, and were relatively invariable once P was greater than ~1000 mm (Fig. 4a). During the growing season, pine canopies in sites of $P_T \leq 128 \pm 58 \text{ mm}$ consumed more water as E_C than that supplied to the soil as P_T (the difference between P and I_C), again noting the P_T needs to also satisfy E_U . As P_T increased, the ratio of canopy transpiration and throughfall (E_C/P_T) decreased and became insensitive to increasing P_T once $P_T \geq 400 \text{ mm}$ (Fig. 4c). At the annual timescale, E_T/P decreased linearly with P with the mean response remaining below 1.0 over the entire range of P , but many stands showing ratio close to 1.0 (Fig. 4b). However, the difference between $E_T - I_C$, representing the sum of growing season E_U , a quantity insensitive to P_T ($p = 0.76$), and canopy transpiration (E_C), exceeded throughfall precipitation input to the soil in regions with $P_T \leq 257 \pm 79 \text{ mm}$ (Fig. 4d).

The analysis producing the results above was inspired by the Budyko framework which is widely used in catchment hydrological studies (Budyko, 1974). The theoretical Budyko curve is the relationship between potential evapotranspiration (PET) and actual evapotranspiration (E_T), each normalized by precipitation (P) of a site (Fig. 5, gray lines). The curve is partitioned to conditions in which E_T is limited by energy supply ($\text{PET}/P < 1$), regulated by climate (net radiation and vapor pressure deficit), or by water supply ($\text{PET}/P > 1$), controlled by vegetation (canopy interception) and soil water storage. An underlying assumption of the Budyko's framework is that mean annual P can be

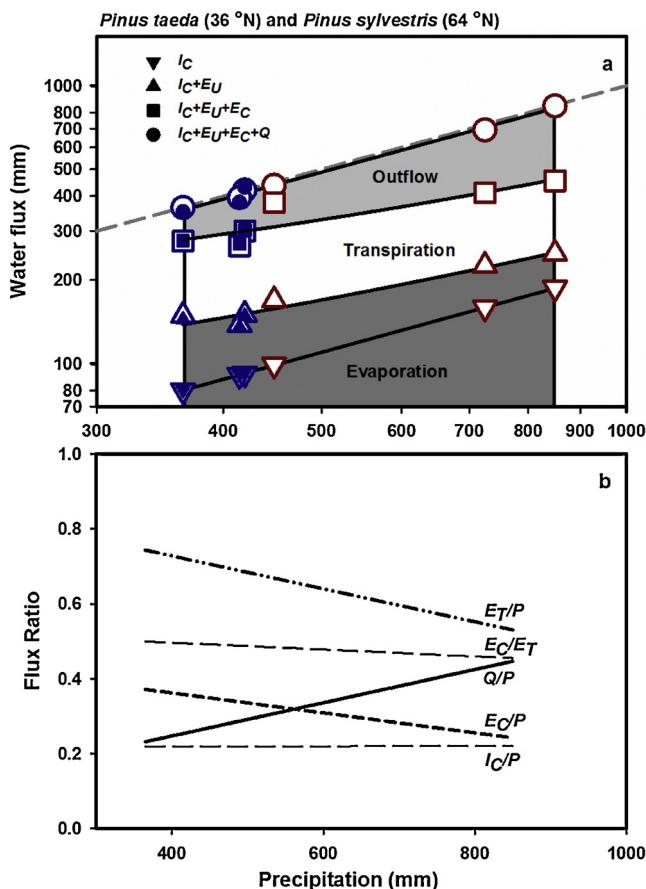


Fig. 2. Water balance of the study sites. (a) Each hydrologic component is shown in growing season totals (mm) as a function of incoming growing season precipitation on a log-log scale. Red symbols represent data for *Pinus taeda* (PT) site from the warm, temperate climate (36°N) while blue ones are for *Pinus sylvestris* (PS) sites from the cold, boreal climate (64°N). Open and closed symbols indicate non-fertilized and fertilized sites, respectively. Note that for the PS sites, values for the control and fertilized sites are relatively similar (see Table 1). (b) Sensitivity of evaporative components as a fraction of either evapotranspiration or precipitation across inter-annual precipitation of the sites (note the linear scale). Long dashed lines represent insignificant results. All regression statistics are presented in Table 2 (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article).

Table 1

Growing season water balance of the study sites. Total growing season estimates (in mm of water) of hydrologic components. P = precipitation; P_T = throughfall; I_C = canopy interception; E_C = canopy transpiration; E_U = below-canopy evaporation, including soil, understory vegetation and litter evaporation; E_T = evapotranspiration including $I_C + E_C + E_U$; Q = drainage; ΔS = change in soil water storage; The residual term R is calculated as $P - I_C - E_C - E_U - Q - \Delta S$.

Site	Growing season year	P	P_T	I_C	E_C	E_U	E_T	Q	ΔS	R
PT	2003	850	663	187	205	62	454	390	-4	10
	2004	725	566	159	187	66	412	280	12	21
	2005	449	350	99	211	70	380	57	-3	15
PS (Control)	2011	420	328	92	158	50	300	120	6	-13
	2012	415	324	91	130	44	265	130	-8	22
	2013	365	285	80	149	47	276	88	-8	-1
PS (Fertilized)	2011	420	328	92	153	57	302	128	19	-23
	2012	415	324	91	129	50	270	111	5	36
	2013	365	285	80	144	53	277	75	11	11

partitioned into E_T and water yield. The larger is PET/P, the less of P is contributed to water yield. We further analyzed the data from the global pine forests in this familiar framework. Our analysis showed that the survey data followed the Budyko curve (Fig. 5, $p = 0.003$, $r^2 = 0.26$), although the saturation regime seems to be mostly driven by only one site. The three sites at the ratio PET/P ≥ 2 (not included in the regression analysis) correspond to those in semi-arid and Mediterranean regions, the inclusion of which would generate a peaking function, a conceptual deviation from the commonly observed saturating Budyko curve (Fig. 5, gray lines).

4. Discussion

Growing season and annual values of canopy transpiration are useful for assessing ecosystem physiological status, and are readily linked to gross primary production (Schäfer et al., 2003; Chiesi et al., 2007; Yan et al., 2016). Coupled with precipitation, values of E_T at these time scales can be utilized for estimating water outflow to downstream aquatic ecosystems and users (Oishi et al., 2010). When soil moisture is not limiting, the variation of the maximum, growing season daily E_C among widely distributed pine forests is explainable by variation of leaf area index (L), decreasing with soil moisture following patterns depending on soil texture (Tor-ngern et al., 2017). Here, using surveyed data of pine forests from around the globe (Table S1), we found that, at growing season and annual timescales, the variable most useful for explaining the spatial variation of E_C remains L . However, accounting for the spatial variability of P significantly increased the explained variation of E_C at both temporal scales (Fig. 3b, e). Given the link between P and soil moisture, these results are consistent with those derived from observations analyzed at finer temporal scales (Tor-ngern et al., 2017). Considering the number of interacting factors controlling transpiration, including atmospheric, soil, and stand variables, it is not surprising that a large fraction of the variation among stands in seasonal and annual E_C remains unexplained. Nevertheless, the results highlight that, during the growing season, pine forests in dry regions use more water than received even though annually these forests consume a similar fraction of P as forests in wetter areas. This finding implies that, if climate change leads to longer growing season and decreased rainfall (Parida and Buermann, 2014), water flow from forests where growing season P currently exceeds E_T may become unreliable.

4.1. Estimates of evaporative components at the study sites

The surfaces in the canopy are the first users of incoming precipitation, a small fraction of which is absorbed (Katz et al., 1989), but a substantial fraction of precipitation is returned to the atmosphere as canopy interception I_C , no longer available to terrestrial or aquatic organisms. Although this section focuses on temporal variation in the fluxes of our three sites, I_C is a relatively conservative flux in time and space – it increased with P temporally within a stand (Fig. 2) and spatially among stands (Fig. 3). The I_C fraction of P in our three stands (0.22) was similar to a Scots pine-dominated stand in central Sweden (0.20, Grelle et al., 1997) but, as expected, was lower than in pine forests with higher L (0.32 with $L \sim 5\text{--}7 \text{ m}^2 \text{ m}^{-2}$ Gash and Stewart, 1977; 0.31 with $L \sim 4 \text{ m}^2 \text{ m}^{-2}$ Benyon and Doody, 2014). Based on the global synthesis, I_C of pine forests was 0.22 of P annually and 0.24 during the growing season (Fig. 3a, d). This value was consistent with the global analysis from satellite observations, showing 0.22 of P returning to the atmosphere as interception loss in needle-leaf forests (Miralles et al., 2010). Thus, despite spatial and temporal variation caused by precipitation type and distribution, and canopy L and energy available for evaporation, the mean I_C at coarse temporal and spatial scales remains a conservative fraction of P .

We estimated below-canopy evaporation (E_U) of the three PT and PS stands to be ~ 0.18 of E_T , similar to previous observations in relatively sparse, low L forests (up to 0.4 of E_T ; Granier et al., 1990; Whitehead

Table 2

Summary of regression statistics. Regression analysis results for the relationships between various hydrologic components and water input as throughfall (P_T) or precipitation for Figs. 2–4. r^2 and p are the coefficient of determination and p value at significant level of 5% for the linear regression analyses. n is the number of data and N is the number of studies involved in each analysis. Notations for the water components are the same as in Table 1. Parameters are reported as estimates with their standard errors.

Figure	Variables	n / N	Relationship	r^2	p
Fig. 2a	I_C vs P	9/1	$y = (0.22 \pm 0.03)x$	0.99	< 0.0001
	$I_C + E_U$ vs P	9/1	$y = (0.23 \pm 0.02)x + (54 \pm 10)$	0.94	< 0.0001
	$I_C + E_U + E_C$ vs P	9/1	$y = (0.37 \pm 0.06)x + (144 \pm 33)$	0.81	0.0006
	$I_C + E_U + E_C + Q$ vs P	9/1	$y = (0.98 \pm 0.02)x$	0.99	< 0.0001
Fig. 2b	I_C/P vs P	9/1	n/a	0.04	0.28
	E_C/E_T vs P	9/1	n/a	0.12	0.19
	E_C/P vs P	9/1	$y = (-0.0003 \pm 0.0001)x + (0.47 \pm 0.06)$	0.39	0.04
	E_T/P vs P	9/1	$y = (-0.0004 \pm 0.0001)x + (0.90 \pm 0.07)$	0.53	0.02
Fig. 3a	Q vs P	9/1	$y = (0.0004 \pm 0.0001)x + (0.07 \pm 0.07)$	0.57	0.01
	I_C vs P (Annual)	58/42	$y = (0.22 \pm 0.01)x$	0.52	< 0.0001
	E_C vs P (Annual)	53/34	$y = (0.33 \pm 0.02)x$	0.23	< 0.0001
	E_T vs P (Annual)	84/62	$y = (0.66 \pm 0.02)x$	0.69	< 0.0001
Fig. 3d	I_C vs P (Growing Season)	21/16	$y = (0.24 \pm 0.02)x$	0.80	< 0.0001
Fig. 3e	E_C vs P (Growing Season)	33/23	$y = (0.27 \pm 0.08)x + (98 \pm 34)$	0.27	0.0011
Fig. 3f	E_T vs P (Growing Season)	38/27	$y = (0.5 \pm 0.08)x + (163 \pm 36)$	0.52	< 0.0001
Fig. 4a	E_C / P vs P	53/34	$y = (1.2 \pm 1.54)\exp((-0.006 \pm 0.004)x) + (0.34 \pm 0.03)$	0.13	0.011
Fig. 4b	E_T/P vs P	84/62	$y = -0.0001x + (0.8 \pm 0.05)$	0.06	0.016
Fig. 4c	E_C/P_T vs P_T	33/23	$y = (3.24 \pm 2.17)\exp((-0.01 \pm 0.004)x) + (0.46 \pm 0.09)$	0.29	0.002
Fig. 4d	$(E_T - I_C) / P_T$ vs P_T	38/27	$y = (1.35 \pm 0.18)\exp((-0.0009 \pm 0.0004)x)$	0.15	0.009

and Kelliher, 1991; Domec et al., 2012). The understory transpiration component of E_U ranges 0.2–0.8 mm d⁻¹ in various *Pinus* stands depending on canopy L (Baldocchi et al., 1997; Constantin et al., 1999; Domec et al., 2012), was not directly quantified in our study, but assumed to contribute little to E_U considering the small fraction of basal area represented by the understory in PT, or the fraction of transpiring L found in stands similar to PS (Kulmala et al., 2011; Palmroth et al., 2014). Although E_U estimates were the least certain among the hydrologic components, of the amount of precipitation reaching the forest floor as throughfall, E_U comprised a small and consistent component of total E_T among years and forests (Table 1; Fig. 2). Thus, in contrast to I_C which diminished as fraction of E_T in dry years and regions, E_U represented an increasing fraction of E_T under dry conditions.

Transpiration (E_C) in the PT and PS stands showed negligible inter-annual variability with P within a site (Fig. 2). The growing season E_C fraction of E_T was ~0.5, lower than the average ratio of 0.75 ± 0.04 found in other PT and PS sites, potentially owing to different site characteristics, such as soil texture and latitudinal locations (Kelliher et al., 1998; Oren et al., 1998a,b; Stoy et al., 2006; Tor-ngern et al., 2017). The apparent insensitivity to variation of inter-annual P is the result of increasing atmospheric evaporative demand for water in periods of low P and, thus, soil moisture (Oishi et al., 2010). Although canopy conductance (and, thus, gross primary production) is lower during these dry periods, E_C varies less, compensated by the higher driving force (Joffre and Rambal, 1993; Oishi et al., 2010; Montaldo and Oren, 2016). The sensitivity of growing season E_T to P at our PT and PS sites was also weak, owing mostly to the insensitivity of E_C to inter-annual variation of P . A relatively weak relationships between E_T and P inter-annually have been shown in a water balance study on a temperate broadleaved deciduous forest (Oishi et al., 2010), a watershed covered with a mosaic of land-cover types, mostly broadleaved deciduous species and *P. taeda* in North Carolina (Palmroth et al., 2010), as well as in a boreal mixed *P. sylvestris* and *P. abies* stand in Sweden (Hasper et al., 2016). As result, the fractional contribution of E_C (as of that of E_U), and therefore E_T , increase with decreasing P (Fig. 2b). Indeed, the temporal variation of P mostly translates into variation in water outflow (Fig. 2), highlighting the fact that, among the flux components, water resources may be particularly sensitive to future changes in P . However, with increasing soil and atmospheric drought severity, duration, and frequency, first leaf area index may decrease (McCarthy et al., 2007), followed by species compositional change

(Pataki and Oren, 2003), as likely are all water, energy and carbon flux components.

The results from the stands in Sweden and North Carolina also demonstrate that, not only is the temporal variation of seasonal and annual evaporative fluxes small at a given location, regardless of the variation of P , but it is also reasonable to consider outflow at coarse temporal scales as the balance between P and E_T (Fig. 2). Thus, assessing the effect of spatial variation of P on water yield estimated from the literature survey as $Q = P - E_T$ seems justified.

4.2. Forest evaporation at growing season versus annual timescales

Spatially across all available studies, the growing season E_C fraction of E_T averaged 0.53 ± 0.17 (SD). In contrast to expectation of lower annual than growing season E_C/E_T , the annual fraction averaged a similar 0.50 ± 0.21 (ranging widely 0.16–0.95). Furthermore, in contrast to the weak inter-annual (i.e., temporal) relationship discussed previously, the mean annual E_C increased across sites (i.e., spatial) with the mean annual P (Fig. 3b).

Total evapotranspiration (E_T) from forests may be influenced by many factors, such as radiation input, canopy leaf area, tree density, canopy conductance, and micrometeorological conditions affecting potential evapotranspiration, which govern the relative contribution of energy and precipitation to E_T (Budyko, 1974; Zhang et al., 2004). However, in contrast to E_C which depends on both P and L , most of the variation of E_T were explained by P (Fig. 3c, f). Thus, both growing season and annual values of E_T can be estimated based on P alone, and other variables, such as L and potential evapotranspiration, did not reduce the unexplained variation (Fig. S3). Evapotranspiration increased linearly with P among sites (Fig. 3c), meaning that Q , the residual flux of water from forests, also increased with P , as it does temporally within a site (Fig. 2). Worldwide, approximately 33% of P falling on pine forests leave the system as outflow, contributing to water table recharge and to streamflow. However, because annual E_T/P tends to increase with decreasing P (Fig. 4b), pine forests in dryer regions contribute a smaller proportion of P to Q . Consistent with this observation, based on the Budyko's curve (Fig. 5), pine forests in dry regions (with annual PET/P > 1) allocate precipitation to E_T more than water yield compared to those in moist regions (with PET/P < 1). Deviations from the theoretical Budyko's curve are likely due to variations in site characteristics such as vegetation type (Zhang et al., 2001), soil

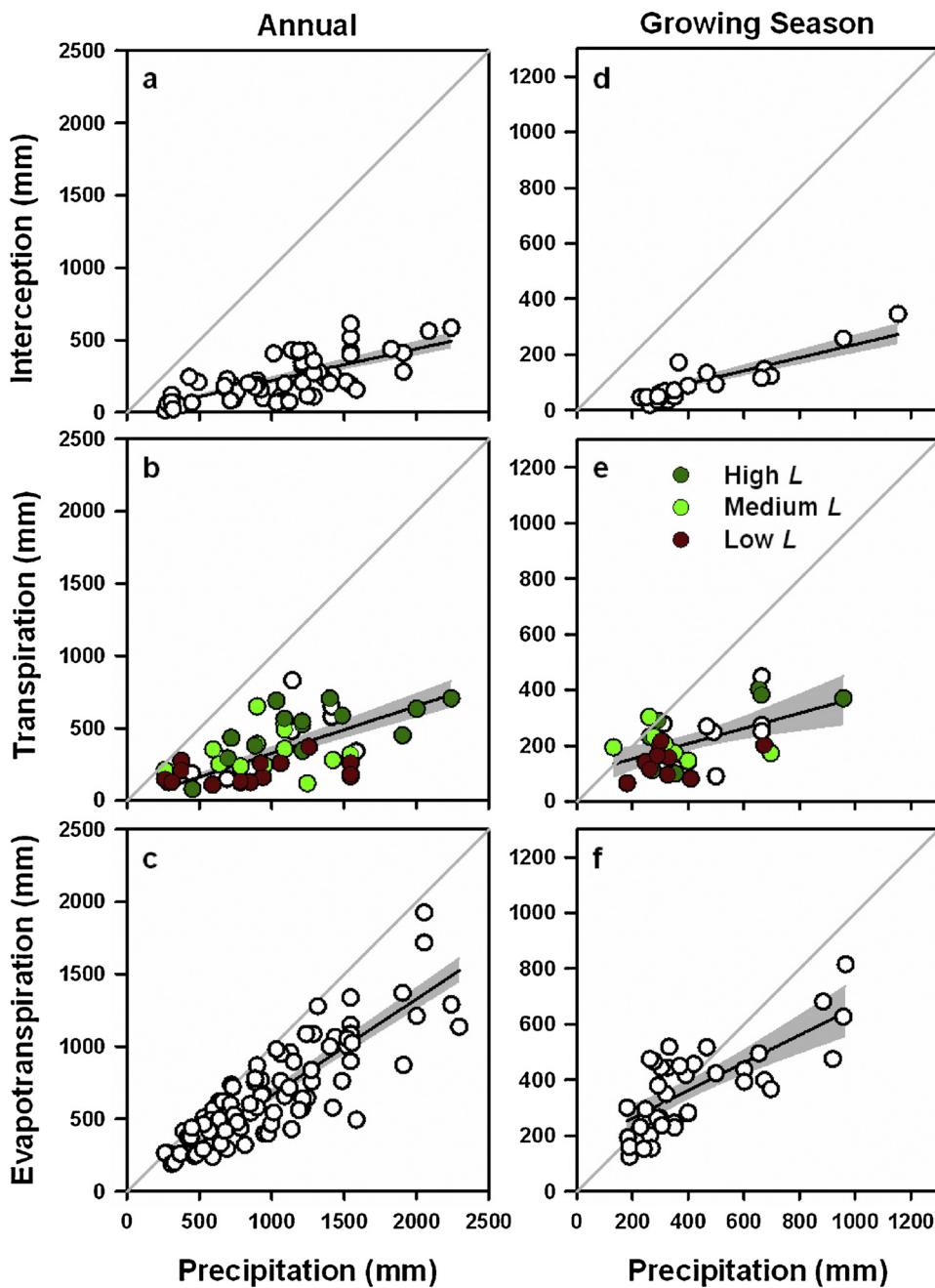


Fig. 3. Synthesis of evaporative components of global pine forests. (a) – (c) Sensitivity of evaporative components to precipitation averaged over annual timescales and (d) – (f) over multiple growing seasons for pine forests at various latitudes. Details of site information are presented in Table S1. Shaded regions indicate the 95% confidence intervals of the regression lines. Regression statistics are listed in Table 2. For the transpiration components in (b) and (e), colors represent different levels of leaf area index (L) of the sites: dark green = high L ($L > 4$), green = medium L ($2 < L < 4$) and dark red = low L ($L < 2$). The non-colored symbols are sites with unknown L . (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article).

type (Wang et al., 2009), water storage capacity (Milly, 1994), and timing of water recharge (Potter et al., 2005).

During the growing season, pine forests growing in dry regions, with $P \leq 134 \pm 37$ mm per growing season (Fig. 3e; or a similar $P \leq 117 \pm 26$ in our three sites), must rely on soil water storage, or access groundwater using deep roots, to meet their E_C rates (Jipp et al., 1998; Luis et al., 2005; Vincke and Thiry, 2008). In reality, however, P also needs to meet other evapotranspiration demands, those of wet canopies, understory and forest floor following rains, and transpiration of the understory. Thus, in the pine forests of dry climates, soil water must balance the water used in evapotranspiration where growing season $P \leq 326 \pm 39$ (Fig. 3f). Since transpiration depends on root access to water stored in the soil, it is more temporally decoupled from P than either I_C or E_U . Thus, if the intra-annual distribution of P changes, but annual P does not, I_C should change relatively little, but the effects on E_C will depend on the degree of soil water recharge before the growing season, and between rain events during the season (Feng

et al., 2012, 2015). However, because growing season E_C (and thus E_T) is not very sensitive to P (Fig. 3e, f), the gap between E_T and P increases when moving progressively towards wetter climates, with the difference supporting increasing water outflow during the season. Such behavior is not evident when integrating E_C to annual fluxes (Fig. 3b, c), showing that the annual supply of water is sufficient to support the transpiration needs of these pine forests, returning on average 33% of annual P back to the atmosphere as E_C (Fig. 3b), and about twice that much (66%) as E_T (Fig. 3c).

These flux ratios, however, are somewhat sensitive to P . Across the wide latitudinal range, the fraction of P transpired annually by pine forests decreased exponentially with P (Fig. 4a), reaching 0.35 at P of ~ 750 mm, and remaining so to an annual P of > 2000 mm, perhaps reflecting the compensating effects of water availability and atmospheric demand for water. In contrast, the annual E_T fraction of P progressively decreased with P (Fig. 4B) despite the increase in its major components (Fig. 3a–c) but, more importantly, shows a large

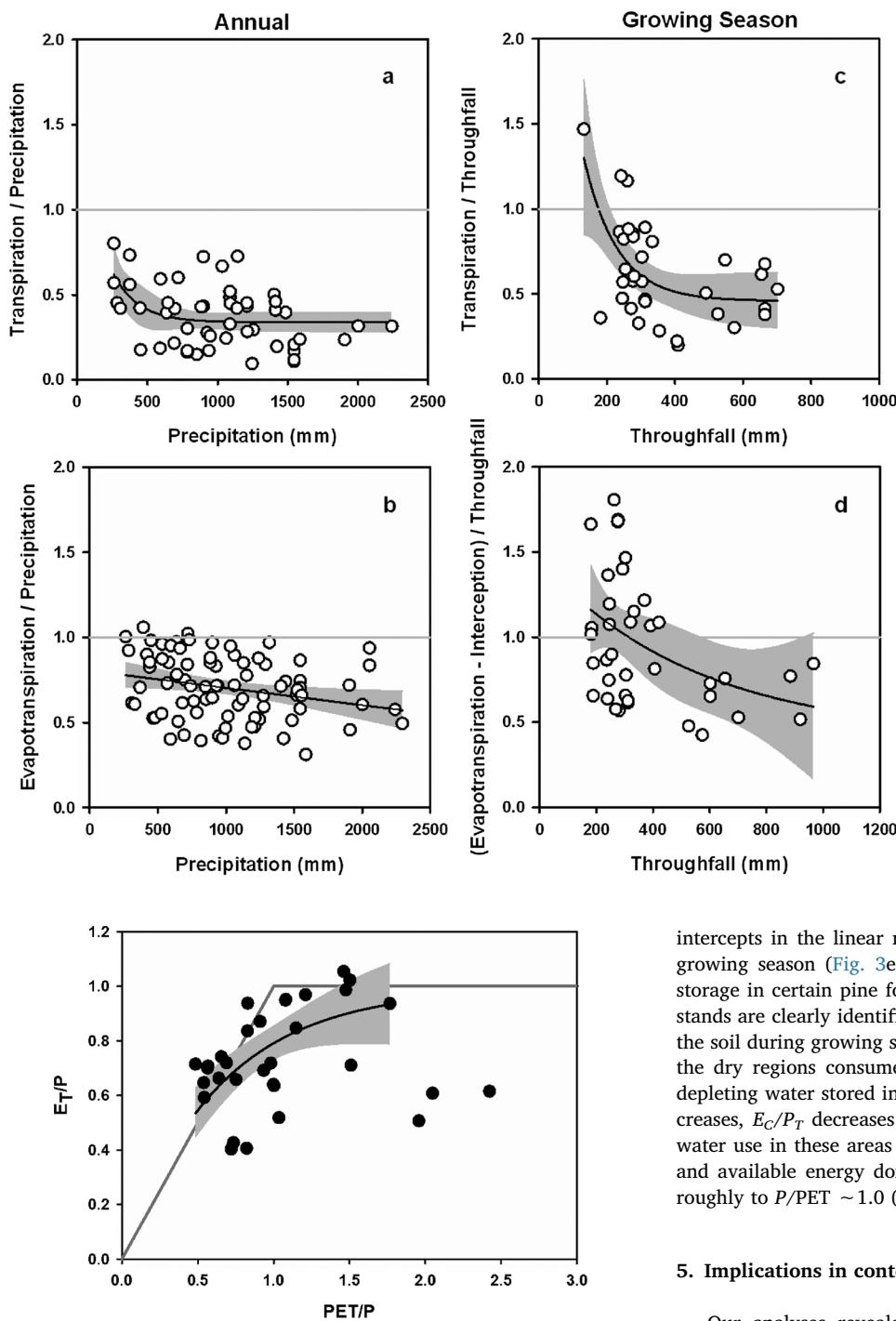


Fig. 4. Fractions of evaporative components to water supply among global pine forests. (a), (b) show variations of fraction of canopy transpiration (E_C) to throughfall (P_T) and that of evapotranspiration (E_T) to precipitation (P) along the gradients of water input as P_T and P , respectively. (c) Sensitivity of the ratio of E_C to P_T to P_T as water input to the soil during growing season. (d) Growing season estimates of the tree transpiration and below-canopy evaporation (including soil and litter evaporation and understory transpiration), expressed as the difference between E_T and canopy interception (I_C), to P_T . Shaded regions indicate the 95% confidence intervals of the regression lines. Regression statistics are shown in Table 2.

Fig. 5. The Budyko's curve derived from the survey data (Table S1). This shows the relationship between the fraction of evapotranspiration (E_T) to precipitation (P) and that of potential evapotranspiration (PET) to P . Dark gray lines show physical boundaries of the curve where dryness index (PET/ P) increases with the evaporative index (E_T/P) over the energy-limited region and where E_T/P is independent of PET/ P over the water-limited region. From the survey data, only 32 studies reported PET. Shaded region corresponds to the 95% confidence interval.

number of stands with a ratio near 1.0 over most of the range of P . The pattern becomes clearer, and more stands suggest potential sensitivity to changing P , when growing season fluxes are considered (Fig. 4c, d). The combined water flux from evapotranspiration from the understory and transpiration of trees exceeded P_T in dry forests where $P_T \leq 257 \pm 79$ mm per growing season (Fig. 4d). The non-zero

intercepts in the linear relationships of E_C and E_T with P during the growing season (Fig. 3e, f; Table 2), suggest reliance on soil water storage in certain pine forests is more than a short-term event. These stands are clearly identified using the ratios of E_C to water supplied to the soil during growing season (E_C/P_T). Thus presented, pine forests in the dry regions consumed more water than they received (Fig. 4c), depleting water stored in the soil, or accessing groundwater. As P_T increases, E_C/P_T decreases and stabilizes at ~ 0.5 , suggesting that tree water use in these areas is no longer controlled by water availability, and available energy dominates E_T (Wu et al., 2017), corresponding roughly to $P/PET \sim 1.0$ (Fig. 5).

5. Implications in context of climate change

Our analyses revealed differences between the inter-annual variability of E_C , and, to somewhat lesser degree, E_T , at a given stand, and the variability of these quantities among stands. These observations likely reflect the ability of forests to tolerate local variation in P . When P declines, however, the buffering capacity of soil water is diminished, and can no longer sustain E_C . Climate change will involve alterations in the spatial and temporal frequency distributions of atmospheric and soil conditions. In the future, increases in air temperature and its variation may be accompanied by similar changes in atmospheric demand for water, while changes in precipitation, and thus water supply to trees, are uncertain. Our results show that pine forests across wide latitudinal gradients return a similar proportion (66%) of the incoming precipitation annually to the atmosphere as evapotranspiration. However, these results do not hold at the seasonal timescale. During the growing season, pine forests in dry regions use more water than they receive as rainfall. This may roughly differentiate between areas supporting

ephemeral streams and those capable of supporting continuous outflow for downstream aquatic ecosystems and users. Thus, depending on future changes in precipitation, the number of areas continuously sponsoring downstream users may increase or decrease with P . However, were P to decrease in regions currently supporting pine forests through usage of stored soil moisture during the growing season ($E_T/P < 1.0$), growing season water needs for supporting L will not be met from storage in the soil, and the following reduction of L will reflect mortality of individuals, and potentially a compositional shift to include species that require and use less water.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at <https://doi.org/10.1016/j.agrformet.2018.04.021>.

References

- Abtew, W., Melesse, A., 2013. Evaporation and Evapotranspiration Measurement and Estimations. Springer, Science + Business Media Dordrecht, pp. 53–62.
- Abrahamson, D.A., Dougherty, P.M., Zarnoch, S.J., 1998. Hydrological components of a young loblolly pine plantation on a sandy soil with estimates of water use and loss. *Water Res. Res.* 34, 3503–3513.
- Baldocchi, D.D., Vogel, C., Hall, B., 1997. Seasonal variation of energy and water vapor exchanges rates above and below a boreal jack pine forest canopy. *J. Geophys. Res.* 102, 28939–28951.
- Barbour, M.M., Hunt, J.E., Walcroft, A.S., Rogers, G.N.D., McSeveny, T.M., Whitehead, D., 2005. Components of ecosystem evaporation in a temperate coniferous rainforest, with canopy transpiration scaled using sapwood density. *New Phytol.* 165, 549–558.
- Benyon, R.G., Doody, T.M., 2014. Comparison of interception, forest floor evaporation and transpiration in *Pinus radiata* and *Eucalyptus globulus* plantations. *Hydro. Processes* 29, 1273–1187.
- Budyko, M.I., 1974. Climate and Life. Academic Press, New York.
- Campbell, G., Norman, J., 1998. An Introduction to Environmental Biophysics. Springer-Verlag New York, Inc.
- Chiesi, M., Maselli, F., Moriondo, M., Fibbi, L., Bindl, M., Running, S.W., 2007. Application of BIOME-BGC to simulate Mediterranean forest processes. *Ecol. Modell.* 206, 179–190.
- Clapp, R.B., Hornberger, G.M., 1978. Empirical equations for some hydraulic properties. *Water Res. Res.* 14, 601–604.
- Constantin, J., Grelle, A., Ibrom, A., Morgenstern, K., 1999. Flux partitioning between understorey and overstorey in a boreal spruce/pine forest determined by the eddy covariance method. *Agric. For. Meteorol.* 98–99, 629–643.
- Delfs, J., 1967. Interception and stemflow in stands of Norway spruce and beech in West Germany. In: Sopper, W.E., Lull, H.W. (Eds.), Aug – Sept 1965. Pergamon Press, New York, USA Forest Hydrology, Proceedings from International Symposium Held at University Park, Pennsylvania, pp. 179–185.
- Domec, J.-C., Sun, G., Noormets, A., Gavazzi, M.J., Treasure, E.A., Cohen, E., Swenson, J.J., McNulty, S.G., King, J.S., 2012. A comparison of three methods to estimate evapotranspiration in two contrasting loblolly pine plantations: age-related changes in water use and drought sensitivity of evapotranspiration components. *For. Sci.* 58, 497–512.
- Ewers, B.E., Oren, R., Sperry, J.S., 2000. Influence of nutrient versus water supply on hydraulic architecture and water balance in *Pinus taeda*. *Plant Cell Environ.* 23, 1055–1066.
- Feng, X., Vico, G., Porporato, A., 2012. On the effects of seasonality on soil water balance and plant growth. *Water Resour. Res.* 48, W05543.
- Feng, X., Porporato, A., Rodriguez-Iturbe, I., 2015. Stochastic soil water balance under seasonal climates. *Proc. R. Soc. A* 471:<http://dx.doi.org/10.1098/rspa.2014.0623>, 2174.
- Ford, C.R., Hubbard, R.M., Vose, J.M., 2011. Quantifying structural and physiological controls on variation in canopy transpiration among planted pine and hardwood species in the southern Appalachians. *Ecohydrology* 4, 183–195.
- Gash, J.H.C., Stewart, J.B., 1977. The evaporation from Thetford Forest during 1975. *J. Hydrol.* 35, 285–396.
- Giesler, R., Lundström, U.S., Grip, H., 1996. Comparison of soil solution chemistry assessment using zero-tension lysimeters or centrifugation. *Eur. J. Soil Sci.* 47, 395–405.
- Granier, A., 1987. Evaluation of transpiration in a Douglas-fir stand by means of sap flow measurements. *Tree Physiol.* 3, 309–320.
- Granier, A., Bobay, V., Gash, J.H.C., Gelpe, J., Saugier, B., Shuttleworth, W.J., 1990. Vapour flux density and transpiration rate comparisons in a stand of Maritime pine (*Pinus pinaster* Ait.) in Les Landes forest. *Agric. For. Meteorol.* 51, 309–319.
- Granier, A., Loustau, D., Bréda, N., 2000. A generic model of forest canopy conductance dependent on climate, soil water availability and leaf area index. *Ann. For. Sci.* 57, 755–765.
- Grelle, A., Lundberg, A., Lindroth, A., Morén, A.-S., Cienciala, E., 1997. Evaporation components of a boreal forest: variations during the growing season. *J. Hydrol.* 197, 70–87.
- Hacke, U.G., Sperry, J.S., Ewers, B.E., Ellsworth, D.S., Schäfer, K.V.R., Oren, R., 2000. Influence of soil porosity on water use in *Pinus taeda*. *Oecologia* 124, 495–505.
- Hasper, T.B., Wallin, G., Lamba, S., Hall, M., Jaramillo, F., Laudon, H., Linder, S., Medhurst, J.L., Ränttörs, M., Sigurdsson, B.D., Uddling, J., 2016. Water use by Swedish boreal forests in a changing climate. *Funct. Ecol.* 30, 690–699.
- Hasselquist, N.J., Höglberg, P., Metcalfe, D.B., 2012. Contrasting effects of low and high nitrogen additions on soil CO_2 flux components and ectomycorrhizal fungal sporocarp production in a boreal forest. *Global Change Biol.* 18, 3596–3605.
- Ilvesniemi, H., Pumpanen, J., Duursma, R., Hari, P., Keronen, P., Kolari, P., Kulmala, M., Mammarella, I., Nikinmaa, E., Rannik, Ü., Pohja, T., Siivola, E., Vesala, T., 2010. Water balance of a boreal Scots pine forest. *Boreal Environ. Res.* 15, 375–396.
- Jackson, R.B., Jobbágy, E.G., Avissar, R., Roy, S.B., Barrett, D.J., Cook, C.W., Farley, K.A., Le Maître, D.C., McCarl, B.A., Murray, B.C., 2005. Trading water for carbon with biological carbon sequestration. *Science* 310, 1944–1947.
- Jasechko, S., Sharp, Z.D., Gibson, J.J., Birks, S.J., Yi, Y., Fawcett, P.J., 2013. Terrestrial water fluxes dominated by transpiration. *Nature* 496, 347–350.
- Jipp, P.H., Nepstad, D.C., Cassel, D.K., Reis De Carvalho, C., 1998. Deep soil moisture storage and transpiration in forests and pastures of seasonally-dry Amazonia. *Climate Change* 39, 395–412.
- Jocher, G., Ottosson-Löfvenius, M., De Simon, G., Hörlund, T., Linder, S., Lundmark, T., Marshall, J., Nilsson, M.B., Näsholm, T., Tarvainen, L., Öquist, M., Peichl, M., 2017. Apparent winter CO_2 uptake by a boreal forest due to decoupling. *Agric. For. Meteorol.* 232, 23–34.
- Joffre, R., Rambal, S., 1993. How tree cover influences the water balance of Mediterranean rangelands. *Ecology* 74, 570–582.
- Johnson, D.W., Binkley, D., Conklin, P., 1995. Simulated effects of atmospheric deposition, harvesting, and species change on nutrient cycling in a loblolly pine forest. *For. Ecol. Manage.* 76, 29–45.
- Kätterer, T., Andrén, O., Jansson, P.-E., 2006. Pedotransfer functions for estimating plant available water and bulk density in Swedish agricultural soils. *Acta Agric. Scand. Sect. B* 56, 263–267.
- Katul, G.G., Todd, P., Pataki, D.E., Kabala, Z.J., Oren, R., 1997. Soil water depletion by oak trees and the influence of root water uptake on the moisture content spatial statistics. *Water Resour. Res.* 33, 611–623.
- Katz, C., Oren, R., Schulze, E.-D., Steudle, E., 1989. Uptake of Water and solutes through bark and needle surfaces. In: In: Schulze, E.-D., Lange, O.L., Oren, R. (Eds.), Forest Decline and Air Pollution: A Study of spruce (*Picea abies* (L.) Karst.) on Acid Soils. Ecological Studies Series, vol. 77. Springer Verlag, Berlin, pp. 218–221.
- Kellihier, F.M., et al., 1998. Evaporation from a central Siberian pine forest. *J. Hydrol.* 205, 279–296.
- Kim, H.-S., Palmroth, S., Thérézien, M., Stenberg, P., Oren, R., 2011. Analysis of the sensitivity of absorbed light and incident light profile to various canopy architecture and stand conditions. *Tree Physiol.* 30, 31–47.
- Komatsu, H., Kume, T., Otsuki, K., 2008. The effect of converting a native broad-leaved forest to a coniferous plantation forest on annual water yield: a paired-catchment study in northern Japan. *For. Ecol. Manage.* 255, 880–886.
- Kulmala, L., Pumpanen, J., Kolari, P., Muukkonen, P., Hari, P., Vesala, T., 2011. Photosynthetic production of ground vegetation in different-aged Scots pine (*Pinus sylvestris*) forests. *Can. J. For. Res.* 41 (10), 2020–2030.
- Laudon, H., Ottosson-Löfvenius, M., 2016. Adding snow to the picture – providing complementary winter precipitation data to the Krycklan Catchment study database. *Hydro. Processes* 30, 2413–2416.
- Laudon, H., Taberman, A., Ågren, A., Futter, M., Ottosson-Löfvenius, M., Bishop, K., 2013.

- The Krycklan catchment study – a flagship infrastructure for hydrological, biogeochemistry, and climate research in the boreal landscape. *Water Resour. Res.* 49, 7154–7158.
- Lim, H., Oren, R., Palmroth, S., Tor-ngern, P., Mörling, T., Näsholm, T., Lundmark, T., Helmisaari, H.-S., Leppälämmi-Kujansuu, J., Linder, S., 2015. Inter-annual variability of precipitation constrains the production response of boreal *Pinus sylvestris* to nitrogen fertilization. *For. Ecol. Manage.* 348, 31–45.
- Luis, V.C., Jiminez, M.S., Morales, D., Cucera, J., Wieser, G., 2005. Canopy transpiration of a Canary Island pine forest. *Agric. For. Meteorol.* 135, 117–123.
- Lundmark, A., Jansson, P.-E., 2009. Generic soil descriptions for modelling water and chloride dynamics in the unsaturated zone based on Swedish soils. *Geoderma* 150, 85–95.
- Mäkelä, A., Kolari, P., Karimäki, J., Nikinmaa, E., Perämäki, M., Hari, P., 2006. Modelling five years of weather-driven variation of GPP in a boreal forest. *Agric. For. Meteorol.* 139, 382–398.
- Manoli, G., Domec, J.-C., Novick, K., Oishi, A.C., Noormets, A., Marani, M., Katul, G., 2016. Soil-plant-atmosphere conditions regulating convective cloud formation above southeastern US pine plantations. *Global Change Biol.* 22, 2238–2254.
- McCarthy, H.R., Oren, R., Finzi, A.C., Ellsworth, D.S., Kim, H.S., et al., 2007. Temporal dynamics and spatial variability in the enhancement of canopy leaf area under elevated atmospheric CO₂. *Global Change Biol.* 13, 2479–2497.
- Mellander, P.-E., Bishop, K., Lundmark, T., 2004. The influence of soil temperature on transpiration: a plot scale manipulation in a young Scots pine stand. *For. Ecol. Manage.* 195, 15–28.
- Milly, P.C.D., 1994. Climate, soil water storage, and the average annual water balance. *Water Res. Res.* 30, 2143–2156.
- Miralles, D.G., Gash, J.H., Holmes, T.R.H., De Jeu, R.A.M., Dolman, A.J., 2010. Global canopy interception from satellite observations. *J. Geophys. Res.* 115, D16122. <http://dx.doi.org/10.1029/209JD013530>.
- Montaldo, N., Oren, R., 2016. The way the wind blows matters to ecosystem water use efficiency. *Agric. For. Meteorol.* 217, 1–9.
- Novick, K.A., Oishi, A.C., Ward, E.J., Siqueira, M., Juang, J.Y., Stoy, P.C., 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, 827–842.
- Oishi, A.C., Oren, R., Novick, K.A., Palmroth, S., Katul, G.G., 2010. Interannual variability of forest evapotranspiration and its consequence to water flow downstream. *Ecosystems* 13, 421–436.
- Oren, R., Phillips, N., Katul, G., Ewers, B.E., Pataki, D.E., 1998a. Scaling xylem sap flux and soil water balance and calculating variance: a method for partitioning water flux in forests. *Ann. For. Sci.* 55, 191–216.
- Oren, R., Ewers, B.E., Todd, P., Phillips, N., Katul, G.G., 1998b. Water balance delineates the soil layer in which moisture affects canopy conductance. *Ecol. Appl.* 8, 990–1002.
- Oren, R., Sperry, J.S., Katul, G.G., Pataki, D.E., Ewers, B.E., Phillips, N., Schäfer, K.V.R., 1999. Survey and synthesis of intra- and interspecific variation in stomatal sensitivity to vapour pressure deficit. *Plant Cell Environ.* 22, 1515–1526.
- Palmroth, S., Katul, G.G., Hui, D., McCarthy, H.R., Jackson, R.B., Oren, R., 2010. Estimation of long-term basin scale evapotranspiration from streamflow time series. *Water Resour. Res.* 46, W10512.
- Palmroth, S., Bach, L.H., Nordin, A., Palmqvist, K., 2014. Nitrogen-addition effects on leaf traits and photosynthetic carbon gain of boreal forest understory shrubs. *Oecologia* 175, 457–470 ri.
- Parida, B.R., Buermann, W., 2014. Increasing summer drying in North American ecosystems in response to longer nonfrozen periods. *Geophys. Res. Lett.* 41, 5476–5483.
- Pataki, D.E., Oren, R., 2003. Species difference in stomatal control of water loss at the canopy scale in a bottomland deciduous forest. *Adv. Water Res.* 26, 1267–1278.
- Phillips, N., Oren, R., 2001. Intra- and inter-annual variation in transpiration of a pine forest. *Ecol. Appl.* 11, 385–396.
- Potter, N.J., Zhang, L., Milly, P.C.D., McMahon, T.A., Jakeman, A.J., 2005. Effects of rainfall seasonality and soil moisture capacity on mean annual water balance for Australian catchments. *Water Res. Res.* 41, W06007.
- Schäfer, K.V.R., Oren, R., Lai, C.-T., Katul, G.G., 2002. Hydrologic balance in an intact temperate forest ecosystem under ambient and elevated atmospheric CO₂ concentration. *Global Change Biol.* 8, 895–911.
- Schäfer, K.V.R., Oren, R., Ellsworth, D.S., Lai, C.-T., Herrick, J.D., Finzi, A.C., Richter, D.D., Katul, G.G., 2003. Exposure to an enriched CO₂ atmosphere alters carbon assimilation and allocation in a pine forest ecosystem. *Global Change Biol.* 9, 1378–1400.
- Stenberg, P., 1996. Correcting LAI-2000 estimates for the clumping of needles in shoots of conifers. *Agric. For. Meteorol.* 79, 1–8.
- Stocker, T.F., Qin, D., Plattner, G.-K., Alexander, L.-V., Allen, S.K., Bindoff, N.L., Bréon, F.-M., Church, J.A., Cubasch, U., Emori, S., Forster, P., Friedlingstein, P., Gillett, N., Gregory, J.M., Hartmann, D.L., Jansen, E., Kirtman, B., Knutti, R., Krishna Kumar, K., Lemke, P., Marotzke, J., Masson-Delmotte, V., Meehl, G.A., Mokhov, I.I., Piao, S., Ramaswamy, V., Randall, D., Rhein, M., Rojas, M., Sabine, C., Shindell, D., Tally, L.D., Vaughan, D.G., Xie, S.-P., 2013. Technical summary. In: Stocker, T.F., Qin, D., Plattner, G.-K., Tignor, M., Allen, S.K., Boschung, J., Nauels, A., Xia, Y., Bex, V., Midgley, P.M. (Eds.), *Climate Change 2013: The Physical Science Basis. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change*. Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA.
- Stoy, P.C., Katul, G.G., Siqueira, M.B.S., Juang, J.-Y., Novick, K.A., McCarthy, H.R., Oishi, A.C., Uebelherr, J.M., Kim, H.-S., Oren, R., 2006. Separating the effects of climate and vegetation on evapotranspiration along a successional chronosequence in the southeastern US. *Global Change Biol.* 12, 1–21.
- Swank, W.T., Douglas, J.E., 1974. Streamflow greatly reduced by converting deciduous hardwood stands to pine. *Science* 185, 857–859.
- Thérizien, M., Palmroth, S., Brady, R., Oren, R., 2007. Estimation of light interception properties of conifer shoots by an improved photographic method and a 3D model of shoot structure. *Tree Physiol.* 27, 1375–1387.
- Tor-ngern, P., Oren, R., Oishi, A.C., Uebelherr, J.M., Palmroth, S., Tarvainen, L., Ottoson-Lövenius, M., Linder, S., Domec, J.-C., Näsholm, T., 2017. Ecophysiological variation of transpiration of pine forests: synthesis of new and published results. *Ecol. Appl.* 27, 118–133.
- Uebelherr, J.M., 2008. The Effects of Plant-Area index on Precipitation Throughfall and Its Spatiotemporal Variation Among Deciduous and Evergreen Forests. MS thesis. University Program in Ecology. Duke University, Durham, North Carolina USA.
- Unsworth, M.H., Phillips, N., Link, T., Bond, B.J., Falk, M., Harmon, M.E., Hinckley, T.M., Marks, D., Kyaw Tha Paw, U., 2004. Components and controls of water flux in an old-growth Douglas-fir-Western-hemlock ecosystem. *Ecosystems* 7, 468–481.
- Vincke, C., Thiry, Y., 2008. Water table is a relevant source for water uptake by a Scots pine (*Pinus sylvestris* L.) stand: evidences from continuous evapotranspiration and water table monitoring. *Agric. For. Meteorol.* 148, 1419–1432.
- Viville, D., Biron, P., Granier, A., Dambrine, E., Probst, A., 1993. Interception in a mountainous declining spruce stand in the Strengbach catchment (Vosges, France). *J. Hydrol.* 144, 273–282.
- Wang, T., Istanbulluoglu, E., Lenters, J., Scott, D., 2009. On the role of groundwater and soil texture in the regional water balance: an investigation of the Nebraska Sand Hills. *USA. Water Resour. Res.* 45, W10413.
- Wear, D.N., Greis, J.G., 2012. The southern forest futures project: summary report. Gen Tech. Rep. SRS-GTR-168, vol. 54. USDA-Forest Service, Southern Research Station, Asheville, NC, pp. 1–54 p., 168.
- Whitehead, D., Kelliher, F.M., 1991. Modeling the water balance of a small *Pinus radiata* catchment. *Tree Physiol.* 9, 17–33.
- Wu, C.H., Hu, B.X., Huang, G., Zhang, H., 2017. Effects of climate and terrestrial storage on temporal variability of actual evapotranspiration. *J. Hydrol.* 549, 388–403.
- Wullschleger, S.D., Hanson, P.J., 2006. Sensitivity of canopy transpiration to altered precipitation in an upland oak forest: evidence from a long-term field manipulation study. *Global Change Biol.* 12, 97–109.
- Wullschleger, S.D., Hanson, P.J., Tschaplinski, T.J., 1998. Whole-plant water flux in understory red maple exposed to altered precipitation regimes. *Tree Physiol.* 18, 71–79.
- Yan, M., Tian, X., Li, Z., Chen, E., Wang, X., Han, Z., Sun, H., 2016. Simulation of forest carbon fluxes using model incorporation and data assimilation. *Remote Sens.* 8 (567). <http://dx.doi.org/10.3390/rs8070567>.
- Zhang, L., Dawes, W.R., Walker, G.R., 2001. Response of mean annual evapotranspiration to vegetation changes at catchment scale. *Water Res. Res.* 37, 701–708.
- Zhang, L., Hickel, K., Dawes, W.R., Chiew, F.H.S., Western, A.W., Briggs, P.R., 2004. A rational function approach for estimating mean annual evapotranspiration. *Water Res. Res.* 40 <http://dx.doi.org/10.1029/2003WR002710>. W02502.