



Partitioning evapotranspiration with concurrent eddy covariance measurements in a mixed forest

Eugénie Paul-Limoges^{a,*}, Sebastian Wolf^b, Fabian D. Schneider^c, Marcos Longo^c, Paul Moorcroft^d, Mana Gharun^e, Alexander Damm^{a,f}

^a Department of Geography, University of Zurich, Winterthurerstrasse 190, 8057 Zurich, Switzerland

^b Institute of Terrestrial Ecosystems, ETH Zurich, Universitaetstrasse 16, 8092 Zurich, Switzerland

^c Jet Propulsion Laboratory, California Institute of Technology, 4800 Oak Grove Drive, Pasadena, CA 91109, USA

^d Department of Organismic and Evolutionary Biology, Harvard University, 26 Oxford Street, Cambridge, MA 02138, USA

^e Institute of Agricultural Sciences, ETH Zurich, Universitaetstrasse 2, 8092 Zurich, Switzerland

^f Eawag, Swiss Federal Institute of Aquatic Science and Technology, 8600 Dübendorf, Switzerland

ARTICLE INFO

Keywords:

Transpiration

Evaporation

Subcanopy

Below canopy

Sap flow

Vapor pressure deficit

ABSTRACT

Plants have an important effect on our climate: as they assimilate atmospheric CO₂ through the process of photosynthesis, they also transpire water to the atmosphere and thereby influence surface temperatures. It is, however, difficult to quantify transpiration from ecosystems due to measurement limitations. Direct eddy covariance (EC) measurements are currently the best available approach to observe interactions linked to biosphere-atmosphere CO₂ and water vapor exchange. While there are well-established methods to partition CO₂ fluxes into the component fluxes of photosynthesis and respiration, there is still no standardized method to partition water vapor fluxes (evapotranspiration, ET) into the component fluxes of evaporation and transpiration.

In this study, we used two years of concurrent below and above canopy EC measurements in a mixed deciduous forest in Switzerland to partition water vapor fluxes into the components of transpiration (biological) and evaporation (physical). We compare our results with transpiration from the ecosystem demographic (ED2) model as well as derived from plot-level sap flow measurements. EC-derived transpiration accounted on average for 74% of ET, emphasizing a considerably lower contribution from evaporation. EC and sap flow measurements showed mid-afternoon reductions in transpiration during periods of high vapor pressure deficit in summer. Reductions in ET and transpiration were found under limiting soil moisture conditions, while the ratio of transpiration to ET remained constant over the years due to the low and rather constant evaporation in this closed canopy forest. Stomatal regulation in response to enhanced atmospheric evaporative demand was also found under water-stressed conditions in the afternoon in summer. When comparing our EC-derived evaporation with the ED2 model, we found large discrepancies linked to the challenge of modeling evaporation in a light limited, yet variable environment below the canopy. A strong correlation was found for transpiration from ED2 with the EC-based estimates. Our results show the potential of concurrent below and above canopy EC measurements to partition ecosystem ET in forests.

1. Introduction

By assimilating carbon dioxide (CO₂) through photosynthesis and releasing water vapor through transpiration, plants have an important dual effect on our climate: mitigating enhanced atmospheric CO₂ concentrations and reducing surface temperatures (Anderegg et al., 2015; Humphrey et al., 2018). As atmospheric CO₂ concentration increases, plants reduce the opening of their stomata, thereby reducing

transpiration rates (Betts et al., 2007; Cao et al., 2010; Field et al., 1995). This reduction in plant transpiration is an additional physiological forcing on top of the radiative forcing linked to increased atmospheric CO₂ concentrations, enhancing the warming of the Earth (Cao et al., 2010; Sellers et al., 1996); as plant transpiration is reduced, there is a reduction in evaporative cooling and this exacerbates the increase in surface temperatures (e.g. Wolf et al., 2016). Warmer and dryer climatic conditions can also lead to earlier plant senescence, thus

* Corresponding author.

E-mail address: eugenie.paul-limoges@geo.uzh.ch (E. Paul-Limoges).

<https://doi.org/10.1016/j.agrformet.2019.107786>

Received 28 February 2019; Received in revised form 26 September 2019; Accepted 30 September 2019

0168-1923/ © 2019 Elsevier B.V. All rights reserved.

further reducing plant transpiration (Zavaleta et al., 2003). On the other hand, an increase in CO₂ concentration can also have a vegetation fertilization effect, leading to increased foliage area and thereby enhancing photosynthesis (Keenan et al., 2013; Piao et al., 2007). There is ongoing debate on how these contrasting effects will influence our climate particularly in forest ecosystems, where transpiration is an important flux of water between the trees and the atmosphere (Schlesinger and Jasechko, 2014).

Ecosystem transpiration is, however, difficult to measure. Due to the overlap of the interests of different disciplines linked to transpiration, various methodologies coming from hydrology, micrometeorology and ecophysiology are used to quantify transpiration or more often, evapotranspiration (ET) (i.e., the combination of plant transpiration, plant evaporation and soil evaporation). These methodologies differ in the components they are measuring (i.e. transpiration or evaporation or evapotranspiration), and in their temporal (i.e. seconds to annual budget) and spatial scales (i.e., leaf to watershed) (Wilson et al., 2001). Soil water budgets (e.g. Cuenca et al., 1997; Eastham et al., 1988; Jaeger and Kessler, 1997) can be used to estimate the total ET from the soil through a balance of water inputs and outputs into the soil, where ET is the remaining unknown (Nolz et al., 2014). Similarly, catchment water budgets (e.g. Bosch and Hewlett, 1982) provide an annual integrated assessment of ET for entire catchments. These budget approaches tend to be relatively inexpensive; however, ET sums derived from hydrological water balances are limited in their ability to inform on biophysical controls at shorter timescales and do not allow the partitioning of ET (Baldocchi and Ryu, 2011). Sap flow measurements (e.g. Smith and Allen, 1996) provide mechanistic details linked to plant transpiration on short temporal scales (i.e., seconds), thereby allowing an understanding of the physiological and environmental controls of transpiration at the plant level (Wullschlegel et al., 1998). This plant-level transpiration then needs to be scaled up to the ecosystem level based on allometry and a detailed knowledge of the forest composition and structure, however often resulting in large uncertainties (e.g. Rouspard et al., 2006; Wilson et al., 2001). Above canopy eddy covariance (EC) measurements (Baldocchi et al., 1988) quantify the total ET from the ecosystem (i.e. vegetation and soil), at scales ranging from typically a few 100 m² in croplands up to 1 km² or more in forests. Although the EC technique measures CO₂ and H₂O exchange simultaneously, only a very small fraction of the efforts within the FLUXNET community has been focused on the water fluxes (Baldocchi and Ryu, 2011). Moreover, while there are well-established methods to partition CO₂ fluxes from EC into the component fluxes of photosynthesis and respiration (e.g. Lasslop et al., 2010; Reichstein et al., 2005), there is currently no standardized method to partition water vapor fluxes into evaporation and transpiration.

In forest ecosystems, concurrent below and above canopy EC measurements can be used to partition the CO₂ and H₂O flux contributions coming from the soil and understory vegetation to the net ecosystem flux measured above canopy (e.g. Black et al., 1996; Misson et al., 2007; Paul-Limoges et al., 2017; Scott et al., 2003). However, only a few studies have partitioned the below canopy contribution for ET. Below canopy ET has been found to range from 10 to 38% of the ecosystem ET (Baldocchi and Vogel, 1996; Black et al., 1996; Constantin et al., 1999; Jarosz et al., 2008; Kilinc et al., 2013; Launiainen et al., 2005), this range being highly influenced by the amount of energy reaching the ground surface of the forest (i.e., the canopy cover). Even fewer studies thus far have attempted to simply use fluxes from below and above canopy to estimate the contribution from the trees (Black et al., 1996; Rouspard et al., 2006; Wilson et al., 2001). With some of the initial EC measurements at the boreal aspen site in Canada, Black et al. (1996) were the first to introduce the concept of using below and above canopy EC measurements to partition the tree component, by simply subtracting the curves for below and above canopy net CO₂ exchange. With regards to tree transpiration, Rouspard et al. (2006) and Wilson et al. (2001) used below and above canopy EC to estimate tree

transpiration and compared their results with other approaches. Rouspard et al. (2006) partitioned the transpiration from a simple architecture, open canopy, row crop coconut palm plantation with high aerodynamic mixing and showed a good agreement with transpiration derived from sap flow measurements. Similarly, Wilson et al. (2001) partitioned transpiration in an uneven-aged mixed deciduous forest in the Southeastern United States and found good agreement on the magnitude of annual ET when compared to a catchment balance approach. Yet, despite these two pioneer studies, the use of below canopy measurements has still not been widely applied to partition tree transpiration due mostly to 1) micrometeorological limitations below the canopy and 2) the ambiguity linked to the ET derived for the canopy being not only transpiration, but also including evaporation of the water intercepted by the canopy.

In this study, we are using two years of concurrent below and above canopy EC measurements in a mixed deciduous forest in Switzerland to partition ET into evaporation and transpiration. We build on the previous approaches using below and above canopy EC measurements in forests and suggest improvements for the known limitations. We compare our results with transpiration modeled from the ecosystem demographic model (ED2) as well as with plot-level sap flow measurements. We develop a systematic approach to use concurrent below and above canopy EC measurements to partition transpiration in forest ecosystems.

2. Methods

2.1. Research site

The Lägeren temperate mixed forest site (47°28'42" N, 8°21'52" E, 682 m a.s.l.) is located on the relatively steep (average 24°) south-facing slope of the Lägeren mountain, approximately 15 km northwest of the city of Zurich in Switzerland. The Lägeren forest is characterized by a relatively high species diversity and a complex canopy structure, with European beech (*Fagus sylvatica* L., 40%), ash (*Fraxinus excelsior* L., 19%), sycamore maple (*Acer pseudoplatanus* L., 13%), European silver fir (*Abies alba* Mill., 8%), large-leaved linden (*Tilia platyphyllos*, 8%) and Norway spruce (*Picea abies* (L.) Karst., 4%) as the dominant species. The mean tree height of dominant trees is 30.6 m (Etzold et al., 2011) and the understory vegetation is dominated by wild garlic (*Allium ursinum* L.) of a maximum height of 0.4 m during spring and early summer (March to June). The open space between the top of the understory vegetation and the bottom of the overstory canopy is about 15 m. The main soil type is a well-drained haplic cambisol. Mean annual temperature is 7.4 °C, and mean annual precipitation is 1000 mm (Etzold et al., 2011). The site is part of the Swiss Air Quality Monitoring Network (NABEL) since 1986 and of the Swiss FluxNet since 2004 (www.swissfluxnet.ch).

2.2. Meteorological measurements

Above canopy measurements of climatic variables were made at a height of 47 m. Air temperature was measured using a temperature probe (Rotronic MP101A, Bassersdorf, Switzerland) inside a radiation shield. Global radiation was measured using a CNR 1 four-way net radiometer (Kipp & Zonen B.V., Delft, The Netherlands). Soil temperature and water content were measured at depths of 10, 20, and 30 cm using Decagon ECH₂O EC-20 probes (Pullman, WA, USA). Measurements were controlled and stored by a data logger (CR10X, Campbell Scientific Inc., Loughborough, UK); measurements were made every 30 s and output averaged every 10 min. Small gaps (< 2 h) in the meteorological time series were gap-filled by interpolation, and larger gaps were filled using mean diurnal variations based on a 14-day moving window. The National Air Pollution Monitoring Network (NABEL) provided precipitation data measured at 47 m height on the same tower at a 10-min resolution.

2.3. Eddy covariance measurements

Turbulent fluxes of water vapor were measured continuously below and above the canopy in 2014 and 2015 using the eddy covariance (EC) technique (Paul-Limoges et al., 2017). The below canopy EC system was at a height of 1.5 m above the soil surface, while the above canopy EC system was at a height of 47 m. The below canopy EC system was within the main footprint of the above canopy EC system. The EC instrumentation at each level consisted of an open-path infrared gas analyzer (IRGA) (model LI-7500, LI-COR Inc., Lincoln, NE, USA) and a three-dimensional ultrasonic anemometer–thermometer (models HS (above) and R3 (below), Gill Instruments Ltd., Lymington, UK). EC measurements were made at a frequency of 20 Hz. The statistical quality of the raw time series was assessed before flux calculations following Vickers and Mahrt (1997). Raw high-frequency data were rejected if (1) spikes accounted for more than 1% of the time series, (2) more than 10% of available data points were statistically different from the overall trend in the half-hour period, (3) raw data values were outside a plausible range, or (4) window dirtiness of the IRGA sensor exceeded 80%. Only raw data that passed all quality tests were used for flux calculations.

Half-hourly fluxes of H_2O were calculated using the *EddyPro* software (v6.1.0, LI-COR Inc., USA). Frequency response corrections were applied to raw fluxes, accounting for high-pass (Moncrieff et al., 2005) and low-pass filtering (Horst, 1997). Spectral corrections were applied to the ET fluxes prior to the WPL correction (Webb et al., 1980). Delays were calculated using the covariance maximization procedure, consisting of the determination of the time lag that maximizes the covariance of two variables, within a window of plausible time lags (see for e.g. Fan et al. (1990)). A conventional two-dimensional coordinate rotation was applied, as this was found to be the best suited rotation for the Lägeren site (Göckede et al., 2008). Half-hourly averaged fluxes were rejected if (1) H_2O fluxes were outside a physically plausible range, (2) the steady-state test statistic was outside the range $\pm 30\%$ (Foken et al., 2005), or (3) the integral turbulence characteristic test was outside the $\pm 30\%$ range (Foken et al., 2005). Small gaps (< 2 h) in the half-hourly flux time series were gap-filled by interpolation, and larger gaps were filled using mean diurnal variations based on a 14-day moving window. The vapor pressure deficit (VPD) was derived from the EC measurements, as the difference between the actual water vapor pressure and its saturation value.

2.4. Partitioning transpiration from EC measurements

Concurrent below and above canopy EC measurements were used to partition ET at the Lägeren mixed forest. Conceptually, above canopy EC systems measure the integrated total ET from the forest, while the below canopy EC systems measure the contribution from the soil and understory vegetation (Fig. 1). In general, ET from the below canopy layer is composed of soil evaporation and understory plant transpiration (if present), while the canopy layer is composed predominantly of tree transpiration and evaporation from the trees, especially following rain events (Fig. 1). It is important to note that transpiration has a physiological (biological) source while evaporation has a physical source. The importance of the evaporation and transpiration components below and above the canopy depends on the ecosystem and time of year. Fig. 2 illustrates the relative importance of the ET components over the course of a year at the Lägeren mixed forest site.

The below canopy EC measurements can therefore be used to remove the contribution from the soil and understory vegetation from the total ET measured for the forest, allowing to partition the contribution from the trees (i.e., $ET_{\text{tree}} = ET_{\text{above}} - ET_{\text{below}}$). However, although the two studies thus far that have estimated transpiration have shown good results (Roupsard et al., 2006; Wilson et al., 2001), there are still important limitations linked to the coupling of the layers (Jocher et al., 2017; Paul-Limoges et al., 2017; Thomas et al., 2013), counter-gradient

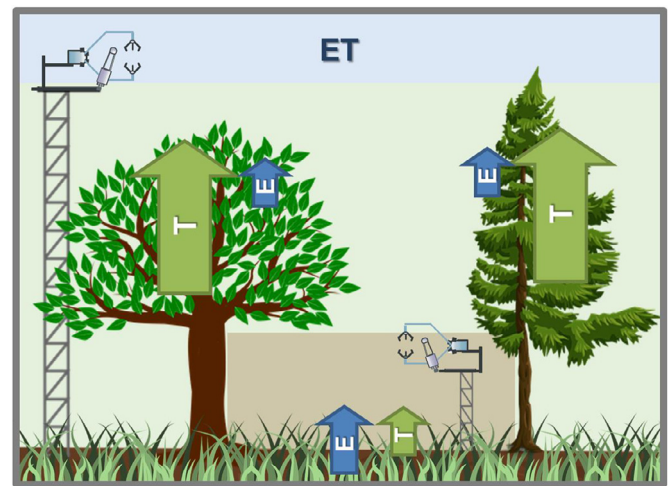


Fig. 1. Conceptual representation of below and within canopy evapotranspiration (ET) contributions to below and above canopy EC measurements. The blue arrows represent the physical evaporation (E) and the green arrows represent the biological transpiration (T). The boxes represent the relative source areas for below canopy (brown), within canopy (green) and above canopy (blue). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

transport below the canopy (Denmead and Bradley, 1985) and evaporation within the canopy that need to be taken into account to improve the accuracy of the transpiration derived. The following section will explain the steps needed to ensure that this conceptual approach is reliable to partition transpiration at an EC site with concurrent below and above measurements.

2.4.1. Coupling assessment

When using concurrent below and above canopy EC systems, assessing the coupling of both layers is essential to ensure reliable conclusions can be made. A previous study using the below and above canopy EC systems to study CO_2 fluxes at the Lägeren site found that the site was subject to decoupling under full canopy closure, thereby leading to errors in the CO_2 fluxes reported when measured only above canopy (Paul-Limoges et al., 2017). Similarly, other studies using concurrent below and above canopy EC systems have also found that decoupling occurred at their sites once below canopy EC measurements were added (Jocher et al., 2017; Thomas et al., 2013). Different stability and turbulence-based indices (e.g. Richardson number, TKE, u^* , σ_w) can be used to assess the coupling of the below and above canopy layers depending on the research sites. At the Lägeren site, the best coupling indicator was found to be the standard deviation of the vertical wind velocity (σ_w) (Paul-Limoges et al., 2017), as the relationship between σ_w below and above canopy is linear when the layers are coupled (Jocher et al., 2017; Thomas et al., 2013). In order to determine the onset and end of the decoupled period, a 5-day moving window was used to determine the change in the linearity of the σ_w relationship (for more details see Paul-Limoges et al., 2017).

2.4.2. Downward moving eddies below the canopy (counter-gradient transport)

Although most eddies tend to be moving upward, there is the possibility below the canopy that some eddies will be coming downward due to counter-gradient transport (e.g. Denmead and Bradley, 1985), either from above the canopy or from the bottom of the canopy crowns. Such downward eddies lead to biases in the below canopy contributions, as they appear as negative water fluxes (i.e. condensation), and therefore, need to be removed from the time series. In order to assess for such conditions, we used two criteria: isolate times (1) when the measured below canopy ET fluxes are negative (w is downward) and (2)

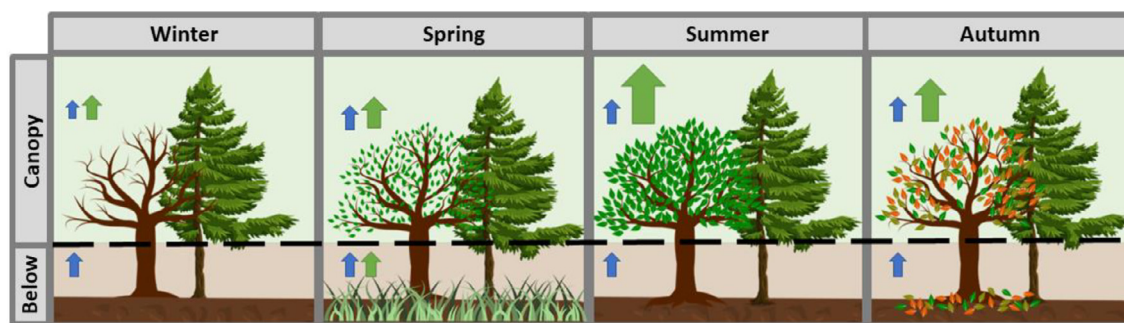


Fig. 2. Conceptual figure illustrating the contributions to evapotranspiration (ET) below and within the canopy at the Lägeren mixed forest site. The blue arrows represent evaporation (E) and the green arrows represent transpiration (T). The black dashed line delimitates the contributions measured below and within the canopy. Seasons are defined as winter (December, January, February), spring (March, April, May), summer (June, July, August) and autumn (September, October, November). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

when the measured below canopy temperature is above the dew point temperature, i.e. when condensation should not occur. As such conditions often represent very short time periods, the gaps can be filled by interpolation.

2.4.3. Removing the contribution of evaporation from the trees

As Fig. 1 indicates, although the water fluxes coming from the trees tend to be dominated by transpiration, there is also a small portion of water that can be evaporated from leaf surfaces. Accounting for the evaporation from the trees often leads to uncertainties in the transpiration derived using below canopy measurements. In order to remove the tree evaporation contribution, two main measurement-based approaches can be applied (1) using leaf wetness sensors or (2) removing periods following rain events. As we did not have leaf wetness sensors, we removed periods after rain events greater or equal to 0.1 mm, which in our case suggested 7% of evaporation from the trees over the two years, assuming that following rain events no transpiration would occur since relative humidity is close to 100% and therefore, there is no water potential for transpiration (i.e., the water on the leaf surface will evaporate first). Removing periods after rain events, however, leads to some uncertainties in tree evaporation estimates, as the duration of the canopy wetness is unknown. To reduce this uncertainty, vertical profiles of leaf wetness sensors could be used to characterise the drying of the canopy, as the different canopy layers will often dry at different rates. In addition, interception models (e.g. Rutter et al. (1971)) could be used in combination with throughfall or stemflow measurements to bound the uncertainties in interception.

2.5. Comparison of transpiration derived with different approaches

In this section, we compare the approach using concurrent below and above canopy EC measurements with other approaches for transpiration (Table 1).

2.5.1. Sap flow measurements

Constant heat flow sensors (SFS2 Type M, UP Ibbenbüren, Germany) were used to measure 16 trees in total, based on the method described by Granier (1985, 1987). One sap flow sensor consisted of two copper-constantan thermocouple needles (20 mm length); the upper needle was constantly heated and the temperature gradient

between the two needles was recorded. The needles were installed vertically at breast height one above the other separated by a distance of 12.5 cm. High xylem sap velocities implied a faster transport of heat and consequently, a smaller temperature difference between the two needles. Sap flow sensors were installed on four trees of four different species (beech, ash, maple and spruce; 16 trees in total). However, the sap flow sensors on the beech trees, the main species, during the two years of this study were found to be faulty and therefore, could not be used. Two sap flow sensors were installed on each tree, one facing north and the other one facing south. Sap flow sensors were covered with a bubble wrap aluminum foil to protect them from rain and influences from air temperature fluctuations. Sap flow data were collected in 2014 and 2015 at 10-min intervals and then averaged half-hourly. Sap flow rates were calculated after Granier (1985, 1987) and for each tree the sap flow rates from north and south sensors were averaged to minimize potential thermal effects of sunshine.

2.5.2. Physiological modeling (ED2 model)

In the Ecosystem Demography model version 2 (ED2), the transpiration fluxes are calculated as part of the photosynthesis model, as described in further detail in Medvigy et al. (2009) and Longo et al. (2019b). The photosynthesis model derives from Farquhar et al. (1980) and Collatz et al. (1991), in which the leaf-level net primary productivity (NPP) and transpiration for each group of plants is constrained by the maximum electron transport rate (which depends mostly on the light availability) and the maximum ability of Rubisco to perform the carboxylase function (primarily a function of temperature). In addition, both NPP and transpiration rates are limited by stomatal conductance. In ED2, stomatal conductance is solved based on the formulation proposed by Leuning (1995) that accounts for both the leaf-level NPP and the supply of CO₂ and water vapor, the latter being a function of VPD. In addition, stomatal conductance is down-regulated depending on the amount of plant available soil moisture, defined as the amount of water in excess of the wilting point in the plants rooting zone (Medvigy et al., 2009). Because NPP and stomatal conductance are interdependent, they are solved simultaneously in ED2 (Longo et al., 2019b). Importantly, both the stand NPP and the stand transpiration are obtained by aggregating each individual tree's NPP and transpiration, and the individual tree's fluxes account for their size (e.g. short trees have shallow rooting depths), their position relative to

Table 1

Comparison of the approach with concurrent EC measurements with different types of methods.

Method	Characteristics
Concurrent EC measurements	Continuously measured ET, ecosystem-level, partitioned T and E
Sap flow measurements	Sap flow measured, tree-level, inferred T given representative sample
Physiological modeling (ED2)	Modeled based on site climate and vegetation structure (biomass, tree heights, species)

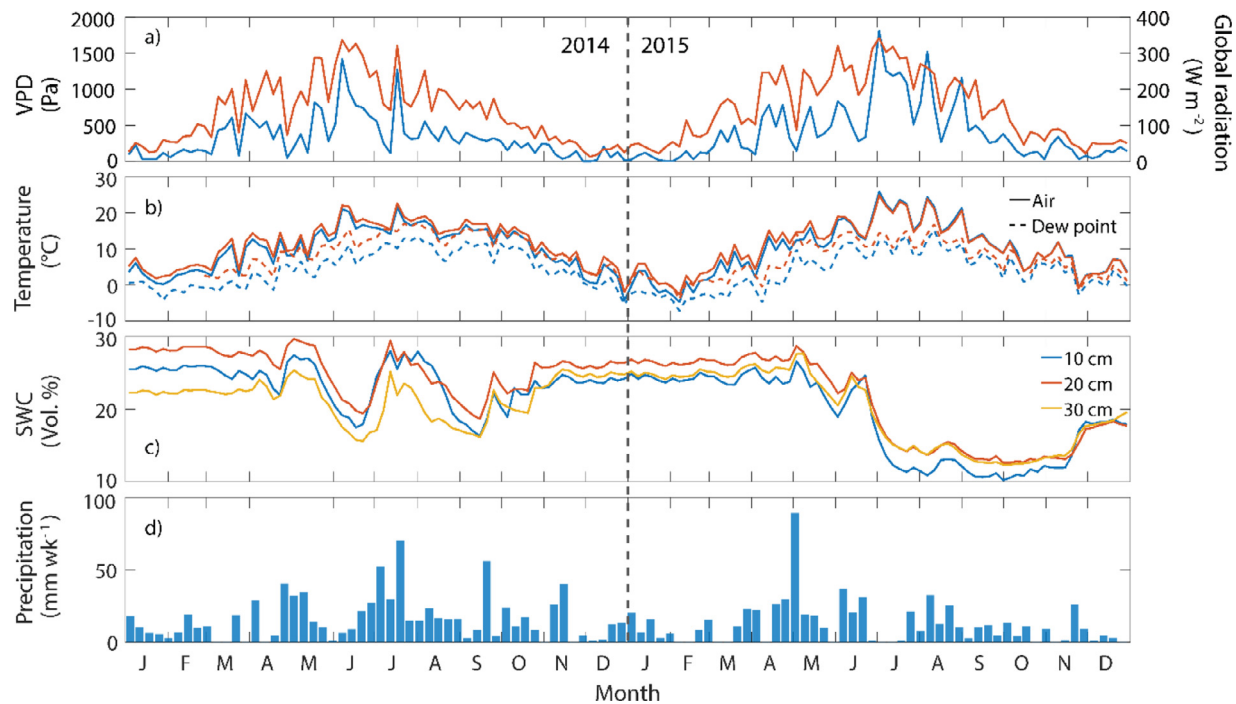


Fig. 3. Environmental conditions at the Lägeren mixed forest site in 2014 and 2015. In panel a), the blue line represents the vapor pressure deficit (VPD) and the red line the global radiation. Red lines in panel b) represent below canopy air temperatures and blue lines represent above canopy air temperatures. Panel c) represents volumetric soil water content (SWC) at 10-cm (blue), 20-cm (red) and 30-cm (yellow) depths. The lines in panels a), b) and c) represent 5-day averages. The bars in panel d) represent total weekly precipitation. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

other trees (e.g. shorter trees will be shaded by taller trees and thus their NPP and transpiration will more likely to be light-limited), and the number of trees in the immediate vicinity (i.e. densely populated patches of forest will experience stronger competition for water than sparsely populated patches, even when soil water content is the same). Additional details on input variables and processes involved in ED2 can be found in Longo et al. (2019a) and Longo et al. (2019b).

3. Results

3.1. Environmental conditions

The 2014 growing season (mid-May to beginning of October) was cooler and wetter, with a mean air temperature of 14.0 °C and 401 mm of rain, compared to the 2015 growing season that had a mean air temperature of 15.6 °C and 252 mm of rain (Fig. 3a and d; Table 2). The contrast between both growing seasons was mostly due to an extended heat wave characterised by low precipitation, high global radiation and high temperatures during the 2015 summer (Fig. 3). Vapor pressure deficit (VPD) and global radiation (R_g) were higher during the 2015

growing season than in 2014 (Fig. 3b). Soil water content at 10-cm depth decreased to 10% in July 2015, being similarly low across depths throughout the soil profile (Fig. 3c). Although air temperature and global radiation decreased after the peak of the heat wave in July–August 2015, soil volumetric water content remained low throughout the fall until November (Fig. 3c). Annual total precipitation was 11% greater during the year 2014 with 1097 mm compared to 977 mm in 2015 (MeteoSwiss station Baden; Table 2), with the end of June-beginning of July period having no precipitation (Fig. 3d).

3.2. Evapotranspiration from eddy covariance measurements

Above canopy annual total evapotranspiration (ET) was slightly greater (8%) in 2014 with 931 mm compared to 863 mm in 2015 (Table 2), in part due to the sharper decrease in ET in August 2015 from the limiting moisture conditions due to the hydrological drought following the meteorological drought from June–July 2015 (Fig. 4). Average above canopy ET was low ($< 1 \text{ mm d}^{-1}$) during the cold winter months (November to February) (Fig. 4). For both 2014 and 2015, above canopy ET started increasing in March and April, before the leaf-out of the deciduous trees in mid-May, due in part to the contribution from the evergreen coniferous trees (Fig. 4). Below canopy ET was consistently low in 2014 and 2015 (Fig. 4) due to the low amount of energy and water available for evaporation at the ground surface. Indeed, average values (based on 7-day running mean) of below canopy ET were always below 0.7 mm (Fig. 4). Higher rates of below canopy ET were found in March–April during the growing season of the wild garlic due to the understory transpiration before leaf emergence of the deciduous canopy (Fig. 4). In some instances, negative below canopy ET values were recorded either due to condensation or to the downward movement of eddies from the canopy (Fig. 4).

Above canopy ET increased from April to June, remained high in summer ($> 0.4 \text{ mm h}^{-1}$ in June to August) and started decreasing again in September (Fig. 5). Compared to 2014, reductions in above canopy

Table 2

Water balance and fractional contributions at the Lägeren mixed forest in 2014 and 2015. Drainage and runoff are estimated as precipitation minus ecosystem ET.

Water balance	2014	2015
Precipitation (P, mm)	1097	977
Ecosystem ET (mm)	931	863
Tree T (mm)	687	642
Tree E (mm)	65	47
Understory ET (mm)	179	174
Estimated drainage and runoff (mm)	166	114
T/ET (%)	74	74
T/P (%)	63	66

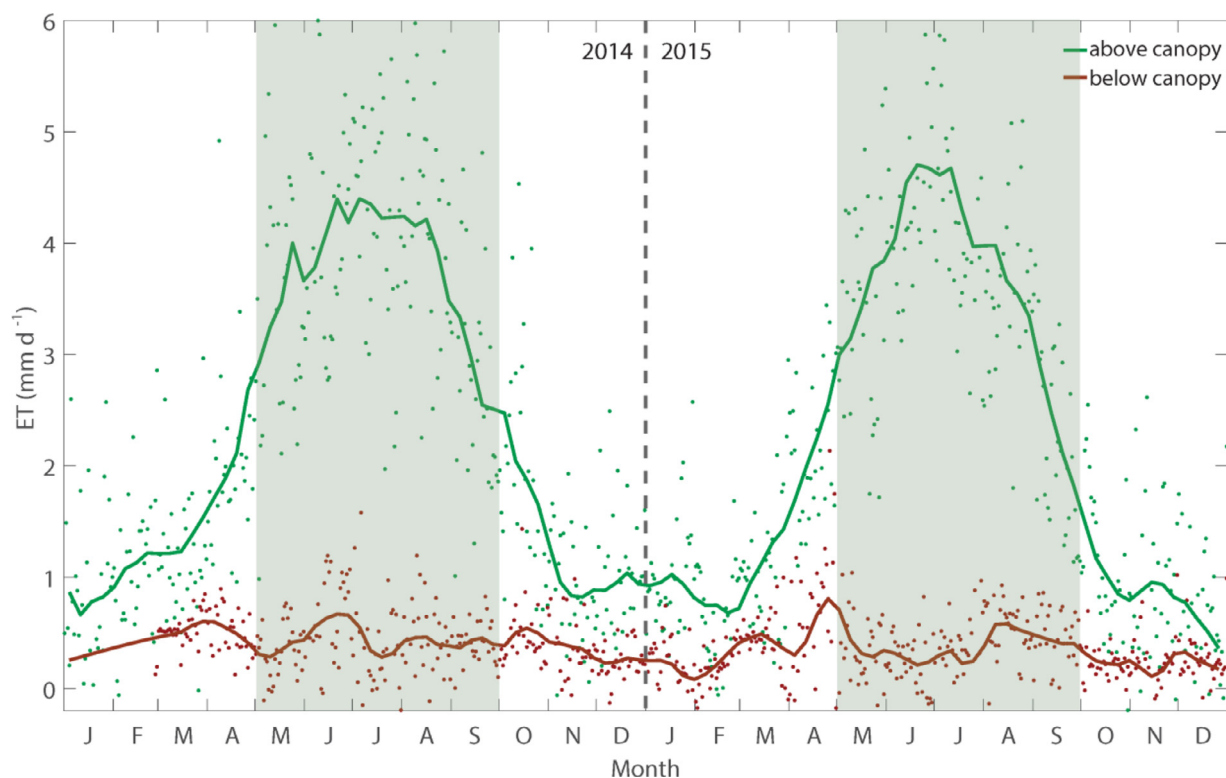


Fig. 4. Evapotranspiration (ET, mm d^{-1}) as measured with the eddy covariance systems above (green) and below (brown) the canopy in 2014 and 2015. The dots represent daily averages and the lines are 7-day running means. The shaded green rectangles represent the period the deciduous trees have leaves (active canopy growing season). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

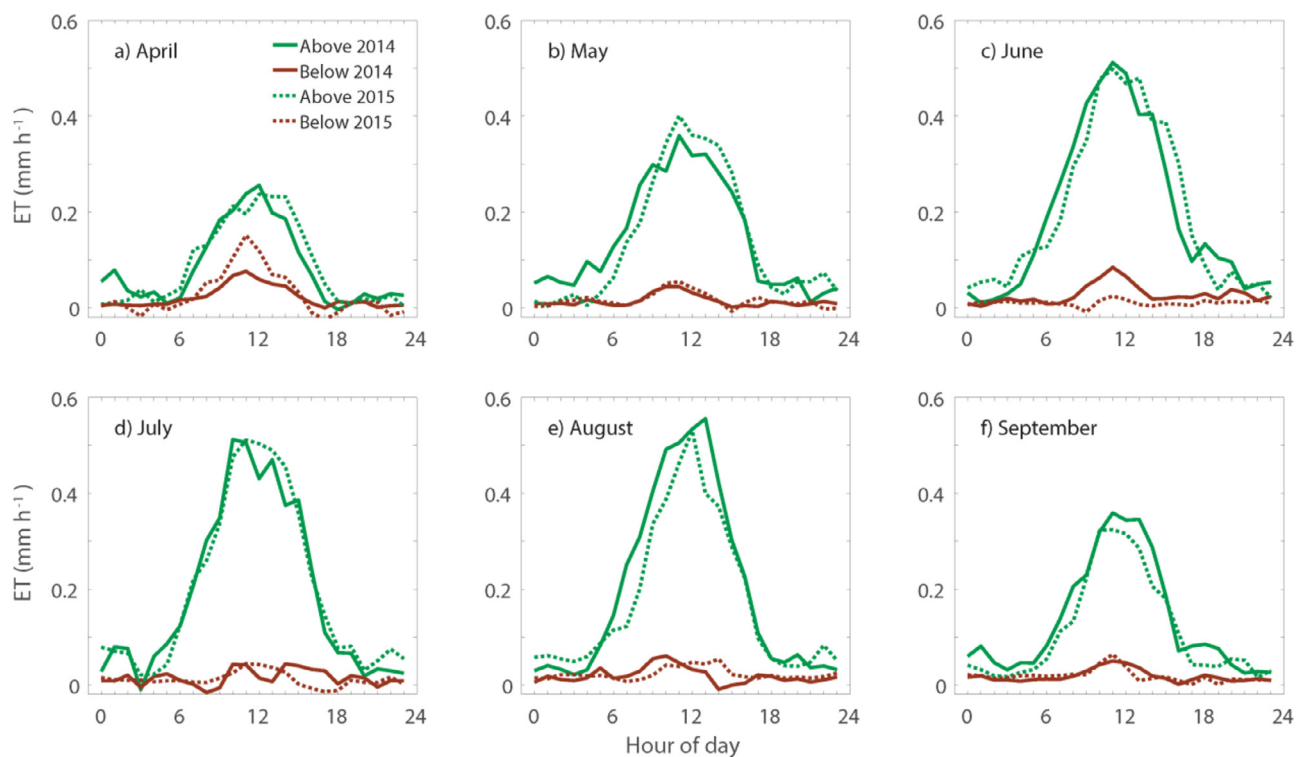


Fig. 5. Mean diurnal evapotranspiration (ET) as measured with the eddy covariance systems above (green) and below (brown) the canopy in 2014 (solid lines) and in 2015 (dotted lines). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

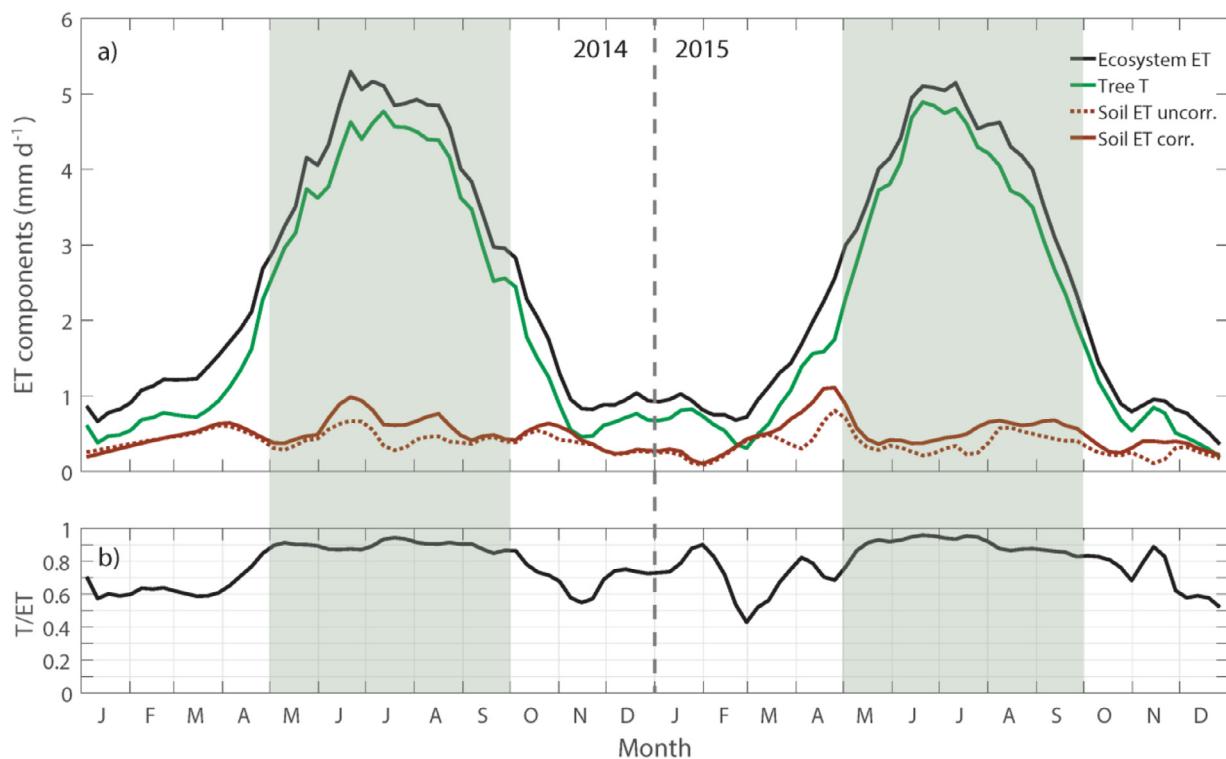


Fig. 6. Evapotranspiration (ET) and its components (T, E) at the Lägeren mixed forest site in 2014 and 2015. In panel a), ecosystem ET (black), tree T (green) and soil ET (brown). The brown dashed line for the soil represents the uncorrected EC measurements and the brown solid line represents the measurements corrected for downward eddies coming from the canopy leading to negative fluxes not linked to condensation (counter-gradient transport). In panel b), ratio of transpiration to evapotranspiration (T/ET). All lines are 7-day running means. The shaded green rectangles represent the period the deciduous trees have leaves (active growing season). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

ET were observed in August and September 2015 linked to a hydrological drought (Fig. 5e and f). In contrast, below canopy ET was highest in April (Fig. 5) due to (1) the presence of active understory vegetation transpiring and (2) the greater amount of energy reaching the soil surface before canopy closure. Reductions in above canopy ET were found in the afternoon with sharper decreases starting around 13:00 during June to August (Fig. 5).

3.3. Transpiration derived from concurrent EC measurements

Transpiration (T) was partitioned from the total ET flux based on the approach outlined in Section 2.4. Tree T was low in April, coming mostly from the active evergreen trees (Figs. 6 and 7). T increased in May with leaf-out, was highest in June–July and reduced with senescence in August–September (Figs. 6 and 7). In 2015, the reduction in T and ET occurred earlier in August due to the limiting moisture conditions (Fig. 6). Reductions in T were found in the afternoon with sharper decreases starting around 13:00 during June to August, and especially in August 2015 (Fig. 7). Soil evaporation (E) was low in general, with average values consistently below 1 mm d^{-1} , and correcting for counter-gradient transport depended on weather conditions (Fig. 6). The correction for counter-gradient transport increased the cumulated annual below canopy E by 35 mm (20%) in 2014 and 52 mm (30%) in 2015.

As a result of the drought conditions in 2015, annual total T was greater in 2014 (687 mm) compared to 2015 (642 mm) (Table 2). Despite the reductions in late summer ET and T in 2015, T represented a similar fraction of ET with 74% in 2014 and in 2015 (Table 2), ranging from 60% in winter to 90% in summer (Fig. 6b). T also represented a similar fraction of precipitation with 63% in 2014 and 66% in 2015 (Table 2). The conservation in T/ET and T/P ratios between 2014 and 2015, despite the reductions in T and ET, was due to the small and

rather invariant amount of summer E from this closed canopy forest.

3.4. Comparison of the transpiration derived with different approaches

When compared with the ED2 model, transpiration was similar, although the ED2 model suggested a faster decrease in transpiration in July and August than what occurred at the site (Fig. 8), likely due to an overestimation of water stress. Overall, ED2 consistently predicted an earlier senescence over the years than what the EC measurements indicated in our mixed forest (Figure S1), possibly due to the parameterized stomatal conductance that is too sensitive to changes in VPD when soils are dry. The ED2 model captured well the diurnal dynamics in T for the site, although with a slight overestimation in April and underestimation in July and August (Fig. 8). When comparing the diurnal cycles from the ED2 model to the T derived from the EC measurements, a faster decrease in T from EC measurements could be seen in the afternoon during May to August, occurring on average about three hours earlier than if only driven by the sun angle (Fig. 8), due to limitations imposed by the VPD. Additional ED2 simulations for beech trees showed that the model predicts a constantly lower T on a diurnal basis under water-stressed conditions, while higher T rates were observed, although sometimes with an afternoon depression when water is less limiting (Figure S2). Overall, the T partitioned from the hourly EC measurements had a strong correlation ($R^2 = 0.78$) to that modeled with ED2 (Figure S3). However, E was constantly overestimated under full canopy closure in ED2 (Figure S1).

Sap flow measurements showed a moderate correlation with the transpiration partitioned from the EC measurements in 2014 ($R^2 = 0.42$) and in 2015 ($R^2 = 0.58$), with similar seasonal dynamics (Fig. 9). Due to the large number of species at the Lägeren site and to some of the sap flow sensors being defective during our study period, it was however not possible to compute a transpiration estimate for the

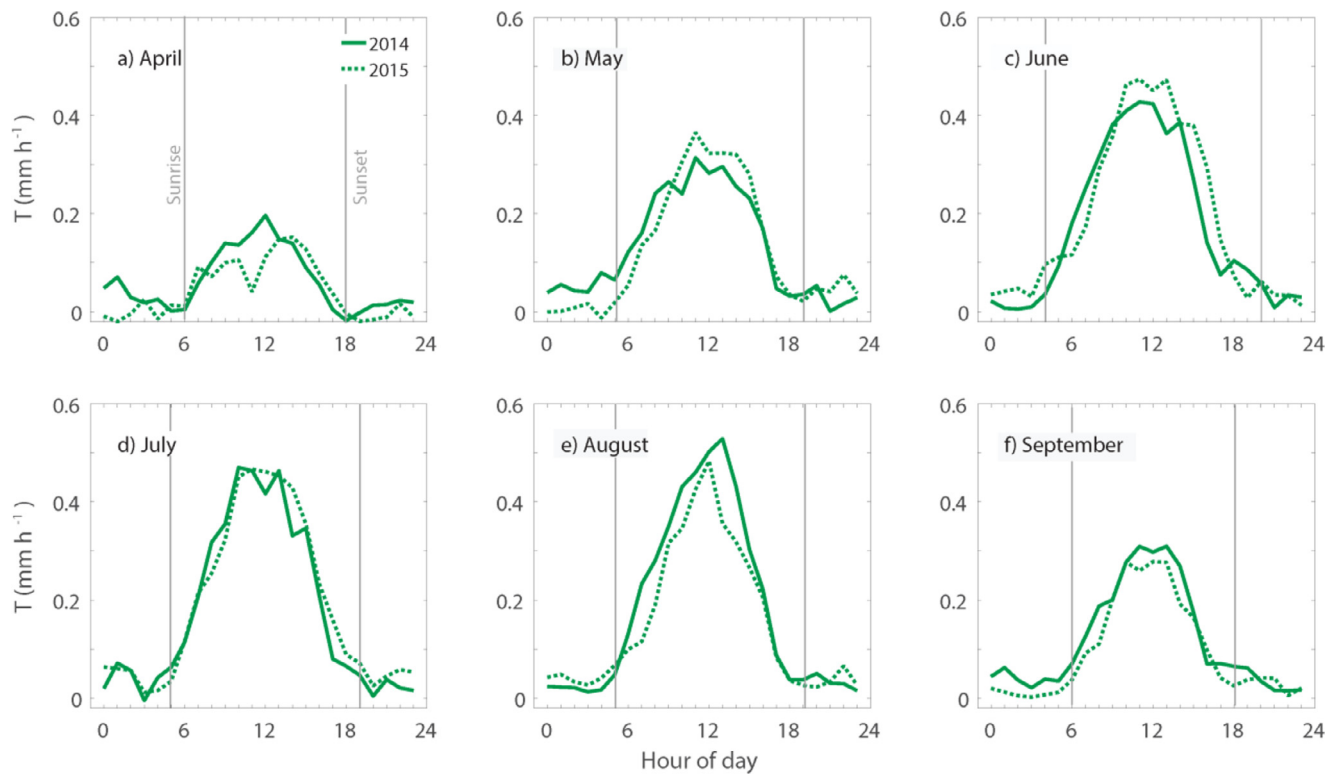


Fig. 7. Mean diurnal transpiration (T) derived from the eddy covariance fluxes below and above the canopy in 2014 and 2015. The solid line represents the 2014 year and the dotted line represents the 2015 year. The thin grey lines represent sunrise and sunset.

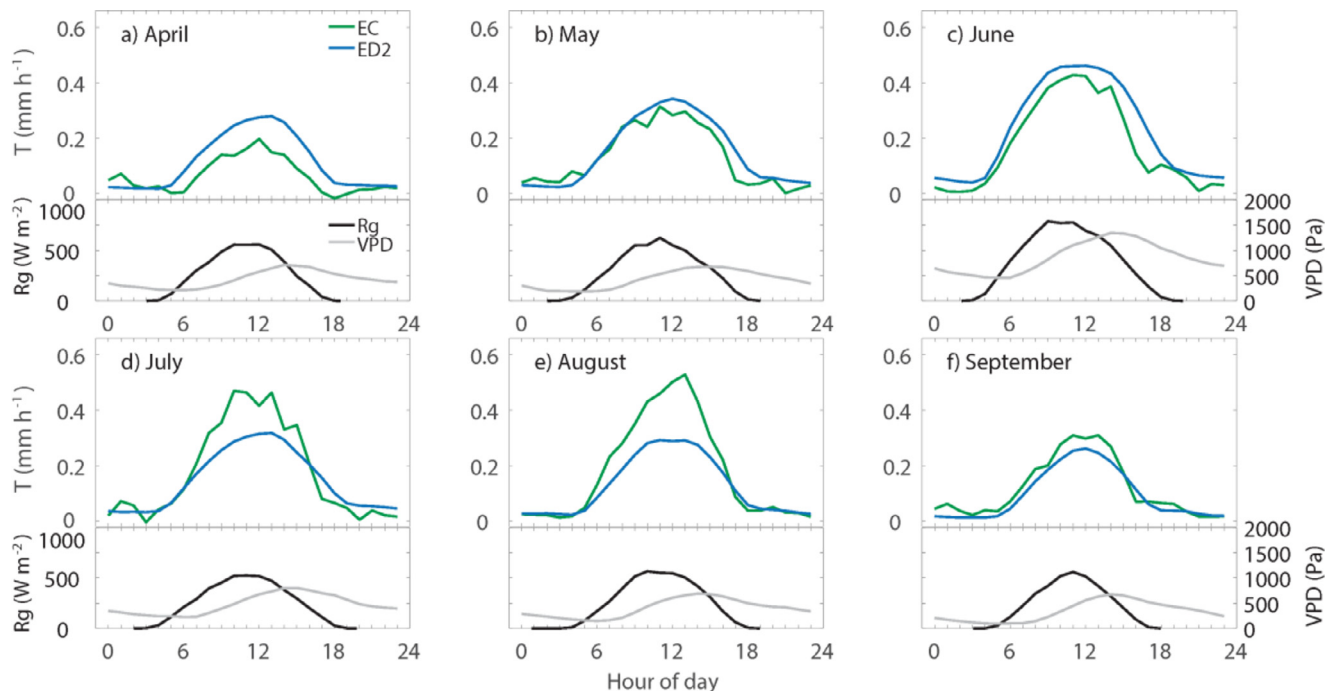


Fig. 8. Top panels: Mean diurnal transpiration in 2014 derived from the eddy covariance fluxes below and above the canopy (green line) and modeled with ED2 (blue line). Bottom panels: Mean diurnal global radiation (black) and VPD (grey) in 2014. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

forest from the sap flow measurements and therefore, the average sap flow measured from all trees (in $\text{L cm}^{-2} \text{d}^{-1}$) is used only as a relative indicator of the sap flow during the study period. Therefore, the sap flow units are not in mm, as they were not scaled up to stand scale.

The sap flow measurements also provided additional insights on

species-specific T as well as stress related dynamics. In April, only spruce trees were actively transpiring before the leaf-out of the deciduous trees (Fig. 10a). In May, all species started transpiring more actively, although this increase was greater in 2015, with sometimes more than twice the amount of sap flow (Fig. 10b). In June, spruce trees were

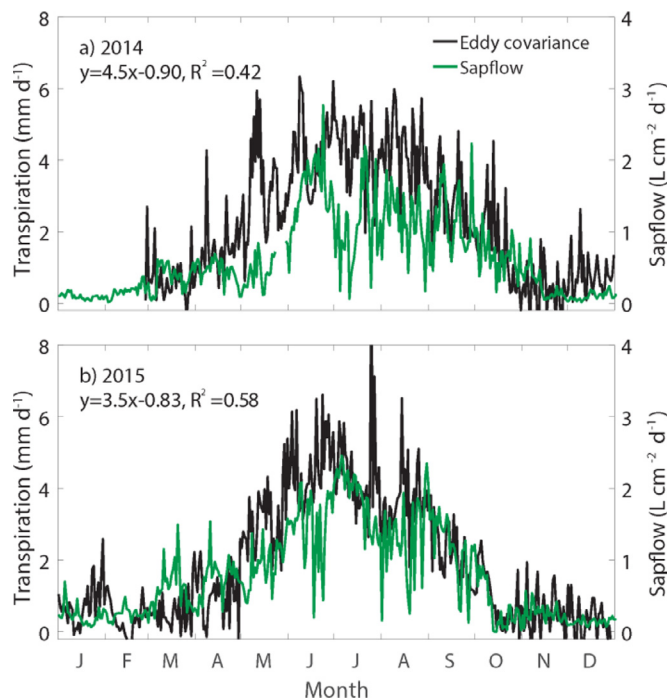


Fig. 9. EC transpiration (mm d^{-1}) vs. sap flow measurements ($\text{L cm}^{-2} \text{d}^{-1}$) in 2014 (a and b) and 2015 (c and d). The sap flow measurements represent an average of 4 ash trees (*Fraxinus excelsior* L.), 2 sycamore maple (*Acer pseudoplatanus* L.), and 3 European silver fir (*Abies alba* Mill.).

found to have lower sap flow than ash and maple trees, and all species showed signs of midday to afternoon depression, with sharper reductions in sap flow in the afternoon (Fig. 10c). Tree-level sap flow was higher and occurred about three hours earlier in July 2015 than in July

2014, probably due to the high VPD and solar radiation in 2015 leading to a reduction in the afternoon (Fig. 10d). A similar pattern was observed in August, with an asymmetrical diurnal shape, shifted towards the morning (Fig. 10e). This pattern was especially found for individual ash trees. In September, all species had a lower sap flow except spruce that increased again, after the deciduous trees became less active (Fig. 10f). This seasonality in the different species transpiring can also be seen in Figure S4. Interestingly, the spruce trees had a marked reduction in sap flow during the peak for ash and maple trees in 2014, while in 2015 their transpiration stayed rather constant over the growing season (Figure S4).

4. Discussion

4.1. Using concurrent below and above EC measurements to partition water fluxes

Concurrent below and above canopy EC measurements enabled us to derive a continuous time series of partitioned T and E for our mixed forest, something only few other direct measurements at ecosystem-level can currently do otherwise. At the Lägeren mixed forest, T was found to represent on average 74% of ET (ranging from 60% in winter to 90% in summer under full canopy closure), emphasizing a considerably lower contribution from E. This high contribution of T of ET at the Lägeren mixed forest site arises from the closed canopy and dry soil in summer leaving little energy and water at the ground surface for evaporation. The haplic cambisol soil is also well-drained leading to the water percolating to the lower layers rather than being lost to the atmosphere. This T/ET proportion is at the higher end of a previously reported range of 40 to 86% by Schlesinger and Jasechko (2014) in temperate deciduous forests, while Wei et al. (2017) found a global average of 84% for broadleaved forests with an LAI of 6. Mid-afternoon reductions in T were found during periods of high VPD and low soil water content in summer as shown by both the EC (Fig. 7) and sap flow

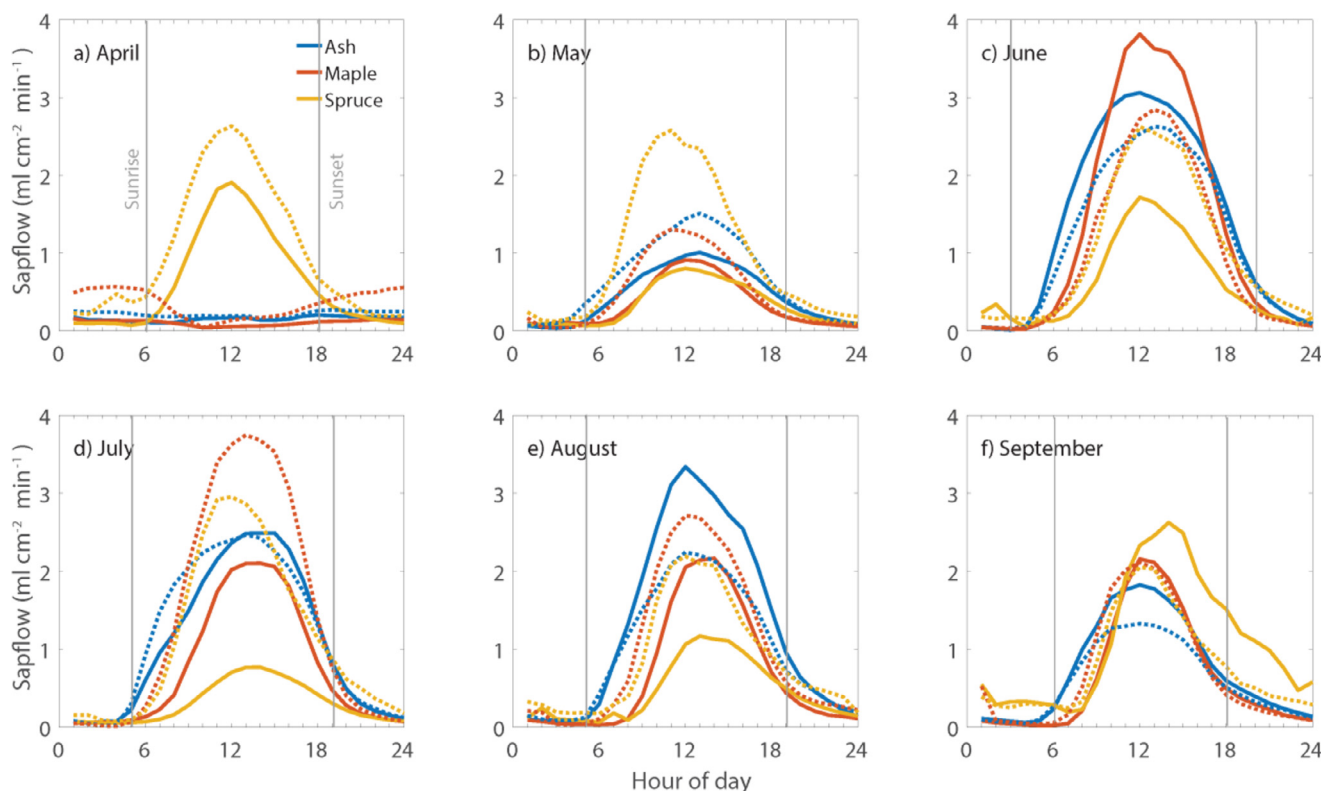


Fig. 10. Average diurnal sap flow for ash (blue), maple (red) and spruce (yellow) trees in 2014 (solid line) and 2015 (dotted line). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

(Fig. 10) measurements. A similar pattern had been previously measured at the site with top-of-canopy sun-induced fluorescence (SIF), an indicator of the photosynthetic activity in photosystem II, where afternoon depressions in SIF had been linked to high VPD under low soil water content (Paul-Limoges et al., 2018). The afternoon depression in transpiration is also consistent with previous studies for example from Granier (1987) that showed midday to afternoon depressions in sap flow in a Douglas-fir forest subject to drought conditions, the depressions increasing as the drought progressed. Similarly, Roupsard et al. (2006) showed a dampening in potential variations in canopy T due to stomatal closure under a high VPD during the warm season in a tropical coconut palm plantation. Despite pronounced differences in environmental conditions during the two observed years, T remained a constant fraction of ET and precipitation in our mixed forest, due to the low and rather constant E below the canopy. Stomatal regulation was also found during summer afternoons in response to enhanced atmospheric evaporative demand in order to mitigate water-stress related damage (i.e. cavitation).

4.2. Comparison with other approaches

The use of concurrent below and above canopy EC measurements in this study agreed relatively well with E and T predicted by the ED2 model, and with sap flow measurements, although it also highlighted some important differences. As mentioned in the introduction, T is difficult to measure at the ecosystem-level, however there are many models currently available that estimate T. Such models are usually based on one (or a combination) of the following basis: (1) water balance, (2) energy balance and (3) physiology. In this study, we compared our results with the ED2 model that is based on vegetation physiology. The ED2 model could well resolve the diurnal scale of T from our mixed forest (Fig. 8), as the model is based on physiology combining equations from Farquhar et al. (1980), Leuning (1995) and Collatz et al. (1991). ED2 however consistently predicted too rapid reductions in T during July–August, because the model predicted an earlier senescence for the forest (Fig. 8 and Figure S1). The model was also limited in estimating E in a low light environment below the canopy, suggesting high E rates in summer under closed-canopy conditions. Such estimates are unrealistic due to the low radiation reaching the ground and low water availability (Figure S1). Both the rapid decline in T in July–August and the E overestimation in summer at Lägeren are consistent with results from the ED2 model applied to the Harvard temperate deciduous forest site (Wehr et al., 2017).

Sap flow sensors provided important additional insights on species-specific and tree-level dynamics; however, due to the large number of species at the Lägeren site, a large number of sap-flow sensors is needed to accurately characterize T from the forest. Although scaling-up sap flow measurements in monospecific and even-aged stands has shown good results when compared to ecosystem T in some studies (e.g. Granier et al., 2000; Köstner et al., 1992), scaling-up is particularly difficult in forests with different age and species (Wilson et al., 2001). Many uncertainties and errors are linked to scaling-up sap flow measured on a small and potentially non-representative sample of trees has been shown to lead to biases in the T derived (e.g. Roupsard et al., 2006; Schlesinger and Jasechko, 2014; Wilson et al., 2001). In this study, measurements from the most abundant species (beech) at our site were also lacking, thereby possibly affecting the dynamics in sap flow measured and precluding us to derive ecosystem-scale estimates of transpiration.

Although some studies have also shown transpiration dynamics independent of biochemical processes, with nighttime stomatal conductance up to 90% of daytime conductance (Caird et al., 2007), transpiration rates at night tend to be lower than during daytime due to a (1) lack of photosynthesis and (2) considerably lower nighttime VPD (e.g. Dawson et al., 2007). Nighttime transpiration rates were found to be low at the Lägeren mixed forest site (despite a relatively high

nighttime VPD), as measured by the EC and sap flow measurements (Fig. 8), indicating strong coupling between stomatal conductance and photosynthesis at the Lägeren site.

4.3. Limitations of the approach with concurrent EC measurements

The approach based on concurrent EC measurements used in this study requires that the turbulence below the canopy is sufficient for the EC measurements to be accurate. Therefore, this method can only be applied at forest sites with sufficient trunk space between the ground surface and the bottom of the tree canopies to allow for turbulence, otherwise the below canopy measurements will be unreliable. Thomas et al. (2013) showed that below canopy measurements could be used even in dense forests subject to decoupling to correct the above canopy CO₂ fluxes with the below canopy CO₂ fluxes, and a similar approach could be used for water. Furthermore, water fluxes are not as affected as by the nighttime systematic biases due to low turbulence that have a large influence on the CO₂ flux measurements, as ET is minimal at night (Moncrieff et al., 1996). At sites where the below canopy environment is not turbulent enough, lysimeters could possibly be used as an alternative to partition E from the soil, although with the limitations imposed from the area measured and the roots biasing the measurements.

Wilson and Meyers (2001) estimated that the errors associated with below canopy measurements of water vapor flux are in the order of 10%. Evidently, special care should be taken regarding the positioning of the EC system below the canopy with regards to the structural obstacles in the proximity affecting the turbulence field. Some studies have shown similar characteristics of spectra and co-spectra below and above the canopy, with spectral peaks occurring at similar natural frequency (e.g. Launiainen et al., 2005; Roupsard et al., 2006), indicating that the turbulence above the canopy was driving the one below. Remaining uncertainties are linked to the downward movement of eddies, which contaminate the below canopy measurements and lead to biases, although such periods can be identified and accounted for based on the methods described in Section 2.4.2. It can however be expected that as the counter-gradient transport (Denmead and Bradley, 1985) increases in the below canopy environment, so will the uncertainty associated with the below canopy measurements and thus, with the transpiration derived.

4.4. Towards better measurements of ecosystem transpiration

With plant T accounting for 60–80% of terrestrial ET, there is no doubt that terrestrial vegetation is a dominant force in the global water cycle (Schlesinger and Jasechko, 2014). As temperature increases and more extreme droughts are expected to occur, it is still unclear in which direction T will evolve in our ecosystems; for example, will the stomata close to reduce water losses (warming effect) or will the atmosphere be able to hold more water vapor and therefore stimulate a cooling effect from increased T (Cao et al., 2010). Overall levels of tree stress and forest disturbances are expected to increase beyond any historic values (Trumbore et al., 2015) and forest responses to these new stresses are not known yet. In order to understand these forest response dynamics and inform models, measurements at ecosystem-level are needed to quantify changes in T.

Nearly all land surface models provide T or E predictions, but without any measurement validations, these predictions are largely unconstrained. Recently, new modeling approaches have been suggested at EC sites to partition ET based on the Penman–Monteith model where ecosystem conductances are decomposed into soil and canopy conductances (Li et al., 2019), based on optimality principles (Perez-Priego et al., 2018) or based on water use efficiency derived from the coupling of gross primary production and T (Nelson et al., 2018). Other studies have suggested to partition global ET using the relationship between T/ET and LAI for different ecosystems

(Wang et al., 2014; Wei et al., 2017). Although such modeling approaches are an important step forward in understanding ET partitioning, ecosystem-based measurements will be needed to improve and validate these models. Consistent T measurements at ecosystem-level are currently lacking, and the approach suggested in this study using concurrent below and above canopy EC measurements could be used in a standardized way at forested FLUXNET sites, while still taking into account the site-specific limitations. Several FLUXNET sites have measured below canopy ET at least for a short period of time and these measurements could be used as a start to understand the transpiration component of those forests.

5. Conclusion

Based on a comprehensive set of observations and model comparisons, we conclude that a rigorous consideration of micro-meteorological constraints relating concurrent below and above canopy EC measurements enables to successfully partition total ecosystem ET into tree transpiration and ecosystem evaporation. On average, EC-derived transpiration accounted for about 74% of ET in our mixed forest, thus emphasizing a considerably lower contribution from evaporation. Transpiration derived from our EC measurements correlated well with that from the ED2 model, yet also highlighted differences linked to the modelled response during water stress. EC and sap flow measurements showed mid-afternoon reductions in transpiration during periods of high vapor pressure deficit in summer. Despite pronounced differences in environmental conditions during the observed years, ET and its transpiration component were relatively similar across years in this mixed forest. This is likely due to (1) low E below the canopy and (2) stomatal regulation in response to enhanced atmospheric evaporative demand during afternoons in summer to avoid damage from hydraulic failure (cavitation).

Our results show the potential of concurrent below and above canopy EC measurements to partition ecosystem ET in forests. We suggest that concurrent below and above canopy EC measurements could be used in a standardized way to help partition ET across forested sites in networks such as FLUXNET. Such network infrastructure could mutually benefit the further development of observational approaches and process models to assess complex ecosystem water and carbon exchange.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgments

We are grateful to T. Baur, P. Meier, and L. Hörtnagl for assistance in the field and in the laboratory. The ED2 research carried out by F.S. and M.L. at the Jet Propulsion Laboratory, California Institute of Technology, was under a contract with the National Aeronautics and Space Administration. Government sponsorship is acknowledged. M.L. was supported by the NASA Postdoctoral Program, administered by Universities Space Research Association under contract with NASA. Reference herein to any specific commercial product, process, or service by trade name, trademark, manufacturer, or otherwise, does not constitute or imply its endorsement by the United States Government or the Jet Propulsion Laboratory, California Institute of Technology. We acknowledge E. Haghighi for comments on a previous version of the manuscript. The authors would also like to thank two anonymous reviewers for their constructive and detailed feedback that helped improve the manuscript.

Supplementary material

Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.agrformet.2019.107786.

References

- Anderegg, W.R.L., et al., 2015. Pervasive drought legacies in forest ecosystems and their implications for carbon cycle models. *Science* 349 (6247), 528–532.
- Baldocchi, D.D., Hincks, B.B., Meyers, T.P., 1988. Measuring biosphere-atmosphere exchanges of biologically related gases with micrometeorological methods. *Ecology* 69 (5), 1331–1340.
- Baldocchi, D.D., Ryu, Y., 2011. A synthesis of forest evaporation fluxes - from days to years - as measured with eddy covariance. *Ecol. Stud. Anal. Synth.* 216, 101–116.
- Baldocchi, D.D., Vogel, C.A., 1996. Energy and CO₂ flux densities above and below a temperate broad-leaved forest and a boreal pine forest. *Tree Physiol.* 16 (1–2), 5–16.
- Betts, R.A., et al., 2007. Projected increase in continental runoff due to plant responses to increasing carbon dioxide. *Nature* 448, 1037.
- Black, T.A., et al., 1996. Annual cycles of water vapour and carbon dioxide fluxes in and above a boreal aspen forest. *Glob. Chang. Biol.* 2 (3), 219–229.
- Bosch, J.M., Hewlett, J.D., 1982. A review of catchment experiments to determine the effect of vegetation changes on water yield and evapotranspiration. *J. Hydrol.* 55 (1), 3–23.
- Caird, M.A., Richards, J.H., Donovan, L.A., 2007. Nighttime stomatal conductance and transpiration in C₃ and C₄ plants. *Plant Physiol.* 143 (1), 4–10.
- Cao, L., Bala, G., Caldeira, K., Nemani, R., Ban-Weiss, G., 2010. Importance of carbon dioxide physiological forcing to future climate change. *Proc. Nat. Acad. Sci.* 107 (21), 9513–9518.
- Collatz, G.J., Ball, J.T., Grievet, C., Berry, J.A., 1991. Physiological and environmental regulation of stomatal conductance, photosynthesis and transpiration: a model that includes a laminar boundary layer. *Agric. For. Meteorol.* 54 (2–4), 107–136.
- 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.* 98–9, 629–643.
- Cuenca, R.H., Stangel, D.E., Kelly, S.F., 1997. Soil water balance in a boreal forest. *J. Geophys. Res. Atmos.* 102 (D24), 29355–29365.
- Dawson, T.E., et al., 2007. Nighttime transpiration in woody plants from contrasting ecosystems. *Tree Physiol.* 27 (4), 561–575.
- Denmead, O., Bradley, E., 1985. Flux-Gradient Relationships in a Forest Canopy. pp. 421–442.
- Eastham, J., Rose, C.W., Cameron, D.M., Rance, S.J., Talsma, T., 1988. The effect of tree spacing on evaporation from an agroforestry experiment. *Agric. For. Meteorol.* 42 (4), 355–368.
- Etzold, S., et al., 2011. The carbon balance of two contrasting mountain forest ecosystems in Switzerland: similar annual trends, but seasonal differences. *Ecosystems* 14 (8), 1289–1309.
- Fan, S.-M., Wofsy, S.C., Bakwin, P.S., Jacob, D.J., Fitzjarrald, D.R., 1990. Atmosphere-biosphere exchange of CO₂ and O₃ in the central Amazon forest. *J. Geophys. Res. Atmos.* 95 (D10), 16851–16864.
- Farquhar, G., von Caemmerer, S., Berry, J., 1980. A biochemical model of photosynthetic CO₂ assimilation in leaves of C₃ species. *Planta* 149 (1), 78–90.
- Field, C.B., Jackson, R.B., Mooney, H.A., 1995. Stomatal responses to increased CO₂: implications from the plant to the global scale. *Plant Cell Environ.* 18 (10), 1214–1225.
- Foken, T., Göckede, M., Mauder, M., Mahr, L., Amiro, B., Munger, W., 2005. Post-field data quality control. In: Lee, X., Massman, W., Law, B. (Eds.), *Handbook of Micrometeorology*. Springer, Netherlands, pp. 181–208.
- Göckede, M., et al., 2008. Quality control of CarboEurope flux data - Part 1: coupling footprint analyses with flux data quality assessment to evaluate sites in forest ecosystems. *Biogeosciences* 5 (2), 433–450.
- Granier, A., 1985. Une nouvelle méthode pour la mesure du flux de sève brute dans le tronc des arbres. *Ann. For. Sci.* 42 (2), 193–200.
- Granier, A., 1987. Evaluation of transpiration in a Douglas-fir stand by means of sap flow measurements. *Tree Physiol.* 3 (4), 309–320.
- Granier, A., Biron, P., Lemoine, D., 2000. Water balance, transpiration and canopy conductance in two beech stands. *Agric. For. Meteorol.* 100 (4), 291–308.
- Horst, T.W., 1997. A simple formula for attenuation of eddy fluxes measured with first-order-response scalar sensors. *Boundary Layer Meteorol.* 82 (2), 219–233.
- Humphrey, V., et al., 2018. Sensitivity of atmospheric CO₂ growth rate to observed changes in terrestrial water storage. *Nature* 560 (7720), 628–631.
- Jaeger, L., Kessler, A., 1997. Twenty years of heat and water balance climatology at the Hartheim pine forest, Germany. *Agric. For. Meteorol.* 84 (1), 25–36.
- Jaros, N., et al., 2008. Carbon dioxide and energy flux partitioning between the understorey and the overstorey of a maritime pine forest during a year with reduced soil water availability. *Agric. For. Meteorol.* 148 (10), 1508–1523.
- Jocher, G., et al., 2017. Apparent winter CO₂ uptake by a boreal forest due to decoupling. *Agric. For. Meteorol.* 232, 23–34.
- Keenan, T.F., et al., 2013. Increase in forest water-use efficiency as atmospheric carbon dioxide concentrations rise. *Nature* 499 (7458), 324.
- Kilinc, M., Beringer, J., Hutley, L.B., Tapper, N.J., McGuire, D.A., 2013. Carbon and water exchange of the world's tallest angiosperm forest. *Agric. For. Meteorol.* 182, 215–224.
- Köstner, B.M.M., et al., 1992. Transpiration and canopy conductance in a pristine broad-leaved forest of Nothofagus: an analysis of xylem sap flow and eddy correlation measurements. *Oecologia* 91 (3), 350–359.

- Lasslop, G., et al., 2010. Separation of net ecosystem exchange into assimilation and respiration using a light response curve approach: critical issues and global evaluation. *Glob. Chang. Biol.* 16 (1), 187–208.
- Launiainen, S., et al., 2005. Eddy covariance measurements of CO₂ and sensible and latent heat fluxes during a full year in a boreal pine forest trunk-space. *Boreal Environ Res* 10 (6), 569–588.
- Leuning, R., 1995. A critical appraisal of a combined stomatal-photosynthesis model for C3 plants. *Plant Cell Environ.* 18 (4), 339–355.
- Li, X., et al., 2019. A simple and objective method to partition evapotranspiration into transpiration and evaporation at eddy-covariance sites. *Agric. For. Meteorol.* 265, 171–182.
- Longo, M., et al., 2019a. The biophysics, ecology, and biogeochemistry of functionally diverse, vertically- and horizontally-heterogeneous ecosystems: the Ecosystem Demography model, version 2.2—part 2: model evaluation. *Geosci. Model Dev. Discuss.* 2019, 1–34.
- Longo, M., et al., 2019b. The biophysics, ecology, and biogeochemistry of functionally diverse, vertically- and horizontally-heterogeneous ecosystems: the Ecosystem Demography model, version 2.2—part 1: model description. *Geosci. Model Dev. Discuss.* 2019, 1–53.
- Medvigy, D., Wofsy, S.C., Munger, J.W., Hollinger, D.Y., Moorcroft, P.R., 2009. Mechanistic scaling of ecosystem function and dynamics in space and time: Ecosystem Demography model version 2. *J. Geophys. Res. Biogeo.* 114 (G1). <https://doi.org/10.1029/2008JG000812>.
- Misson, L., et al., 2007. Partitioning forest carbon fluxes with overstory and understorey eddy-covariance measurements: a synthesis based on FLUXNET data. *Agric. For. Meteorol.* 144 (1–2), 14–31.
- Moncrieff, J., Clement, R., Finnigan, J., Meyers, T., 2005. Averaging, detrending, and filtering of eddy covariance time series. In: Lee, X., Massman, W., Law, B. (Eds.), *Handbook of Micrometeorology*. Atmospheric and Oceanographic Sciences Library. Springer, Netherlands, pp. 7–31.
- Moncrieff, J., Malhi, Y., Leuning, R., 1996. The propagation of errors in long-term measurements of land-atmosphere fluxes of carbon and water. *Glob. Chang. Biol.* 2 (3), 231–240.
- Nelson, J.A., et al., 2018. Coupling water and carbon fluxes to constrain estimates of transpiration: the tea algorithm. *J. Geophys. Res. Biogeo.* 123 (12), 3617–3632.
- Nolz, R., Cepuder, P., Kammerer, G., 2014. Determining soil water-balance components using an irrigated grass lysimeter in NE Austria. *J. Plant Nutr. Soil Sci.* 177 (2), 237–244.
- Paul-Limoges, E., et al., 2018. Effect of environmental conditions on sun-induced fluorescence in a mixed forest and a cropland. *Remote Sens. Environ.* 219, 310–323.
- Paul-Limoges, E., Wolf, S., Eugster, W., Hörtnagl, L., Buchmann, N., 2017. Below-canopy contributions to ecosystem CO₂ fluxes in a temperate mixed forest in Switzerland. *Agric. For. Meteorol.* 247 (Supplement C), 582–596.
- Perez-Priego, O., et al., 2018. Partitioning eddy covariance water flux components using physiological and micrometeorological approaches. *J. Geophys. Res. Biogeo.* 123 (10), 3353–3370.
- Piao, S., et al., 2007. Changes in climate and land use have a larger direct impact than rising CO₂ on global river runoff trends. *Proc. Natl. Acad. Sci.* 104 (39), 15242–15247.
- Reichstein, M., et al., 2005. On the separation of net ecosystem exchange into assimilation and ecosystem respiration: review and improved algorithm. *Glob. Chang. Biol.* 11 (9), 1424–1439.
- Roupsard, O., et al., 2006. Partitioning energy and evapo-transpiration above and below a tropical palm canopy. *Agric. For. Meteorol.* 139 (3–4), 252–268.
- Rutter, A.J., Kershaw, K.A., Robins, P.C., Morton, A.J., 1971. A predictive model of rainfall interception in forests, 1. Derivation of the model from observations in a plantation of Corsican pine. *Agric. Meteorol.* 9, 367–384.
- Schlesinger, W.H., Jasechko, S., 2014. Transpiration in the global water cycle. *Agric. For. Meteorol.* 189–190, 115–117.
- Scott, R.L., et al., 2003. The understory and overstory partitioning of energy and water fluxes in an open canopy, semiarid woodland. *Agric. For. Meteorol.* 114 (3–4), 127–139.
- Sellers, P.J., et al., 1996. Comparison of radiative and physiological effects of doubled atmospheric CO₂ on climate. *Science* 271 (5254), 1402–1406.
- Smith, D.M., Allen, S.J., 1996. Measurement of sap flow in plant stems. *J. Exp. Bot.* 47 (305), 1833–1844.
- Thomas, C.K., Martin, J.G., Law, B.E., Davis, K., 2013. Toward biologically meaningful net carbon exchange estimates for tall, dense canopies: multi-level eddy covariance observations and canopy coupling regimes in a mature Douglas-fir forest in Oregon. *Agric. For. Meteorol.* 173, 14–27.
- Trumbore, S., Brando, P., Hartmann, H., 2015. Forest health and global change. *Science* 349 (6250), 814–818.
- Wang, L.X., Good, S.P., Caylor, K.K., 2014. Global synthesis of vegetation control on evapotranspiration partitioning. *Geophys. Res. Lett.* 41 (19), 6753–6757.
- Webb, E.K., Pearman, G.I., Leuning, R., 1980. Correction of flux measurements for density effects due to heat and water-vapor transfer. *Q. J. Roy. Meteor. Soc.* 106 (447), 85–100.
- Wehr, R., et al., 2017. Dynamics of canopy stomatal conductance, transpiration, and evaporation in a temperate deciduous forest, validated by carbonyl sulfide uptake. *Biogeosciences* 14 (2), 389–401.
- Wei, Z.W., et al., 2017. Revisiting the contribution of transpiration to global terrestrial evapotranspiration. *Geophys. Res. Lett.* 44 (6), 2792–2801.
- Wilson, K.B., Hanson, P.J., Mulholland, P.J., Baldocchi, D.D., Wullschlegel, S.D., 2001. A comparison of methods for determining forest evapotranspiration and its components: sap-flow, soil water budget, eddy covariance and catchment water balance. *Agric. For. Meteorol.* 106 (2), 153–168.
- Wilson, K.B., Meyers, T.P., 2001. The spatial variability of energy and carbon dioxide fluxes at the floor of a deciduous forest. *Boundary Layer Meteorol.* 98 (3), 443–473.
- Wolf, S., et al., 2016. Warm spring reduced carbon cycle impact of the 2012 US summer drought. *Proc. Natl. Acad. Sci. U.S.A.* 113 (21), 5880–5885.
- Wullschlegel, S.D., Meinzer, F., Vertessy, R., 1998. A review of whole-plant water use studies in tree. *Tree Physiol.* 18 (8–9), 499–512.
- Zavaleta, E.S., et al., 2003. Plants reverse warming effect on ecosystem water balance. *Proc. Natl. Acad. Sci.* 100 (17), 9892–9893.