Methods

Association between sap flow-derived and eddy covariance-derived measurements of forest canopy CO2 uptake

Tamir Klein1,2, Eyal Rotenberg1, Fyodor Tatarinov1 and Dan Yakir1

1Department of Earth and Planetary Sciences, Weizmann Institute of Science, Rehovot 76100, Israel; 2 Present address: Institute of Botany, University of Basel, Schoenbeinstrasse 6, Basel 4056, Switzerland

Author for correspondence:
Tamir Klein
Tel: +41 76 4886212
Email: tamir.klein@unibas.ch

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Introduction

Forests play a major role in the terrestrial carbon cycle through CO2 assimilation, respiration, and sequestration (Luyssaert et al., 2007; Bonan, 2008; Canadell & Raupach, 2008; Reichstein et al., 2013). Gross primary productivity (GPP) of forest canopies has hence become an important measure of the carbon uptake of forests. Considering the effects of the increase in atmospheric CO2, on the one hand, and the influence of climate change, on the other, GPP is central to our understanding of the responses of ecosystem and biosphere to change (Gais et al., 2005; Asaf et al., 2013; Reichstein et al., 2013). Currently, GPP is routinely calculated using eddy covariance (EC) from the difference between measured net ecosystem CO2 exchange (NEE) and inferred daytime ecosystem respiration (Rd) extrapolating night-time EC measurements of respiration based on empirical temperature response equations (Aubinet et al., 2000; Baldocchi, 2003; Reichstein et al., 2005). For the past two decades, the EC method has been providing essential GPP data from sites across all major biomes and climate types (Luyssaert et al., 2007). However, the EC approach has several limitations and uncertainties. Its application is limited to relatively large, homogeneous and flat terrains, and it is critically dependent on empirical extrapolation of the night-time measurements with significant uncertainties (e.g., Van Gorsel et al., 2009). The difficulties in using the EC methodology to obtain a balanced ecosystem energy budget has also indicated significant uncertainties in EC flux estimates, with estimated precision of c. ±20% at best (Baldocchi et al., 2001), and in the range of corrections for the basic wind speed and direction (e.g. Nakai & Shimoyama, 2012). Although EC flux measurements are widely used, such estimates cannot yet be used as the accurate reference points for GPP and, ultimately, the large range of global GPP estimates (c. 100 to c. 150 Pg C yr−1; Beer et al., 2010) indicates the critical need for more constraints on GPP estimates across all scales.

Indeed, alternative approaches are being continuously developed. For example, recent new developments include flux measurements of carbonyl sulfide (Asaf et al., 2013) and remotely sensed solar-induced chlorophyll fluorescence (Parazoo et al., 2014). Recent studies pointed out the potential utility of using independent estimates of water use efficiency, WUE, and transpiration, T, to estimate GPP from the relationship of WUE = GPP/T (Hu et al., 2010; Wang et al., 2013), where GPP is nearly identical with canopy photosynthetic assimilation (see the Materials and Methods section) and T is obtained from sap flow (SF) time series. For simplicity, this approach is termed here ‘SF-derived GPP’. In contrast with the EC-derived GPP, the CO2 uptake estimated by the SF-derived GPP approach relates directly to the trees (Fig. 1). Therefore, it has the potential to

Summary

- The carbon sink intensity of the biosphere depends on the balance between gross primary productivity (GPP) of forest canopies and ecosystem respiration. GPP, however, cannot be directly measured and estimates are not well constrained. A new approach relying on canopy transpiration flux measured as sap flow, and water-use efficiency inferred from carbon isotope analysis (GPPSF) has been proposed, but not tested against eddy covariance-based estimates (GPPEC).
- Here we take advantage of parallel measurements using the two approaches at a semi-arid pine forest site to compare the GPPSF and GPPEC estimates on diurnal to annual timescales.
- GPPSF captured the seasonal dynamics of GPPEC (GPPSF = 0.99 ± 0.01 × GPPEC, R2 = 0.78, RMSE = 0.82, n = 457 d) with good agreement at the annual timescale (653 vs 670 g C m−2 yr−1). Both methods showed that GPP ranged between 1 and 8 g C m−2 d−1, and the GPPSF/GPPEC ratio was between 0.5 and 2.0 during 82% of the days. Carbon uptake dynamics at the individual tree scale conformed with leaf scale rates of net assimilation.
- GPPSF can produce robust estimations of tree- and canopy-scale rates of CO2 uptake, providing constraints and greatly extending current GPPEC estimations.
partition the CO₂ uptake between overstory and understory and among co-occurring tree species.

Photosynthetic CO₂ assimilation (A) occurs via plant stomata in parallel with transpiration. At the leaf level, CO₂ uptake by photosynthesis is readily measured, along with leaf transpiration and stomatal conductance (gₛ), using a chamber equipped with an infrared gas analyzer (Von Caemmerer & Farquhar, 1981). However, a chamber technique cannot be easily applied to mature forest trees, and is difficult to scale up to tree and canopy scales. Alternatively, transpiration (T) from a forest canopy can be more easily estimated by upscaling of SF measurements in individual trees (Granier, 1985; Cermak et al., 2004; Tatarinov et al., 2005; Cohen et al., 2008). The ratio A/T, defined as water-use efficiency (WUE), is calculated at the leaf scale using simultaneous chamber measurements of A and T. Alternatively, an integrated value of intrinsic water use efficiency (WUEᵢ) can be calculated from the carbon isotope ratio (δ¹³C) in the assimilated carbon (Farquhar & Richards, 1984). The isotopic approach takes advantage of the inherent relationships between plant CO₂ discrimination and leaf internal CO₂ concentration, and the constant ratio of the diffusivities of CO₂ and water in air (Farquhar & Richards, 1984; Seibt et al., 2008; Maseyk et al., 2011). A tree-scale CO₂ uptake can be estimated if concurrent estimates of T and WUE values are obtained (Aᵣₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑعكسültexts tends to our analysis: Although 2005 was a peak growth year, 2009–2010 followed two consecutive drought years, resulting in c. 5% mortality (Klein et al., 2014). Although significant uncertainties are still associated with the GPPEC as noted above, estimates for our specific forest site have been constrained by a range of independent measurements: latent heat flux measurements with fully closed energy balance indicated high reliability of the EC measurements at the site (Rotenberg & Yakir, 2010); estimating changes in biomass based on aerial photography (Bar Massada et al., 2006); biomass inventories and long-term sum of respiration fluxes (Grünzweig et al., 2003, 2007); and carbon sink estimates at the tree scale (Klein & Hoch, 2015). For example, an annual GPPEC of 670 g C m⁻² yr⁻¹, which is translated into 22.3 kg C per tree yr⁻¹, consistent (±5%) with the sum of tree C sinks of 23.5 kg C per tree yr⁻¹ (Klein & Hoch, 2015). Our study site offered parallel, long-term, continuous measurements of EC and SF, with minimum contribution of the understory vegetation and groundwater to the forest fluxes, and detailed T estimates, verified by a balanced water budget (T = precipitation – (evaporation + interception); Raz-Yaseef et al., 2010; Klein et al., 2014). Our objective was to exploit SF time series, combined with ¹³C data, to estimate photosynthetic CO₂ uptake at the tree level and, consequently, GPP at the canopy scale, in comparison to the traditional GPPEC.

Materials and Methods

Site description

Our study was conducted in Yatir forest, a 45-yr-old Aleppo pine (Pinus halepensis Miller) plantation located at the northern edge of the Negev desert, Israel (31°20’N, 35°20’E). The climate is hot and dry (40-yr average mean annual temperature and precipitation are 18.2°C and 285 mm). Stand density is c. 300 trees ha⁻¹, mean tree height is 10.2 ± 2.49 m and mean diameter at breast height (DBH) is 19.8 ± 5.61 cm. In 2000, an instrumented flux tower was erected in the geographic center of the forest, allowing continuous measurements of NEE and GPP (Grünzweig et al., 2003; Rotenberg & Yakir, 2010). Unless specified, all measurements and samples were taken within the flux tower footprint. The study site offered an ideal setting to compare the two GPP estimation methods, because: (1) EC and SF were measured continuously during most of the period under study; (2) Canopy CO₂ uptake at the study site is almost entirely attributed to the trees’ photosynthesis, with only minor contribution of understory vegetation (Grünzweig et al., 2007); (3)
Changes in needle and wood δ13C that were used for deriving the WUEi were based on a 7-yr dataset (1997–2003) and therefore provided a robust representation of the seasonal changes in WUEi; and (4) A phenological decoupling between stem wood growth in the wet season and needle formation in the dry season (Klein et al., 2005; Maseyk et al., 2008) ensured year-round availability of fresh plant material with carbon isotopic signals for WUEi calculation.

Sap flow-derived canopy-scale assimilation rates

We developed an approach to estimate GPP in which we use the well-established physiological relationship: WUEi = A/gs, (μmol CO2 mol−1 H2O). We wish to scale up to the ecosystem scale and solve for Astand assuming that at this scale Astand = GPP. Leaf mitochondrial respiration, Rl, in the light is subtracted from the leaf-scale assimilation measurements (A). Rl is added back in estimating canopy GPP, with significant uncertainty (e.g. Speckman et al., 2014), and neglecting downregulation of Rl in the daytime (e.g. Heskel et al., 2014) when canopy-scale GPP is estimated based on extrapolating night-time ecosystem respiration, Rl (see more detail in Asaf et al., 2013). Thus, GPPSF was calculated from:

\[ \text{GPP}_{SF} = \text{WUE}_{i \text{stand}} / \text{gs}_{\text{stand}} \]  

Eqn 1

which can be solved by obtaining independent estimates of WUEi and gs (Fig. 1; see Table 1 for list of variables used in this study). Here we estimate WUEi from δ13C measurements of organic material averaged for the stand (based on 11 P. halepensis trees growing on two plots in Yatir forest; see Supporting Information Methods S1), using the following equation (adapted from Farquhar & Richards, 1984; Seibt et al., 2008):

\[ \text{WUE}_{i} = \frac{C_a}{r} \times \frac{[b - \Delta - pr \times (\Gamma^r / C_a)]/[b - a + (b - a_{in}) \times (g_s / (r \times g_s))]}}{ \} \]  

Eqn 2

Table 1 List of main variables used in this study

<table>
<thead>
<tr>
<th>Symbol</th>
<th>Description</th>
<th>Units</th>
<th>Value range</th>
</tr>
</thead>
<tbody>
<tr>
<td>Aleaf</td>
<td>Needle CO2 assimilation</td>
<td>μmol CO2 m−2 s−1</td>
<td>0.2–12.7</td>
</tr>
<tr>
<td>Atree</td>
<td>Tree CO2 assimilation</td>
<td>g CO2 per tree d−1</td>
<td>2.3–410.2</td>
</tr>
<tr>
<td>GPP</td>
<td>Gross primary productivity</td>
<td>g CO2 m−2 d−1</td>
<td>0.1–9.1</td>
</tr>
<tr>
<td>gs</td>
<td>Stomatal conductance</td>
<td>mol H2O m−2 s−1</td>
<td>N/A</td>
</tr>
<tr>
<td>NEE</td>
<td>Net ecosystem CO2 exchange</td>
<td>g CO2 m−2 d−1</td>
<td>N/A</td>
</tr>
<tr>
<td>Rl</td>
<td>Ecosystem respiration</td>
<td>g CO2 m−2 d−1</td>
<td>N/A</td>
</tr>
<tr>
<td>SF</td>
<td>Sap flow</td>
<td>kg H2O d−1</td>
<td>0.2–127.1</td>
</tr>
<tr>
<td>SFD</td>
<td>Sap flow density</td>
<td>cm3 H2O d−1</td>
<td>6.4–291.6</td>
</tr>
<tr>
<td>SWA</td>
<td>Sapwood area</td>
<td>cm2 ha−1</td>
<td>66 377–66 599</td>
</tr>
<tr>
<td>Tl</td>
<td>Stand-level transpiration</td>
<td>cm3 H2O m−2 d−1</td>
<td>N/A</td>
</tr>
<tr>
<td>VPD</td>
<td>Vapor pressure deficit</td>
<td>kPa</td>
<td>0.0–6.9</td>
</tr>
<tr>
<td>WUEi</td>
<td>Intrinsic water-use efficiency</td>
<td>μmol CO2 mol−1 H2O</td>
<td>75.0–120.0</td>
</tr>
</tbody>
</table>

N/A, not available.

\( C_a \), atmospheric CO2 concentration in ppm (continuously measured on site); r, ratio of the diffusivities of CO2 and water vapor in air (1.6); a, a_{in}, b and pr, leaf-level discriminations against 13C in the diffusion through the stomata (4.4%), during dissolution and liquid phase diffusion (1.8%), in biochemical CO2 fixation (29%o), and in photo-respiratory CO2 release (8%o), respectively; \( \Delta \), tree discrimination against 13C; \( \Gamma^r \), temperature-dependent CO2 compensation point of c. 30–45 ppm (Maseyk et al., 2008); g/gs, ratio between stomatal and internal conductances to CO2 respectively (0.5 according to Maseyk et al., 2011).

In order to obtain an estimate of \( g_s \), we used measured tree transpiration and continuously monitored vapor pressure deficit (VPD) and the general relationship (Beer et al., 2009):

\[ g_s = T / \text{VPD} \]  

Eqn 3

\( T \) was measured as sap flow (SF) of individual trees integrated over the daily cycle (to overcome 1–6 h offset between SF and \( T \) in the dry season). Notably, SF and δ13C-derived WUEi (Eqn 2) integrate different spatial and temporal micro-meteorological changes across the canopy such as variations in light levels and aerodynamic conditions. SF sensors were installed on 16 trees in Yatir forest, 10–70 m from the flux tower in 2004 and again in 2009. Trees were chosen to capture the distribution of DBH and height of trees growing at the footprint of the flux tower. For our analysis, 10 out of 16 trees with the longest SF time-series were chosen. Lab-manufactured thermal dissipation sensors (Granier, 1985) were applied to all trees, and commercial heat balance sensors (Cermak et al., 2004; EMS, Brno, Czech Republic) were also used on six of these trees. The correlation between the two methods had \( r^2 = 0.90 \), with heat balance sensors producing values 2.5 times higher than thermal dissipation sensors. The ratio of 2.5 was in agreement with the forest-scale water flux partitioning to tree transpiration calculated for the site (Klein et al., 2014) and, independently, with earlier validations of the thermal dissipation method (Kanety, 2010; Steppe et al., 2010; Paudel et al., 2013) and was therefore used as a calibration factor. Radial and sapwood depth gradients of SF were measured and analyzed in these trees in a former study (Cohen et al., 2008) and were used for the length compensation factor below. Measurements were taken every 30 s and the 30-min average was saved on a local CR1000 data-logger (Campbell Scientific Inc., Logan, UT, USA). Sap flux densities on the diurnal scale (SFD, in cm3 d−1 cm−2) were calculated from thermal dissipation sensors in relation to the minimum sap flux during the day:

\[ \text{SFD} = \text{LCF} \times \text{CF} \times \sum_{\text{day}} 0.04284 \times (\text{Δ} T_{\text{max}} - \text{Δ} T_{\text{i}}) / \text{Δ} T_{\text{i}}^{1.231} \]  

Eqn 4

\( 0.04284 \) (kg m−2 s−1) and 1.231 are empirical constants (Granier, 1985); LCF = 1/0.65, the length compensation factor due to the inability of the 2-cm probes to capture the entire active sapwood depth, but rather 65% of it (for P. halepensis in Yatir; Cohen et al., 2008; Paudel et al., 2013) and calculated specifically for individual trees; CF, a calibration factor of 2.5; \( \Delta T_{\text{i}} \), average...
half-hourly temperature difference between heated and non-heated probes; $\Delta T_{\text{max},i}$, maximum temperature difference measured during the day (assumed to be at a negligible sap flow rate, below sensor sensitivity threshold) as in the empiric equation (Granier, 1985)). Radial SF gradients were observed in these trees, but were inconsistent with specific azimuths and smaller than differences between similar-size individuals (Cohen et al., 2008). SFD was then scaled to the stand scale, after adjusting to total sapwood area per hectare, $\Sigma \text{SWA}_i$, based on the DBH distribution in forest inventory surveys conducted in 2005 and 2010 in the plots around the flux tower:

$$\sum \text{SWA} = \sum_{i=5}^{35} (f_i \times \text{SWA}_i)$$

Eqn 5

($f_i$, number of trees per hectare in DBH class $i$, between 5 and 35 cm, in 1 cm increments; $\text{SWA}_i$, sapwood area of a tree at a certain DBH class in cm, considering a measured sapwood depth of 6 cm below the cambium (Cohen et al., 2008)). Based on Eqn 4, the 2005 and 2010 $\Sigma \text{SWA}$ were 66 377 and 67 599 cm$^2$ ha$^{-1}$, respectively. These rather similar values were the result of a tradeoff between drought-induced growth reductions and tree mortality, on the one hand, and some diameter increment, on the other. $T_{\text{stand}}$ was thus obtained:

$$T_{\text{stand}} = \sum \text{SWA} \times \text{SFD}_{\text{mean}}$$

Eqn 6

In order to solve for $g_{\text{stand}}$, diurnal $T_{\text{stand}}$ values were divided by VPD, which was continuously monitored at the flux tower and averaged for each day with the following criteria, based on a previous study in the study site (Maseyk et al., 2008): (1) Because CO$_2$ uptake is restricted to daytime hours, night-time VPD values were disregarded; (2) Because stomatal closure restricts CO$_2$ uptake to VPD < 4.0 kPa in $P$. halepensis in Yatir, the value of 4.0 kPa was used when measured VPD was above 4.0 kPa; and (3) Because CO$_2$ uptake is unaffected by VPD at VPD < 1.5 kPa in $P$. halepensis in Yatir, the value of 1.5 kPa was used when measured VPD was below 1.5 kPa. Using these criteria, the diurnal mean VPD avoided the bias associated with averaging low and high values that had negligible effect on CO$_2$ uptake. Similar procedures were also applied in earlier studies (Ewers & Oren, 2000; Drake et al., 2011). The extent to which the continuously measured air VPD represented the actual VPD across the canopy and at the needle surface was further tested (Methods S2).

Tree-scale carbon assimilation and canopy-scale monthly and annual GPP

Tree-scale carbon assimilation rate ($A_{\text{tree}}$) was calculated similarly on diurnal timescale from the ratio WUE$_{i,\text{stand}}$/g. To test the seasonal dynamics of $A_{\text{tree}}$, leaf photosynthesis ($A_{\text{leaf}}$) was measured using the LiCor 6400 on the sample trees in the morning (09:00–11:00 h) and afternoon (12:00–14:00 h) during eight field days between 22 October 2009 and 8 December 2010. Both $A_{\text{tree}}$ and the SF-derived GPP estimates were based on SF data availability, that is for 235 d in the calendar year 2005, and for the entire period between 1 October 2009 and 31 December 2010. Diurnal GPP$_{\text{SF}}$ estimates were summed into an annual estimate for the hydrological year of 2010 (October 2009–October 2010) but not for 2005 due to large data gaps. Monthly GPP$_{\text{SF}}$ values were calculated for all months except for March–June 2005 due to large data gaps. In other months of 2005, data gaps of 1–3 d were filled by the mean GPP$_{\text{SF}}$ of the day before and the day after the gap. Two larger gaps of 12 and 11 d in July and September 2005, respectively, were filled by monthly mean values. In spite of the large gaps this approach was still safe considering the negligible GPP$_{\text{SF}}$ variance in those months (1.0 ± 0.06 and 0.8 ± 0.05 g C m$^{-2}$ d$^{-1}$, respectively).

Eddy covariance-derived GPP

Eddy covariance-derived GPP (GPP$_{\text{EC}}$) was calculated from:

$$\text{GPP}_{\text{EC}} = \text{NEE} - R_c$$

Eqn 7

(NEE, net ecosystem CO$_2$ exchange; $R_c$, ecosystem respiration). The NEE was measured continuously at the Yatir flux tower (Rotenberg & Yakir, 2010). Data gap filling and carbon flux partitioning were performed using an algorithm specially developed for the study site (Afkh, 2009). Night-time NEE values with the friction velocity $U^* < U_{\text{crit}}$ were excluded. $U_{\text{crit}}$ was defined for each month as the value where the night-time NEE ($U^*$) dependence reached a plateau. Missing NEE values (including NEE night-time values when $U^* < U_{\text{crit}}$) were replaced by averages of NEE values for the day before and the day after the current day and for the same hour and minutes as the missing value ($\pm 1/2$ h only if it was still in the same day). If the corresponding values in the closest days were also missing, longer series of close days were checked. The largest gaps that remained after the previous step were filled by the overall mean for a given hour taken within 30 d in the wet season (November to April) and within 60 d in the dry season. Specifically, night-time ecosystem respiration, $R_{\text{sec}}$, used for estimating $R_c$ was calculated for each day as mean of the first 3 × 30-min periods of each night. In these periods, turbulent conditions are typically the highest during the night (Van Gorsel et al., 2009) and better represent the previous daytime photosynthetic activities. Daytime respiration, $R_{\text{dt}}$, for each 30-min period was then calculated as:

$$R_{\text{dt}} = R_{\text{sec}} \times (\alpha_1 g_s^{dT} + \alpha_2 q_{\text{air}}^{dT} + \alpha_3 q_f^{dT})$$

Eqn 8

(coefficients $q_s$, $q_{\text{air}}$, and $q_f$ correspond to soil, wood and foliage Q10 values; $dT$ and $dT_{\text{a}}$, differences of temperatures between the target time of $R$ estimate, and that at the beginning of the night for soil and air temperatures, respectively; partitioning coefficients $\alpha_1$, $\alpha_2$, and $\alpha_3$ are 0.5, 0.1 and 0.4, respectively, representing the relative contribution to ecosystem CO$_2$ exchange of soil, wood, and foliage). $q_s$, $q_{\text{air}}$, and $q_f$ were calculated based on Grünzweig et al. (2009): $q_s$ = 2.45 for wet soil (soil water content in upper 30 cm above 20% v/v) and $q_s$ = 1.18 for dry soil; $q_f$ = 3.15–0.36 $T_{\text{a}}$; and
$g_w = 1.34 + 0.46 \cdot \exp\left(-0.5 \cdot \left((\text{DoY} - 162)/66.1\right)^2\right)$ (DoY, day of year). Needle respiration was measured directly using a gas exchange chamber over 24-h periods on seasonal and annual timescales, also accounting for needle phenology (Maseyk et al., 2008). Profile CO$_2$ measurements showed that CO$_2$ storage in Yatir forest is rather small and can be ignored. Being an evergreen forest ecosystem at the dry timberline, interannual leaf area index variations are low and the contribution of understory vegetation is insignificant (Grünzweig et al., 2003). This approach (Afik, 2009) was found to provide for our specific semi-arid site better results than the more conventional approach (Reichstein et al., 2005) based on comparing predicted and measured soil respiration over the daily and seasonal cycles.

**Statistical analysis**

The significance of seasonal and interannual variations in $\delta^{13}$C-derived WUE$_i$ were tested in ANOVA using JMP Pro 11 (Cary, NC, USA) with WUE$_i$ as response and month, or year (nested by month) as model effects, respectively. Variations in the estimation of GPP from Eqn 1 were calculated using the variations in its components (SFD, WUE$_i$, and VPD) and applying error propagation rules (Taylor, 1997). If $x$ and $y$ have independent errors $\delta x$ and $\delta y$, then the error in $z = x + y$ is $\delta z = (\delta x^2 + \delta y^2)^{1/2}$, and the error in $z = x \cdot y$ is $((\delta x/x)^2 + (\delta y/y)^2)^{1/2}$. In this analysis, we used standard errors of each component. Errors in the daily mean SFD were those associated with variations among the ten individual trees; errors in the monthly mean WUE$_i$ were from interannual variations in 2001–2003; and errors in the daily mean VPD were from fluctuations in the half-hourly VPD values during daytime. The relationships between GPP$_{SF}$ and GPP$_{EC}$ were studied in ANOVA using JMP Pro 11. The interdiurnal co-variability between GPP$_{SF}$ and GPP$_{EC}$ and the relationships between the ratio GPP$_{SF}$/GPP$_{EC}$ and environmental variables were studied using STATISTICA (StatSoft Inc., Tulsa, OK, USA).

**Results**

The seasonal SF dynamics of *Pinus halepensis* in Yatir forest have been described, and specifically for 2010 (Klein et al., 2014). The SF rate correlated well with tree size (Fig. S1; $r^2 = 0.97$ in 1 May 2010 and $r^2 \approx 0.95$ and 0.70 during the wet and the dry seasons, respectively). As expected, when expressed on a sapwood area basis, that is, as sap flux density (SFD), the variation among trees decreased considerably, although it still existed (Fig. S1). Changes in *P. halepensis* $\delta^{13}$C-derived WUE$_i$ followed a seasonal pattern with minimum of 81.7 $\mu$mol CO$_2$ mol$^{-1}$ H$_2$O in December, and maximum of 101.5 $\mu$mol CO$_2$ mol$^{-1}$ H$_2$O in April (Fig. S2). The seasonal dynamics of $\delta^{13}$C-derived WUE$_i$ was significant ($P=0.008$) but the interannual variation was not significant ($P=0.574$). The $\delta^{13}$C-derived WUE$_i$ pattern was similar to that of the WUE$_i$ calculated from chamber gas exchange measurements, but was more stable and had mostly lower values (Fig. S2). This was expected considering that gas exchange measurements were performed under saturating light conditions, thereby promoting higher $A$ and WUE$_i$ than under ambient conditions; and that the organic matter integrated the isotopic signals of CO$_2$ throughout the day and the month, which in the dry season (May–October) was assimilated under very low flux conditions.

In a tree with DBH of 22 cm during 2010, $A_{tree}$ rates were 10–50 g C d$^{-1}$ during the dry season (June–November; Fig. 2a). $A_{tree}$ increased to 220 g C d$^{-1}$ during the first major rain events marking the onset of the wet season in January, and up to 410 g C d$^{-1}$ by the end of March. By the end of April, $A_{tree}$ did not exceed 150 g C d$^{-1}$ again, and decreased to dry season rates during May. In comparison, needle photosynthesis ($A_{needle}$) measured in eight field days in 2010 showed a similar pattern (Fig. 2a). Both estimated $A_{tree}$ and measured $A_{needle}$ had minimum rates during the dry season, with five-fold increase in rates in May, and 10-fold increase during March–April. The seasonal dynamics of tree transpiration (Fig. 2b) were generally similar to those of tree carbon uptake. The ratio $A_{tree}/T_{tree}$ fluctuated between 1.9 mmol CO$_2$ mol$^{-1}$ H$_2$O in early September–October and 5.7 mmol CO$_2$ mol$^{-1}$ H$_2$O in April–May (Fig. 2b). $A_{tree}/T_{tree}$ had many short-term oscillations reflecting the high variability of VPD. Overall, the range in $A_{tree}/T_{tree}$ was three-fold, whereas $T_{tree}$ changes were 10-fold or higher. This meant that the $T_{tree}$ and $A_{tree}$ curves were generally well correlated.

![Fig. 2](https://example.com/fig2.png)

**Fig. 2** Tree-scale (22 cm diameter at breast height (DBH) *Pinus halepensis* tree at the observation plot in Yatir forest in 2010) CO$_2$ uptake ($A_{needle}$, a), transpiration ($T_{tree}$, b), and WUE$_{tree}$ ($A_{tree}/T_{tree}$, gray area in b), derived from sap-flow measurements, and leaf-scale rates of CO$_2$ uptake ($A_{needle}$; a) obtained from eight field measurements days between 22 October 2009 and 8 December 2010 on needles of the same tree (or trees of similar age and size, and at the same stand density) in the morning (closed circles) and afternoon (open circles). Error bars represent standard errors of the mean ($n = 3–6$).
Variations in GPP\textsubscript{SF} and GPP\textsubscript{EC}

GPP values produced by the SF and EC estimations were in good agreement in 2010, with the regression producing a highly significant linear fit (Fig. 3; RMSE = 0.82). The 2005 comparison also produced similar GPP values for the two methods, with a linear regression slope of 1.045 (r\textsuperscript{2} = 0.64, P < 0.0001, n = 457 d). GPP\textsubscript{SF}/GPP\textsubscript{EC} ratio (logarithmic scale; black line) and wind speed (7-d moving average; dashed line) are shown in (f).

GPP\textsubscript{EC} by up to 3.3 g C m\textsuperscript{-2} d\textsuperscript{-1} on 8 March. To test the interdiurnal co-variability of GPP\textsubscript{SF} and GPP\textsubscript{EC}, a cross-correlation analysis was performed assuming time lags of 0–15 d (Fig. S3) producing the highest cross-correlation result at zero time lag (r\textsuperscript{2} = 0.82). Figure 3(f) shows the GPP\textsubscript{SF}/GPP\textsubscript{EC} ratio, on a logarithmic scale, for 2010. The 10-fold GPP\textsubscript{SF} overestimation on 28 January 2010 is evident, along with underestimations in October and December. The seasonal trend of good agreement between the methods in and after the wet season (February–June) and lesser agreement in the dry season (June–December) might indicate a limitation on the GPP\textsubscript{SF} method at very low fluxes. The trends in the GPP\textsubscript{SF}/GPP\textsubscript{EC} dynamics (Table 2; Fig. 3f) hinted at possible contributions of environmental factors. The average wind speed showed some similarities to these dynamics (Fig. 3f). GPP\textsubscript{SF}/GPP\textsubscript{EC} was smaller than 1.0 in 73% of the days when wind speed < 2.5 m s\textsuperscript{-1}. Other environmental factors, such as VPD and soil moisture, were not related to GPP\textsubscript{SF}/GPP\textsubscript{EC} (Fig. S4). But generally both methods provided similar GPP estimates, as the GPP\textsubscript{SF}/GPP\textsubscript{EC} ratio was between 0.5 and 2.0 during 82% of the time.
Variations in GPP\textsubscript{SF} and its components

The standard errors associated with variations among trees in SFD, interannual variations in WUE\textsubscript{e}, and daytime fluctuations in VPD, were used in the calculation of the sources of variance in the GPP\textsubscript{SF} estimation (Table 3). As expected, variations in GPP\textsubscript{SF} were attributed mainly to variations in SFD, with VPD as the second source of variance, and smaller variance associated with WUE\textsubscript{e}. The propagated error in GPP\textsubscript{SF} estimation was relatively high, between 6.8% and 41.3% (Table 3). But notably, the higher relative errors were associated with the lower carbon fluxes in VPD\textsubscript{c} and in late April (Fig. 3f). These and other, smaller deviations were from fluctuations in the half-hourly VPD values during daytime.

We presented the first comparison between SF-derived GPP and EC-derived GPP for a forest canopy. The GPP\textsubscript{SF} captured the seasonal trends similarly to those measured by the GPP\textsubscript{EC}, with GPP\textsubscript{SF} values only slightly lower than GPP\textsubscript{EC} values. This is noteworthy, especially considering that measurements are completely independent of each other: H\textsubscript{2}O-based vs CO\textsubscript{2}-based; and although in a uniform forest stand, the GPP\textsubscript{SF} approach is tree-based near the flux tower and the EC-based one is atmospheric-based, capturing a fetch area away from the tower. The consistent agreement between the methods across seasons and years (Fig. 3a–e) provides some confidence in the robustness of the new GPP\textsubscript{SF} approach. The annual GPP\textsubscript{EC} and GPP\textsubscript{SF} of 670 and 653 g C m\textsuperscript{-2} yr\textsuperscript{-1} translated into 22.3 and 21.8 kg C per tree yr\textsuperscript{-1}, reasonably close to the reported sum of tree C sinks of 23.5 kg C per tree yr\textsuperscript{-1} (Klein & Hoch, 2015). The high interdiurnal co-variability of GPP\textsubscript{SF} and GPPEC supports the idea that SF and EC-based WUE can produce a mechanistically based proxy for GPP. Possible caveats are also indicated by the similar patterns of the GPP\textsubscript{SF}/GPP\textsubscript{EC} ratio and wind speed over part of the record. This may be related to increased EC measurement error at low wind speed (Nakai & Shimoyama, 2012) or increased transpiration (and hence GPP\textsubscript{SF}) disproportional to CO\textsubscript{2} uptake at high wind speed. Variations in GPP\textsubscript{SF} were mostly related to changes in SFD (Fig. 4; Table 3). Marked deviations were observed during the growth season onset, and in late April (Fig. 3f). These and other, smaller deviations were further tested (Fig. 4). As expected, GPP\textsubscript{SF} correlated linearly with SFD, with some values along a maximum GPP\textsubscript{SF} line and others distributed below this line (Fig. 4a). Most of these lower GPP\textsubscript{SF} values were estimated for wet season days with increased VPD\textsubscript{c}, potentially inducing partial stomatal closure and reduced assimilation. The association between GPP\textsubscript{SF} and VPD\textsubscript{c} was less strong (Fig. 4b), in line with the lesser role of VPD\textsubscript{c} in determining GPP\textsubscript{SF} (Table 3). Note that in our analysis VPD\textsubscript{c} was constrained between 1.77 and 4.72 kPa, which are 1.18 of 1.5 and 4.0 kPa (see the Materials and Methods section). At any VPD\textsubscript{c}, there was large variance in GPP\textsubscript{SF}, highlighting the role of additional drivers such as light, soil moisture and temperature. For example, GPP\textsubscript{SF} < 2.0 g C m\textsuperscript{-2} d\textsuperscript{-1} was sometimes estimated on days with low VPD\textsubscript{c} of 2.0 kPa. Such conditions prevailed during autumn, when VPD was decreasing but soil moisture was still too low to allow high assimilation rates. High rates of CO\textsubscript{2} uptake were usually related to mild VPD\textsubscript{c}, and the maximum GPP\textsubscript{SF} decreased by 1.64 g C m\textsuperscript{-2} d\textsuperscript{-1} for each 1.0 kPa increment in VPD\textsubscript{c}.

Table 2

<table>
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<tr>
<th>Year</th>
<th>Month</th>
<th>GPP\textsubscript{EC}</th>
<th>GPP\textsubscript{SF}</th>
<th>GPP\textsubscript{SF}/GPP\textsubscript{EC} ratio</th>
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<td>2005</td>
<td>January</td>
<td>122.1</td>
<td>96.5</td>
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<td>N/A</td>
</tr>
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</tr>
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<tr>
<td></td>
<td>December</td>
<td>17.5</td>
<td>19.9</td>
<td>1.14</td>
</tr>
</tbody>
</table>

Wet season months are given in boldface (May being wet in 2005 but not in 2010). GPP\textsubscript{SF} values were not available (N/A) in March–June 2005 due to large data gaps.

Table 3

<table>
<thead>
<tr>
<th>Parameter (unit)</th>
<th>SE range</th>
<th>Relative SE range (%)</th>
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</thead>
<tbody>
<tr>
<td>SFD (cm\textsuperscript{3} d\textsuperscript{-1} cm\textsuperscript{-2})</td>
<td>0.5–32.0</td>
<td>2.8–40.4</td>
</tr>
<tr>
<td>WUE\textsubscript{e} (µmol CO\textsubscript{2} mol\textsuperscript{-1} H\textsubscript{2}O)</td>
<td>0.3–7.0</td>
<td>0.3–7.9</td>
</tr>
<tr>
<td>VPD (kPa)</td>
<td>0.6–288.6</td>
<td>0.0–16.4</td>
</tr>
<tr>
<td>GPP (g C m\textsuperscript{-2} d\textsuperscript{-1})</td>
<td>0.0–1.0</td>
<td>6.8–41.3</td>
</tr>
</tbody>
</table>

Errors in the daily mean SFD were those associated with variations among the 10 individual trees; errors in the monthly mean WUE\textsubscript{e} were from interannual variations in 2001–2003; and errors in the daily mean VPD were from fluctuations in the half-hourly VPD values during daytime.

Discussion

We presented the first comparison between SF-derived GPP and EC-derived GPP for a forest canopy. The GPP\textsubscript{SF} captured the seasonal trends similarly to those measured by the GPP\textsubscript{EC}, with GPP\textsubscript{SF} values only slightly lower than GPP\textsubscript{EC} values. This is noteworthy, especially considering that measurements are completely independent of each other: H\textsubscript{2}O-based vs CO\textsubscript{2}-based; and although in a uniform forest stand, the GPP\textsubscript{SF} approach is tree-based near the flux tower and the EC-based one is atmospheric-based, capturing a fetch area away from the tower. The consistent agreement between the methods across seasons and years (Fig. 3a–e) provides some confidence in the robustness of the new GPP\textsubscript{SF} approach. The annual GPP\textsubscript{EC} and GPP\textsubscript{SF} of 670 and 653 g C m\textsuperscript{-2} yr\textsuperscript{-1} translated into 22.3 and 21.8 kg C per tree yr\textsuperscript{-1}, reasonably close to the reported sum of tree C sinks of 23.5 kg C per tree yr\textsuperscript{-1} (Klein & Hoch, 2015). The high interdiurnal co-variability of GPP\textsubscript{SF} and GPP\textsubscript{EC} supports the idea that SF and δ\textsuperscript{13}C-derived WUE can produce a mechanistically based proxy for GPP. Possible caveats are also indicated by the similar patterns of the GPP\textsubscript{SF}/GPP\textsubscript{EC} ratio and wind speed over part of the record. This may be related to increased EC measurement error at low wind speed (Nakai & Shimoyama, 2012) or increased transpiration (and hence GPP\textsubscript{SF}) disproportional to CO\textsubscript{2} uptake at high wind speed. Variations in GPP\textsubscript{SF} were mostly related to changes in SFD (Fig. 4; Table 3). Marked deviations were observed during the growth season onset, and in late April (Fig. 3f). These and other, smaller deviations

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occurred throughout the year and hence do not directly depend on seasonality (Table 2). In late January 2010 there was a 1-wk delay between the increase in GPP_{SF} on 21 January and the increase in GPP_{EC} on 28 January. If there was a decoupling between the trees’ hydraulic and photosynthetic systems during the first week of the growing season, there should have been a transient decrease in WUE. It is possible that the December minimum in WUE_{i} (Fig. S2) is related to such scenario, but due to its short term, the transient low WUE_{i} values were potentially diluted by higher values during the same month. In mid-December 2001, a low WUE_{i} value of 70.5 μmol CO_{2} mol^{-1} H_{2}O was calculated from chamber needle gas exchange measurements, immediately following a major rain event marking the onset of the growing season (Klein et al., 2005). WUE_{i} values preceding and following this minimum by c. 1 month were 137.5 and 88.2 μmol CO_{2} mol^{-1} H_{2}O, respectively. It is possible that following the dry season, the recovery of photochemistry and photosynthetic components in the needles (e.g. pigments, enzymes) was slower than that of the xylem, as shown elsewhere in olives and in oaks (Giorio et al., 1999; Galle et al., 2007). Although these details need further studies and probably higher temporal resolution in the WUE estimates, it shows the potential in obtaining additional insights by constraining GPP using the two independent approaches.

It is difficult to relate our observations to those of earlier studies that measured GPP_{SF} but not GPP_{EC} (Hu et al., 2010; Wang et al., 2013). The forest settings of these earlier studies likely involved larger variations in the measured parameters than our semi-arid pine forest, for example related to a multiple number of tree species (Hu et al., 2010). Nevertheless, both studies provided comparisons with other methodologies, and both reported consistently large underestimation of GPP by the SF-based method. The mean GPP_{SF} of a subalpine conifer forest (Hu et al., 2010) was 0.97 g C m^{-2} d^{-1}, whereas the mean modeled GPP applied at the same site was 2.15 g C m^{-2} d^{-1}. In a subtropical acacia plantation (Wang et al., 2013), the mean GPP_{SF} was 2.13 g C m^{-2} d^{-1}, whereas the mean GPP estimated from carbon balance for a similar ecosystem (Nouvellon et al., 2012) was 8.77 g C m^{-2} d^{-1}. Here we estimated the mean GPP_{SF} and GPP_{EC} at 1.79 and 1.84 g C m^{-2} d^{-1}, respectively. A relatively good agreement between GPP_{EC} and GPP modeled using SF data (but not δ^{13}C-derived WUE_{i}) was also reported for a temperate pine species but not for deciduous species, possibly indicating higher complexity in GPP estimation in the latter (Schäfer et al., 2003). Clearly this study benefitted from a combination of three SF measurement methods providing a robust T estimate verified by a closed water balance. For example, using noncalibrated readings from thermal dissipation SF probes would yield c. 60% lower SF values and GPP underestimation to match. Our calculation of WUE also improved on earlier studies (Hu et al., 2010; Drake et al., 2011), which didn’t account for the advanced model of δ^{13}C discrimination.

Uncertainties associated with the GPP_{SF} methodology

Our analysis highlighted the major contribution of the variations in SFD to the GPP_{SF} estimation (Table 3), also in agreement with the earlier applications of this methodology (Hu et al., 2010; Wang et al., 2013). At the single tree scale, SF integrates variations in transpiration rates across the tree crown, providing a rather robust T_{tree} flux for estimation of A_{tree}. However, at the canopy scale, differences among individual trees come into play, and can increase with competition for resources. The low water inputs in the semi-arid pine forest mean that even small structural changes in the soil and rhizosphere can translate into considerable differences in water uptake among neighboring trees. Evidence for such heterogeneity comes from a patchy spatial pattern of tree mortality observed in Yatir forest following the 2008–2009 drought (Klein et al., 2014). Considering the observed variations in SFD (Fig. S1; Table 3), our analysis could benefit from a larger number of study trees.

The use of a single diurnal VPD value is a simplification that also increases the uncertainty of GPP_{SF}. Variations in VPD exist both in time (along the day and the year; Table 3) and space (across the canopy, from top to bottom, in shaded vs sunlit needles; Methods S2). Therefore, higher resolution data may produce more reliable estimates. Stomatal and photosynthetic effects were accounted for in our analysis, thereby limiting the VPD values to 1.5–4.0 kPa. We also calculated that the actual VPD at the leaf surface was c. 18% higher than the measured atmospheric VPD. Differences between air and needle temperatures, which were smaller than observed here, have been reported (Drake et al., 2011), but increased with temperature. Note that the relationship between GPP_{SF} and VPD (Fig. 4a) is similar to the relationship between g_{s} and VPD reported earlier (Maseyk et al., 2008), with the majority of values at low rates of g_{s} and GPP, associated with the long dry season, and a gradual decrease in the maximum values of g_{s} and GPP with increasing VPD.
The relatively small variations in $\delta^{13}$C-derived WUE$_t$ meant a smaller effect on the GPP$_{SF}$ error propagation than that of SF and VPD (Table 3). Nevertheless, it is possible that concurrent, high-resolution wood sampling could improve our GPP estimations, as discussed above for the onset of the growth season. Concurrent sampling for $\delta^{13}$C should also significantly reduce the number of samples by avoiding the need for a multi-annual average (Methods S1) but more work is needed to recommend a specific sampling density. Earlier studies provided alternative approaches in the sampling of organic matter for WUE estimation. The $\delta^{13}$C signal of fresh leaf compounds might better represent the WUE of the photosynthates than the whole wood and needle samples used here, yet sugars are a relatively complex and dynamic pool and are not as integrative. The ratio WUE$_t$/VPD$_r$, which is equivalent to $A_h/T_{\text{tree}}$, reproduced the $A_h/T$ dynamics in these trees well, with wet season and dry season means of 4.5 and 3.1 mmol CO$_2$ mol$^{-1}$ H$_2$O, respectively (Maseyk et al., 2008).

At the forest scale, the GPP estimate is sensitive to variations in additional parameters, such as stand density and carbon uptake by understory vegetation. The latter parameter was estimated as very small in our study site (Grünzweig et al., 2007), but water balance calculation showed that water use in the understory during the short wet season (and usually earlier than peak canopy activity) can be as high as 13% of the water budget (Klein et al., 2014). Assuming that most of the understory gas exchange is indeed associated only with wet season growth of annuals and geophytes, its WUE should be lower than that of the pine trees, and hence the expected effect on GPP smaller than 13%. Nevertheless it must be recognized that relying on SF precludes consideration of the understory vegetation, which in some cases can be significant. When the contribution of the understory component is small, such as observed here, the GPP$_{SF}$ and GPP$_{EC}$ are expected to show high agreement and provide constraints and validation to either one of the approaches. Once faith in the robustness of the methodology is gained, the distinction between the two estimates should provide additional insights to ecosystem functioning.

Implications and perspectives

The encouraging outcome of our GPP$_{SF}$ comparison study should motivate similar comparisons in other forest sites. Notably, such estimates can prove more complex than presented here due to higher ecosystem complexity. A major recommendation arising from this study is the requirement of intimate knowledge of the eco-physiology of the tree species in the studied canopy. For example, the response of $g_i$ to VPD was critical for constraining high VPD values. The key role of GPP as a measure of the photosynthetic capacity of forests and its implications on the terrestrial carbon cycle, as conditions are changing, highlight the need to constrain and improve current GPP estimates. Although pronounced effort has been invested in setting up a global network of flux towers (www.fluxnet.orl.gov), there is great need to increase the resolution of our observation across different vegetation types, land uses and climates. Recently, flux measurements of carbonyl sulfide (COS) have been utilized to infer ecosystem-scale GPP, and were in agreement with simultaneous GPP$_{EC}$ within $\pm$15% (Asaf et al., 2013). GPP$_{COS}$ was usually higher than GPP$_{EC}$, especially in our semi-arid forest site. It seems that applying a combination of complementary approaches (e.g. GPP$_{COS}$, GPP$_{SF}$ and GPP$_{EC}$) can produce a powerful measurement tool, both to constrain estimates of GPP and to provide additional insights based on the specific processes that control each methodology. Similarly, SF-measuring research stations, with and without flux towers, can become an important tool in terrestrial carbon budgeting. The potential for enhancement and constraining of the global GPP monitoring network and database, and ultimately of global-scale GPP of the terrestrial biosphere, is hence considerable. Finally, the method presented here also offers a reasonable approach with which to reconstruct GPP using existing and archived datasets of SF and WUE, and to calculate additional parameters that are hard to obtain: for example, $A_h$, the whole-tree C uptake and the mean stomatal conductance at the stand level.

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Supporting Information

Additional supporting information may be found in the online version of this article.

Fig. S1 Variations in sap flow and sap flux density as a function of tree diameter at breast height among the 10 measured Pinus halepensis trees in Yatir forest.

Fig. S2 Changes in intrinsic water-use efficiency of Pinus halepensis in Yatir forest, from chamber measurements of assimilation and stomatal conductance and from δ¹³C of needles and stem wood.

Fig. S3 Cross-correlation analysis between GPPSF and GPPEC and between dlnGPPSF and dlnGPPEC, where dlnGPP = (GPP_{day i} – GPP_{day i-1})/GPP_{day i-1}.

Fig. S4 Relationships between the GPPSF/GPPEC ratio and the prevailing vapor pressure deficit and soil water content.

Methods S1 Estimation of WUEᵢ from wood and needle δ¹³C.

Methods S2 Validations of the vapor pressure deficit (VPD) measurement.

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