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Response of water use efficiency to summer drought in boreal Scots pine forests in Finland

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Abstract. The influence of drought on plant functioning has received considerable attention in recent years, although our understanding of the response of carbon and water coupling in terrestrial ecosystems remains unclear. In this study, we investigated the response of water use efficiency to summer drought in boreal forests at daily time scales mainly using eddy covariance flux data. In addition, simulation results from the JSBACH land surface model were evaluated against the observed results. Two Scots pine (*Pinus sylvestris*) sites at Hyytiälä (southern Finland) and Sodankylä (northern Finland) were used in the study. Based on observed data, the ecosystem level water use efficiency (EWUE) showed a decrease only during a severe soil moisture drought at Hyytiälä, whereas the inherent water use efficiency (IWUE) increased when there was a severe soil moisture drought at Hyytiälä and a moderate soil moisture drought at Sodankylä. This indicates a decrease in surface conductance at the ecosystem level, but the decrease in evapotranspiration (ET) was alleviated because of the increased vapour pressure deficit (VPD) during drought. Moreover, the changes in IWUE implied that Scots pine has weaker response to drought in the southern site than in the northern site. Thus, IWUE is a more appropriate metric than EWUE for capturing the impact of soil moisture drought on plant functioning at daily time scales. In general, the results from transpiration based ecosystem level water use efficiency (EWUEt) and IWUE, and the transpiration based inherent water use efficiency (IWUEt) from JSBACH simulations were similar to the observed results. The deviated groups of gross primary production (GPP) and evapotranspiration (ET) under severe soil moisture drought in observed data at Hyytiälä were also successfully captured in the simulated results. However, deficiencies in the model were clearly seen by the limitation effect of air humidity on stomatal conductance in observed data. Our study provides a deeper understanding of carbon and water dynamics in the major boreal ecosystem. These findings highlight the importance of choosing a suitable plant functioning indicator when investigating the effects of drought, and suggest possible improvements to land surface models, which play an important role in the prediction of biosphere-atmosphere feedbacks in the climate system.

Keywords: drought response, boreal forests, eddy covariance, water use efficiency, soil moisture drought, land surface model

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1. Introduction

Terrestrial plants assimilate carbon through photosynthesis accompanied by a loss of water in transpiration. Both processes are strongly regulated by plant physiology (e.g. stomatal conductance; g_s) and local environmental conditions. Plants protect themselves from excessive water (H_2O) losses (diffusion out of the leaf) under water-limited environments through a reduction of stomatal conductance, which in turn leads to less carbon uptake (diffusion of carbon dioxide (CO_2) into the leaf) and physiological stress (McDowell et al., 2008; Will et al., 2013).

Soil water deficit can induce a reduction of transpiration (Bréda et al., 1993; Clenciala et al., 1998; Granier et al., 2007; Irvine et al., 1998), and it has been recognized as the main environmental factor limiting plant photosynthesis at global scale (Nemani et al., 2003). The occurrence of drought is low in northern Europe. However, the summer of 2006 in Finland was extremely dry, and 24.4 % of the 603 forest health observation sites over entire Finland showed drought damage symptoms in visual examination, in comparison to 2–4 % damaged sites in a normal year (Muukkonen et al. 2015). The spatial distribution of the drought damages has been found to be closely related to the plant available soil moisture (Gao et al., 2016).

Water Use Efficiency (WUE) is a critical metric that quantifies the trade-off between photosynthetic carbon assimilation and transpiration at the leaf level (Farquhar et al., 1982). WUE describes ecosystem functioning, which is closely related to the global cycles of water, energy and carbon (Keenan et al., 2013). With the use of the eddy covariance technique (EC) and associated data processing, i.e. the derivation of gross primary production (GPP) and evapotranspiration (ET) from measurements of CO_2 flux and latent heat flux, WUE can be calculated at the ecosystem scale (EWUE) as the ratio of GPP and ET. EWUE is broadly adopted as a surrogate for WUE due to data availability (Arneth et al., 2006; Law et al., 2002; Lloyd et al., 2002).

Reichstein et al. (2007) observed a small decrease in EWUE in the majority of the 11 studied EC sites during the 2003 summer heatwave in Europe. However, their findings are at odds with many models that describe the environmental controls on stomatal conductance, with increased EWUE predicted during drought periods (Reichstein et al., 2002; Schulze et al., 2005). Many of those models are based on the optimality theory by Cowan and Farquhar (1977) who proposed that plants are able to regulate stomatal conductance in order to maximize WUE. Granier et al. (2008) reported that EWUE increased linearly with soil water deficit duration and intensity at a young beech forest site in north-eastern France. Moreover, EWUE also increased substantially at two forest sites, but not at grassland sites, during the 2011 spring drought in Switzerland (Wolf et al., 2013). However, no differences in EWUE were shown between abundant- and low-rainfall years at a boreal Scots pine forest site in south-eastern Finland, even though GPP was reduced during low-rainfall years with long-lasting drought periods (Ge et al., 2014). Therefore,

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the impact of drought on EWUE remains unclear. Moreover, Beer et al. (2009) have proposed the ecosystem level inherent water use efficiency (IWUE), which has been found to increase during short-term moderate drought.

Given the need to understand and project feedbacks between climate change and plant physiological responses, it is crucial to be able to realistically model the plant controls of stomatal conductance, and photosynthesis and transpiration responses under water stress (Berry et al., 2010; Knauer et al., 2015; Zhou et al., 2013). Contrasting results that are produced by the various land ecosystem models highlight the current uncertainty in regard to plant physiology (water use) in response to drought in simulations (Huang et al., 2015; Jung et al., 2007).

The objectives of this study are (1) to understand the environmental controls on GPP and ET fluxes, especially during drought, in boreal Scots pine (*Pinus sylvestris*) forests at two EC sites in Finland, (2) to investigate the relationship of EWUE and IWUE to drought, (3) to evaluate how accurately plant functioning responses to changes in environmental variables are captured by the JSBACH land surface model (LSM).

2. Data and methods

2.1 Study sites

Scots pine (*Pinus sylvestris*) is the dominating species in southern Finland, covering more than half of the forest area (Vesala et al., 2005). Two Scots pine forest sites in Finland were studied in this work. Hyytiälä and Sodankylä are situated in the southern and northern boreal zone, respectively. The mean annual temperature and precipitation (Table 1) in Hyytiälä are higher than in Sodankylä (Aurela, 2005; Vesala et al., 2005), reflecting the latitudinal difference between the sites. The total leaf area index (LAI) at Hyytiälä is 8 m^2/m^2, approximately twice of that at Sodankylä (3.6 m^2/m^2). Both sites are located on mineral soils. More details of the two sites can be found in Table 1.

We analysed the summer period (June-August) from an 11-year dataset for Hyytiälä (1999-2009) and from an 8-year dataset for Sodankylä (2001-2008) according to data availability.

2.2 Flux measurement and data processing

Ecosystem carbon and water fluxes at Hyytiälä and Sodankylä were measured with the micrometeorological EC method. Turbulent fluxes were calculated as half-hourly averages following standard methodology (Aubinet et al., 2012) with EddyUH software at Hyytiälä (Mammarella et al., 2016) and PyBarFlux software at Sodankylä (Aurela et al., 2015). Data recorded during periods of low-turbulence mixing and instrument failures were screened. The vertical CO_2 flux was obtained as the covariance of high-frequency (10 Hz) observations of vertical wind speed and the CO_2 concentration (Baldocchi, 2003). The CO_2 flux was corrected for storage change to obtain net ecosystem CO_2 exchange (NEE), which was then partitioned into total ecosystem respiration (TER) and GPP. Missing or poor quality GPP flux data was gap-filled according to Kolari et al. (2009) for Hyytiälä and Reichstein et al. (2005) for Sodankylä. ET was inferred from the measured latent heat flux. The ET flux was gap-filled with the mean diurnal variation method at both sites. For our analysis, daily values of GPP and ET fluxes were calculated as daily sums of half-hourly values and only good quality gap-filled data were used.

In addition to the EC measurements, a set of supporting meteorological variables were adopted as half-hourly averages; incoming shortwave and longwave radiations, air temperature, humidity, precipitation at both sites were used as meteorological forcing for the site level simulations.

The soil water content was monitored with the Time Domain Reflection (TDR) technique at Hyytiälä, and with the ThetaProbe technique at Sodankylä. The measured soil layers were: Hyytiälä: 0 to −5, −5 to −23 and −23 to −60 cm, Sodankylä: −10, −20 and −30 cm. In this study, soil moisture at the two lower levels at Hyytiälä was averaged, and the average of the three levels at Sodankylä was adopted.

2.3 JSBACH land surface model

JSBACH (Raddatz et al., 2007; Reick et al., 2013) is the LSM of the Max Planck Institute for Meteorology Earth System Model (MPI–ESM) (Roeckner et al., 1996; Stevens et al., 2013). The land physics of JSBACH mainly follow those of the global atmosphere circulation model ECHAM5 (Roeckner et al., 2003), and the biogeochemical components are mostly taken from the biosphere model BETHY (Knorr, 2000). In JSBACH, land vegetation cover is described as plant functional types (PFTs) and a set of properties (e.g. maximum LAI, albedo) is attributed to each PFT with respect to the processes that are accounted for by JSBACH. A five layer soil hydrology scheme was implemented in JSBACH by Hagemann and Stacke (2015). The models of Farquhar et al. (1980) is used for photosynthesis of C3 plants. The limitation from soil water availability on stomatal conductance is also considered in the photosynthesis module. Unlike the BETHY approach (Knorr, 2000), the control of stomatal conductance in JSABCH does not include the influence of atmospheric humidity (see detailed description in Knauer et al., 2015).

2.4 Site level simulations by JSBACH

The simulations of JSBACH for the two sites were carried out using the half-hourly local meteorological observations as model forcing. Based on the site-specific information, PFT was assigned as evergreen needleleaf forest and the soil type was set as loamy sand in JSBACH for both sites. The maximum LAI was set according to observed values. Also, the maximum carboxylation rate (Jmax) and maximum electron transport rate (Vmax) at 25 °C were adjusted, for the simulated GPP to match the magnitude of the observed GPP. The Vmax was set to be 37.5 and 30 for Hyytiälä and Sodankylä, respectively. The Jmax was 71.3 for Hyytiälä and 64.2 for Sodankylä. The soil depth and root depth at the two sites were derived from maps for the regional JSBACH simulation presented in Gao et al. (2016) (see also Hagemann and Stacke, 2015). Those parameter settings in the JSBACH site level simulations for the two sites are listed in Table 1. Prior to the actual simulations, long-term spin-up runs were conducted to obtain equilibrium for soil water and soil heat, as well as ecosystem carbon pools.

To analyse the response of simulated GPP and ET to environmental variables, daily air temperature (Ta), incoming solar radiation (Rs) and VPD were calculated from the JSBACH forcing data, and the Soil Moisture Index (SMI) was derived from simulated soil moisture and soil parameters in JSBACH.

2.5 Soil Moisture Index (SMI)

In this study, the soil moisture dynamics are represented by SMI (also referred to as Relative Extractable Water – REW), which has been demonstrated to be able to represent summer drought in boreal forests in Finland (Gao et al., 2016). The SMI describes the ratio of plant available soil water content to the maximum volume of water available to plants in the soil (Betts, 2004; Seneviratne et al., 2010):

$$\mathrm{SMI} = (\theta - \theta_{WILT})/(\theta_{FC} - \theta_{WILT}), \quad (1)$$

where θ is the volumetric soil moisture [m^3 H_2O m^{-3}], θ_{FC} is the field capacity [m^3 H_2O m^{-3}], θ_{WILT} is the permanent wilting point [m^3 H_2O m^{-3}]. When θ exceeds θ_{FC}, soil water cannot be retained against gravitational drainage, while below θ_{WILT}, the soil water is strongly held by the soil matrix and cannot be extracted by plants (Hillel, 1998).

The SMI calculated from the simulated soil moisture is based on the model soil parameters. We used the average of the second layer (layer-2; 6.5–31.9cm) and the third layer (layer-3; 31.9–123.2 cm) of the simulated soil moisture for Hyytiälä, and layer-2 for Sodankylä, to correspond with the depth of the observed soil moisture. Soil moisture conditions can be classified as: severe drought: $0 \leq \mathrm{SMI} < 0.2$, moderate drought: $0.2 \leq \mathrm{SMI} < 0.4$, mid-range: $0.4 \leq \mathrm{SMI} < 0.6$, moderate wet: $0.6 \leq \mathrm{SMI} < 0.8$, very wet: $0.8 \leq \mathrm{SMI} <1$.

For the SMI derived from the observed soil moisture at Hyytiälä, the measured soil parameters were adopted (i.e. water content at saturation (θ_{SAT}) = 0.50 m^3 H_2O m^{-3}, θ_{FC} = 0.30 m^3 H_2O m^{-3}, θ_{WILT} = 0.08 m^3 H_2O m^{-3}). As θ_{FC} acts as a proxy for θ_{SAT} in the model, θ_{SAT} was used instead of θ_{FC} for consistency when calculating SMI based on the observed soil moisture data (Hagemann and Stacke, 2015). The same classification mentioned above for simulated SMI was applied for the observed SMI at Hyytiälä. Due to the lack of measured soil parameters, the observed volumetric soil moisture at Sodankylä was directly adopted and categorized according to its value with respect to the simulated SMI (i.e., severe drought: 0 m^3 H_2O m^{-3} $\leq \theta <$ 0.032 m^3 H_2O m^{-3}, moderate drought: 0.032 m^3 H_2O m^{-3} $\leq \theta <$ 0.064 m^3 H_2O m^{-3}, mid-range: 0.064 m^3 H_2O m^{-3} $\leq \theta <$ 0.096 m^3 H_2O m^{-3}, moderate wet: 0.096 m^3 H_2O m^{-3} $\leq \theta <$ 0.128 m^3 H_2O m^{-3}, very wet:

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$0.128\ m^3\ H_2O\ m^{-3} \leq \theta < 0.16\ m^3\ H_2O\ m^{-3}$).

2.6 Ecosystem Water Use Efficiency (EWUE) and Inherent Water Use Efficiency (IWUE)

At the ecosystem level, water use efficiency is calculated as

$$EWUE = GPP/ET, \quad (2)$$

The inherent water use efficiency (IWUE) is defined as EWUE multiplied by VPD, and ET/VPD is a hydrological measure of the surface conductance at the ecosystem level (Beer et al., 2009),

$$IWUE = GPP \times VPD/ET, \quad (3)$$

From EC data EWUE and IWUE can only be calculated with ET, which contains the effects of interception and soil evaporation. However, process-based ecosystem models can be used to reveal plant physiological processes by separating evaporation and transpiration. Therefore, transpiration-based ecosystem water use efficiency (EWUEt) and inherent water use efficiency (IWUEt) were also calculated using simulated transpiration instead of ET in equations (2) and (3).

3. Results

3.1 The relationship of GPP to ET/transpiration(T) categorized by environmental variables

3.1.1 Hyytiälä results

At Hyytiälä, the observed daily GPP ranged from 1 to 12 g C m^{-2} day^{-1}, and the observed daily ET ranged from 0 to 4.5 kg H_2O m^{-2} day^{-1} during the study period. In general, GPP increased with increasing ET with a non-linear response (Fig. 1; see fitting method description in the Supplementary Material). When categorized according to the ranges of environmental variables, an increase in Rs, Ta and VPD led to an increase in GPP and ET in general, whereas soil moisture conditions showed no clear impact on the relationship of GPP to ET (Fig. 1).

Moreover, in the relationship between daily observed GPP and ET at Hyytiälä, two groups of data deviated from typical plant functioning under normal conditions (i.e. the data with residuals from the fitted line were outside the 2.5th-97.5th percentile band as shown in Fig. 1). The two groups both have small daily ET values (less than 2 kg H_2O m^{-2} day^{-1}), although the daily GPP for group a is above normal and for group b is below normal. Group a is found in an environment that has favorable Ta (10 to 25 °C), sufficient Rs (above 150 W/m^2 generally), low VPD (mostly below 0.8 kPa) and non-water limited condition (SMI > 0.4 mostly), while the most data points in group b experience slightly higher Ta and Rs values, high VPD (0.8 to 2 kPa mostly) and soil moisture indicating severe drought (SMI < 0.2). The deviated group a occurred at the beginning of the summer and almost all the days were in June. The deviated group b occurred at the end of the summer in 2006 (end of July to the middle of August), and this year was the only year in the 11-year dataset at Hyytiälä where SMI values were under 0.2 (Fig. 2 in Gao et al., 2016).

The simulated daily GPP and ET at Hyytiälä are similar to the observed data in terms of their extent and relationship, as well as their correlations with the environmental variables (Fig. S1 in the Supplementary Material). However, the groups a and b that were visible in observed results are not differentiated from other days in the simulations. Nevertheless, the relationship between GPP and transpiration from the simulations shows that the two groups have similar quantities of transpiration (less than 2 kg H_2O m^{-2} day^{-1}) but exhibit above- and below-normal levels of GPP under sufficient and deficient soil moisture conditions, respectively. However, the deviation of the simulated GPP of those two groups from the majority of the GPP values is not as large as that in the ET-based observed dataset.

3.1.2 Sodankylä results

The observed relationship between daily GPP and ET at Sodankylä (Fig. S2 in the Supplementary Material) is more scattered than at Hyytiälä, and does not contain deviated GPP and ET groups that could be reasonably explained by environmental conditions. The values of GPP and ET are concentrated at lower magnitudes at Sodankylä than at Hyytiälä. This is partly due to generally lower Ta values at Sodankylä in comparison to Hyytiälä, with less days above 20 °C and more days below 10 °C observed at that site. In addition, the number of days with Rs values above 250 W m^{-2} was much less at Sodankylä than at Hyytiälä. Moreover, the growing season was shorter and the forest LAI value was lower in Sodankylä than in Hyytiälä. No severe soil moisture deficit at Sodankylä ($\theta < 0.032$ m^3 H_2O m^{-3}) were observed during the study period.

In comparison to the observed data at Sodankylä, the simulated GPP and ET/T relationship was less scattered. The range of simulated daily GPP (1.5 to 8 g C m^{-2} day^{-1}) was smaller than the observed GPP (0 to 10 g C m^{-2} day^{-1}). In the simulation, GPP and ET/T both increased concomitant with increasing Rs and VPD values, a trend that was more evident than in observed data. Although severe drought days (SMI<0.2) were seen in the simulation, the GPP and ET/T relationship did not deviate from plant functioning under normal conditions. This was because we only used layer-2 soil moisture from the JSABCH simulation in order to match with the depth of observed soil moisture at Sodankylä, and the severity of drought does not reach layer-3 that also belongs to the root zone depth at the site. However, in the model, the whole root zone soil moisture plays a role in regulating the plant stomatal conductance.

In the following, we concentrate on the results from group b at Hyytiälä, where the impact of soil moisture was clearly seen in the relationship between GPP and ET.

3.2 Response of GPP and ET/T to environmental variables categorized by SMI

The impact of soil moisture on GPP and ET/T were further investigated by separating the dependence of GPP and ET on environmental variables under different soil moisture conditions. Regression functions were fitted for each group, and the regression parameters and coefficients of determination are summarized in Table S1 and S2 in the Supplementary Material.

At Hyytiälä, severe soil moisture drought (SMI < 0.2) led to a distinct response in both observed GPP and ET to Rs, Ta and VPD, when compared to the groups with SMI values greater than 0.2 (Fig. 2 and 3). For the relationship between GPP and Rs, the Michaelis-Menten type equation was used (e.g. Markkanen et al., 2001). The group that had SMI values less than 0.2 displayed lower GPP values in relation to increased Rs values and had a lower coefficient of determination than the other groups. The relationship between Ta and GPP was rather scattered and we used linear regression to determine the general trends of GPP dependence on Ta under different soil moisture conditions. In contrast to the positive correlations seen with the other SMI groups, GPP was negatively correlated with Ta under severe soil moisture drought. Exponential decay equations were fitted to the response of GPP to VPD for the groups with SMI values greater than 0.2, whereas a linear response with a negative slope was found for the group under severe soil moisture drought. Furthermore, for the relationship between GPP and SMI, decreasing SMI values led to a linear decrease in GPP with a high correlation ($r^2 = 0.62$) when SMI were lower than 0.2, while the other SMI groups showed scattered patterns. The GPP value tended to be highest when SMI was between 0.4 to 0.6, and decreased with lower or higher SMI.

For the simulated GPP, the group under severe soil moisture drought (SMI < 0.2) also deviated from the other SMI groups, but not to the same extent as that in the observed GPP. The response of simulated GPP to VPD in the group under severe soil moisture drought was positive, in contrast to the negative relationship seen for the observed GPP.

The response patterns of the observed ET to environmental variables were similar to those of GPP (Fig. 3). As with GPP, the group under severe soil moisture drought deviated strongly from the other SMI groups. However, the decrease in ET under severe soil moisture drought relative to the environmental variables was not as large as in GPP.

Some differences existed in the response of the simulated ET/T to environmental variables compared to the observed ET (Fig. S1 in the Supplementary Material). The dependence of simulated ET/T on Rs tended to be more linear in contrast to the observed ET and Rs relationship. In addition, the simulated ET and T increased with a concomitant increase in VPD when VPD was high, which was not the case with observed ET. Nevertheless, simulated ET/T of the group under severe soil moisture drought deviated strongly from the other SMI groups, but to a less extent than observed ET/T. Additionally, both observed and simulated

ET/T showed a small decrease when SMI indicated moderate drought ($0.2 \leq SMI < 0.4$), compared to days with higher soil moisture conditions ($SMI \geq 0.4$) and under the same VPD.

At Sodankylä, the response of the observed GPP and ET to environmental variables showed the same response patterns as those at Hyytiälä (Fig. S3 and Fig. S4 in the Supplementary Material). When Rs, Ta and VPD values were high, simulated GPP and T were higher for the group with SMI values between 0.2 and 0.4 in comparison to the other SMI groups.

3.3 Soil moisture drought impacts on EWUE and IWUE

According to the observed data at Hyytiälä, when SMI was higher than 0.2, daily EWUE showed values (about 2-4 g C kg^{-1} H_2O) within the typical ET range, and higher values when ET was low (Fig. 4). However, at severe soil moisture drought conditions ($SMI < 0.2$), significant decreases in EWUE were seen, which indicates a stronger decrease in GPP than in ET compared to normal plant functioning. In the simulation, the EWUE did not show an obvious decrease when SMI was lower than 0.2, whereas EWUEt showed a much smaller decrease than the observed data. The observed and simulated IWUE, as well as the simulated IWUEt increased when SMI was lower than 0.2 at Hyytiälä. The increase was more obvious in the simulated IWUE. The IWUEt showed a narrower range than IWUE as the influence of evaporation was not included.

Low soil moisture conditions did not lead to changes in the observed and simulated EWUE, as well as simulated EWUEt at Sodankylä (Fig. S5 in the Supplementary Material). The observed and simulated IWUE at Sodankylä increased when soil moisture was under moderate drought (i.e. observed $\theta < 0.064$ m^3 H_2O m^{-3} and simulated $SMI < 0.4$, respectively). However, the increase was not seen in the simulated IWUEt. This would suggest that soil moisture drought was not severe enough to influence transpiration and GPP through stomatal conductance in the simulation.

4. Discussion

4.1 Drought impacts on GPP and ET

Both GPP and ET were suppressed when there was severe soil moisture drought ($SMI<0.2$) at Hyytiälä. In addition, the response of GPP and ET to the changes in environmental variables under severe water stress differed from those under other soil moisture conditions. The dominant reason is that low soil moisture leads to stomatal closure of the plants, which further limits plant assimilation and transpiration. The consequence of decreased ET due to soil moisture drought would be increased atmospheric VPD, which in turn accelerates stomatal closure (Eamus et al., 2013; Jarvis, 1976). Moreover, the coupling between GPP and ET was disturbed and EWUE decreased due to the soil moisture limitation (shown as the deviated group b).

In high latitude regions, such as Finland, snowmelt water normally saturates the soil at the beginning of the growing season, and thus soil moisture drought is more likely to occur at the end of the summer. The favourable environmental conditions for plant growth at the beginning of summer have a major influence on annual plant growth. There was no severe soil moisture drought observed in the 8-year dataset at Sodankylä. Therefore, there was no disturbance on GPP, ET and EWUE from low soil moisture conditions. As the Sodankylä site is located in the north of Finland, the lower summertime mean Ta, Rs and VPD values in comparison to those at Hyytiälä, together with a low LAI, resulted in lower GPP and ET in general.

In contrast to EWUE, IWUE increased when there was a severe soil moisture drought at Hyytiälä and a moderate soil moisture drought at Sodankylä. This means that the intrinsic water use efficiency at the ecosystem level is enhanced during soil moisture drought. The moderate soil moisture drought did not enhance IWUE at Hyytiälä, which could be evidence of a higher drought tolerance of boreal Scots pine forest in the south than in the north.

Our findings indicate that IWUE is a more appropriate metric to capture the impact of soil moisture drought impact on plant functioning at daily time scales than EWUE. For the latter, the impacts of drought on plant functioning can be misinterpreted due to the strong dependence of ET on atmospheric VPD.

4.2 Differences between observations and site simulations

The soil moisture drought impacts on plant functioning at Hyytiälä were only demonstrated when the relationship between GPP and transpiration rather than ET was investigated from JSBACH simulation. The simulated daily ET data is disturbed because of frequent negative night-time values especially at the beginning of the summer. A likely reason for those is that the offline coupling for the JSBACH simulation tends to overestimate night-time condensation, which consequently leads to an underestimation of daily mean latent heat flux (Dalmonech et al., 2015).

The model successfully showed the strong limitations on GPP and ET/T under severe soil moisture drought ($0 \leq \mathrm{SMI} < 0.2$) at Hyytiälä. In addition, the relationships between ET/T and VPD from both observation and simulation at the two sites showed that ET/T decreased slightly when soil moisture under moderate drought. However, the discrepancies in response between observed and simulated GPP and ET to changing environmental variables were obvious (Fig. 2 and 3). That is because the functions for calculating stomatal conductance in JSBACH do not include air humidity as a variable, therefore the stomatal conductance in JSBACH is insensitive to atmospheric VPD (Knauer et al., 2015). In Knauer et al. (2015), Ball-Berry model (Ball et al., 1987) has been found to be best in a few stomatal conductance models in its response to atmospheric drought under non-limited soil moisture conditions. In reality, low soil moisture and high temperature during drought are closely coupled with high atmospheric VPD. Our results indicate that the combined effects of soil moisture and atmospheric drought on stomatal conductance have to be taken into account. Moreover, model performance could be improved through the inclusion of non-stomatal limitations on plant photosynthesis, which have been considered to be important for the simulation of short-term plant responses to drought (Egea et al., 2011; Manzoni et al., 2011; Zhou et al., 2013).

Soil moisture content was not a strong limiting factor on GPP and ET/T in either observed or simulated dataset at Sodankylä. The SMI at Sodankylä was calculated with the layer-2 soil moisture and values under 0.2 only occurred on sporadic days, thus moisture values deep in the soil profile were not low and did not persist long enough to cause strong deviations in GPP and ET (T).

Moreover, when utilizing EC data, it should be kept in mind that the EC method has its own uncertainties. Due to the stochastic nature of the turbulent flow, there is always a random error component in the observations. In addition, there may be systematic errors source from imperfect spectral corrections and gap-filling procedures or calibration problems (Richardson et al. 2012, Wilson et al. 2002).

5. Conclusions

In general, IWUE was found to be a more sensitive metric than EWUE in capturing the impact of soil moisture drought on plant functioning at daily time scales. Under a very severe soil moisture drought at Hyytiälä, the decrease in GPP became stronger than the decrease in ET as the drought developed, which resulted in low EWUE values. In contrast to EWUE, IWUE increased as a whole when there was a severe soil moisture drought at Hyytiälä and a moderate soil moisture drought at Sodankylä in the observed dataset. As IWUE is inversely related to the surface conductance at the ecosystem level, it is sensitive to stomatal closure during drought.

Further developments are needed in ecosystem modelling in order to adequately capture the impacts of drought in boreal forests. The simulated response in plant functioning to severe soil moisture drought predicted by JSBACH was weaker than those in the observed dataset, even though the strong limitation effects on GPP and ET through stomatal closure were shown at the severe soil moisture drought condition ($0 \leq \text{SMI} < 0.2$) as in the observed data. Also, in the relationships between ET/T and VPD at the two sites, both observed and simulated ET/T showed a small decrease under moderate soil moisture drought, compared to days with higher soil moisture conditions. The main reason for the differences in the model results is that the stomatal conductance model in JSBACH is insensitive to air humidity. This suggests that combined formulations of atmospheric and soil moisture drought are needed in the model to adequately simulate effects of drought on plant functioning. In addition, inclusion of non-stomatal limitations on photosynthesis during drought, e.g. reduced mesophyll conductance or carboxylation capacity, could also lead to an improvement of the model results (Keenan et al., 2010).

This study gives a view of the response of boreal forests to summer drought, and further suggests that choosing the appropriate indicator, and improving our knowledge of ecosystem processes in land surface models are of great importance when estimating biosphere-atmosphere feedbacks of terrestrial ecosystems under climate change.

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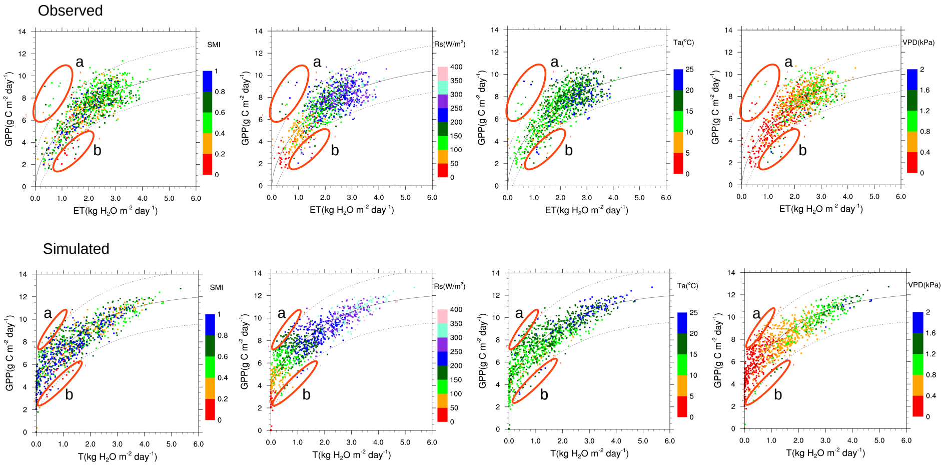

Figure 1: Relationship between daily gross primary production (GPP) and evapotranspiration/transpiration (ET/T) at Hyytiälä. Data are categorized according to soil moisture index (SMI), solar radiation (Rs), air temperature (Ta) and vapour pressure deficit (VPD). The solid lines are fitted regression lines, and the dashed lines show the 97.5th (upper dashed line) and 2.5th (lower dashed line) percentiles of the data. The two deviated groups (a and b) are marked with red circles.

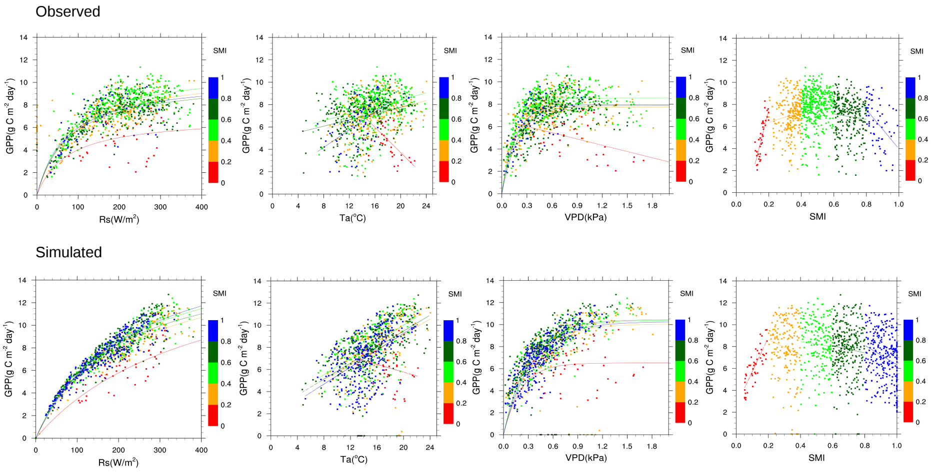

Figure 2: Response of daily gross primary production (GPP) to incoming solar radiation (Rs), air temperature (Ta), vapour pressure deficit (VPD) and soil moisture index (SMI) at Hyytiälä, categorized with soil moisture conditions. The lines are fitted regression lines for the categorized SMI groups.

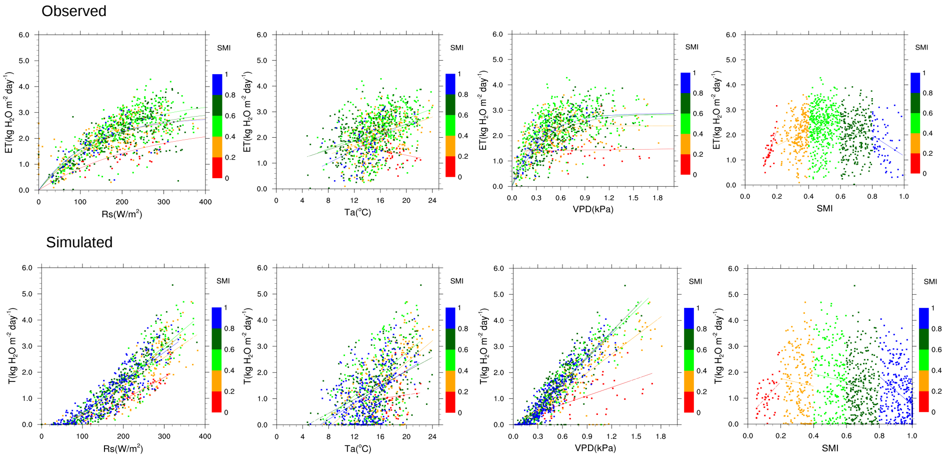

Figure 3: Response of daily evapotranspiration/transpiration (ET/T) to incoming solar radiation (Rs), air temperature (Ta), vapour pressure deficit (VPD) and soil moisture index (SMI) at Hyytiälä, categorized with soil moisture conditions. The lines are fitted regression lines for the categorized SMI groups.

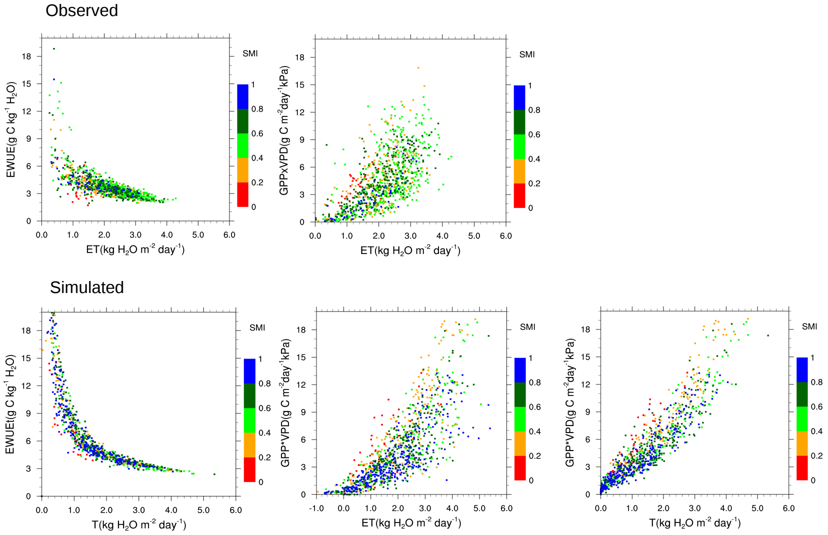

Figure 4: Relationship between daily ecosystem water use efficiency (EWUE) and evapotranspiration (ET), and between daily gross primary production multiplied by vapour pressure deficit (GPP × VPD) and ET based on the observed dataset at Hyytiälä; relationship between transpiration-based ecosystem water use efficiency (EWUEt) and transpiration (T), and between GPP × VPD and evapotranspiration/transpiration (ET/T) using the simulated dataset at Hyytiälä.

Table 1: Key characteristics relevant to this study at the two measurement sites; and the parameter settings in the JSBACH site level simulations for the two sites.

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Observation									
Site	Location	Vegetation type	LAI (m^2/m^2) (all-sided, annual)	Canopy height (m)	Measurement height (m)	Mean annual temperature (◦C) and precipitation (mm) (30 year average)	Soil type	Analysed measurement depth of soil moisture (cm)	References
Hyytiälä	61°51'N, 24°17'E	Scots pine	8	13-16	23	2.9; 709	Mineral (Haplicpodzol)	−5 to −23; −23 to −60	Markkanen et al.(2001); Vesala et al. (2005)
Sodankylä	67°22'N, 26°38'E	Scots pine	3.6	13-18	23.5	-1.0; 500	Mineral (Sandy Podzol)	−10, −20, −30 (averaged)	Aurela (2005)

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