

The role of climatic variability in controlling carbon and water budgets in a boreal Scots pine forest during ten growing seasons

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This study reports eddy-covariance measurements of carbon and water fluxes in a boreal Scots pine (*Pinus sylvestris*) forest during the 1999–2008 growing seasons. We found that gross primary productivity (GPP) was limited by low rainfall and low summer temperatures, whereas evapotranspiration (ETP) was limited by temperature and precipitation. GPP was less sensitive to increased ETP in the years with little rainfall than in the years with abundant rainfall. During low-rainfall years with long-lasting drought periods and few rainy days (2000 and 2003), GPP was reduced, whereas during the low-rainfall year (2006) with evenly distributed seasonal precipitation it remained at the same level as that during the abundant-rainfall years. Ecosystem water-use efficiency (WUE) was found to be sensitive to increased ETP and vapour-pressure deficits. However, there was no difference between abundant- and low-rainfall years in the responses of WUE to climatic and edaphic variables, most likely due to the coupled feedback of the carbon and water cycles to drought. This study suggested that combined frequency (also seasonality) of precipitation and total amount of rainfall are needed to better evaluate the feedback of carbon and water budgets in boreal forests to drought, especially under expected climate change.

Introduction

Numerous studies based on the eddy-covariance (EC) technique have addressed the seasonal and annual variations in the carbon balance of various forest ecosystems in response to climatic variability (Law *et al.* 2002, Kolari *et al.* 2009). In the boreal zone, forest growth is greatly limited by low summer temperatures, and the dynamics of carbon and water fluxes are clearly affected by

climatic variability during the short growing seasons (Barr *et al.* 2007, Granier *et al.* 2007).

Carbon and water fluxes in forest ecosystems are intrinsically linked. Gross primary production (GPP) is determined by the balance between atmospheric transpirational demand and soil water supply, which are controlled by meteorological conditions (Barr *et al.* 2007, Gerten *et al.* 2008). In this context, forest evapotranspiration (ETP) plays an important role in controlling eco-

system water and energy balances (Ilvesniemi *et al.* 2009). Furthermore, water-use efficiency (WUE) dictates the carbon and water budgets of an ecosystem based on the relationship between the amount of carbon fixed by photosynthesis and the amount of water lost through evaporation and transpiration. The feedback between WUE and environmental conditions such as drought varies. For example, Granier *et al.* (2008) reported a significant effect of drought intensity on WUE, whereas Reichstein *et al.* (2007) found only a small year-to-year change in WUE at European forest sites across non-drought and drought years. Therefore, multiple information sources on the carbon, water and energy exchanges between ecosystems and the atmosphere can provide valuable insight into the variability and interrelationships of these fluxes. Such insight is needed to understand how key eco-physiological processes will respond or adapt to climatic variability and climate change (Wu *et al.* 2011, Ge *et al.* 2013).

We previously introduced a long-term (1999–2008) EC measurement of the CO₂ component of flux and water and heat exchange (Kellomäki and Wang 1999, 2000a, Wang *et al.* 2004a, Ge *et al.* 2011b, 2011c) in a homogeneous Scots pine (*Pinus sylvestris*) stand representative of boreal forests in eastern Finland. In the present study, we used measurements from the same site to investigate how the coupled carbon and water budgets are affected by climatic variability under a wide range of weather and soil conditions. We focused on identifying how the variability in climatic factors (e.g., air temperature, vapour-pressure deficit, precipitation amount and rainfall distribution and intensity) control carbon and water budgets on daily, monthly and annual scales during the April–September growing season. We also briefly discuss the potential effects of future climate change on boreal forests.

Material and methods

Site description

The experimental site for the eddy-covariance measurements was established in 1999 in a 50-year-old, even-aged Scots pine stand. The

stand is located in Huhus (62°52′N, 30°49′E, 145 m a.s.l.), which is 30 km north of the Mekrijärvi Research Station (University of Eastern Finland) in eastern Finland. The stand extends uniformly over a zone with a radius of at least 1–2 km surrounding the EC measurement tower. The terrain has a slope of 2%–5%. A stand inventory was performed based on 49 forest plots (10 × 10 m) around the measurement tower in 1998–1999 (Kellomäki and Wang 1999, 2000a). This inventory revealed that the mean stand density was 1175 trees ha⁻¹. The mean height of the dominant trees (the upper 10%) was 17.6 m (for more information on the stand, see Ge *et al.* 2011b). The understory mainly comprised mosses (*Dicranum* spp., *Pleurozium schreberi*) and dwarf shrubs (*Vaccinium vitis-idea*, *Calluna vulgaris*). The forest floor was further covered by small patches of litter and lichens. The soil was poor, belonging to the *Vaccinium* type, according to the classification system of Cajander (1949). During the study period, the leaf area index (LAI) increased from 2.4 m² m⁻² ground area in 1999 to 3.3 m² m⁻² ground area in 2008 as a result of tree growth (Ge *et al.* 2011b).

The climate at the site is characterised by cold winters with persistent snow cover and a brief growing season (April–September, approximately 140–175 days). The mean annual precipitation in the area (1961–2000) is approximately 700 mm, of which approximately 38% is received as snow. The monthly mean temperatures of the coldest (January) and hottest (July) months are –10.4 °C and 15.8 °C, respectively.

Measurement of fluxes and meteorological variables

Continuous carbon dioxide and water vapour fluxes were measured using an eddy-tower system mounted 32 m above the ground (approximately 20 m above the canopy). The instrumentation, flux calculations and corrections applied have been reported in detail by Kellomäki and Wang (1999, 2000a), Wang *et al.* (2004a, 2004b) and Zha *et al.* (2007). In brief, wind velocity and virtual temperature were measured using a three-axis sonic anemometer (model Solent A1012R, Gill Instruments, Lymington, UK). The CO₂ and

water vapour fluctuations at 32 m were continuously monitored using a closed-path dual CO₂/H₂O analyser (IRGA, model LI-6262, LiCor, Lincoln, NE, USA). Air was brought to the analyser from a point near the sonic anemometer through a heated sampling tube (35 m in length, 3 mm in inner diameter, Dekabon Ltd., Glasgow, UK) at a flow rate of 6 l min⁻¹. The resulting gauge pressure in the sample cell, maintained with a pressure transducer, was 20.0 kPa. The data were sampled at 10 Hz, and half-hour fluxes were calculated using specially written software, in which the fluxes (e.g., vertical velocity, CO₂ and water vapour) were computed as the differences between the instantaneous and respective mean scalar quantities. The mean scalar values were calculated in real time using a digital recursive filter time constant of 200 s and a time lag of 5 s to account for the delay in drawing air down the tower. Baselines were calibrated weekly using dry N₂ gas. The CO₂ channel was calibrated using a standard CO₂ gas bottle, and the water vapour channel was calibrated using a dew-point generator (model Li-610, LiCor, Lincoln, NE, USA).

The meteorological data were recorded by a Vaisala weather station (MILOS 500, Vaisala Oy, Helsinki, Finland) placed approximately 20 m from the tower. Air temperature (HMP45D and DTR13) profiles were measured individually at heights of 32, 20, 18, 12, 9 and 4 m. Humidity (HMP45D) and wind data (WAA15A and WAV15A) were obtained from sensors mounted at heights of 20, 18, 12, 9 and 4 m. Atmospheric pressure (AP1) and radiation sensors (CM21, CG1, CM6B/1, LI-190SA/1 and QT1) were mounted at heights of 20, 18 and 4 m. Precipitation above and below the forest canopy was measured using eight rain gauges (RG13). The soil heat flux and temperature were measured at four depths (5, 10, 20 and 60 cm) in four locations near the measuring tower using soil heat plates and temperature probes (HFPO1, Hukseflux, The Netherlands). The volumetric water content of the soil was monitored at depths of 10 cm using soil-moisture probes (ThetaProbe ML1, Delta-T Devices Ltd., UK).

The net ecosystem CO₂ exchange (NEE) and the total water vapour flux arising from evapotranspiration (ETP) were measured from 1999 to 2008. NEE was defined as the sum of the eddy

flux recorded by the eddy-covariance instrument and the flux associated with CO₂ storage in the underlying air layer, which was calculated as the integral with respect to height of the rate of change of the CO₂ concentration profile over time (Aubinet *et al.* 2000). ETP was defined as the sum of the evaporation from the ground and canopy surfaces and the transpiration from trees, expressed in terms of the weight (kg H₂O m⁻²) of liquid water. The Bowen ratio (the ratio between sensible heat and latent heat) based on the EC measurements was within the range of 0.5–3.0 for more than 80% of each growing season. The half-hour ETP fluxes revealed an energy balance closure of approximately 77%–87% (Kellomäki and Wang 1999, Wang *et al.* 2004a).

The EC flux data were screened to remove possible errors arising from instrument malfunctions or sampling errors. It is widely accepted that under stable conditions, nighttime CO₂ flux is underestimated by EC measurements (Reichstein *et al.* 2005). Therefore, the CO₂ flux data collected during periods of low friction velocity ($u^* < 0.25$ m s⁻¹) were discarded. The u^* threshold value for the rejection of nighttime CO₂ flux data was determined using the bootstrapping technique described by Reichstein *et al.* (2005). For the water vapour fluxes, the data screening procedure consisted of the following steps: (1) Data with turbulence intensities greater than 0.5 were omitted to satisfy the requirements for the applicability of Taylor's frozen turbulence hypothesis. (2) Data were rejected when the absolute differences between the total available energy and the ETP were greater than 50 W m⁻² or if the averaging time was less than 30 min. (3) Data were screened out when the absolute difference in the water vapour was greater than 30% or when the water vapour concentration was constant (e.g., unchanging over time). (4) Data collected during rainy periods were also set aside. After data screening, approximately 70% of the CO₂ flux data and 80% of the H₂O flux data from the 1999–2008 growing seasons remained for further analysis.

To integrate the daily CO₂ fluxes, short (1- to 2-hour) gaps were filled by linear interpolation. Larger gaps were filled by applying a non-rectangular hyperbolic function between NEE and the photosynthetically active radi-

tion absorbed by the canopy (APAR) during the daytime. Following Zha *et al.* (2004) and Wang *et al.* (2004b), the underestimation was compensated for by replacing the measured NEE during stable nighttime periods ($u^* < 0.25 \text{ m s}^{-1}$) with a parameterisation obtained from regressions of the CO_2 flux vs. the air temperature at a height of 12 m, measured during turbulent periods ($u^* > 0.25 \text{ m s}^{-1}$). Gaps in the water flux data were filled based on the functional relationship of ETP to the incident solar radiation and canopy vapour-pressure deficit, determined by calculating the monthly model parameter values from valid flux data obtained for the surrounding days (Kellomäki and Wang 1999, Wang *et al.* 2004a).

Estimation of GPP and WUE

The gross primary production (GPP) was calculated as the sum of the net ecosystem exchange (NEE) and the total ecosystem respiration (TER):

$$\text{GPP} = \text{NEE} + \text{TER} \quad (1)$$

$$\text{TER} = R_l + R_{(b+w)} + R_s \quad (2)$$

where NEE is the eddy-covariance measurements and TER is the sum of the respiration in leaves (R_l), branches, sapwood ($R_{(b+w)}$) and soil (R_s).

Ecosystem WUE represents the ability of the ecosystem to assimilate carbon while limiting water loss. WUE was calculated as the ratio of GPP to ETP:

$$\text{WUE} = \text{GPP}/\text{ETP} \quad (3)$$

The values of the TER flux components (respiration flux from leaves, branches, sapwood and the forest floor) were estimated using a process-based ecosystem model [FinnFor, described in detail in Kellomäki and Wang (2000) and Ge *et al.* (2011a, 2011b, 2011c)]. Based on the component carbon fluxes of TER in the Scots Pine ecosystem determined from chamber and EC measurements under climatic variations (Zha *et al.* 2002, 2003, 2004, 2007), the meteorological data were used to model the flux of the above-ground components, and the variables of soil

temperature and moisture were used to model the flux from the forest floor. With the model parameterisation, the simulated mean daily respiration for branches, stems and the soil surface matched the corresponding measured respiration well ($r^2 = 0.87$) for the period 1999–2004 (Zha *et al.* 2007). The validation analysis confirmed that the FinnFor model is able to capture the variation in TER between drought and non-drought conditions and between different years.

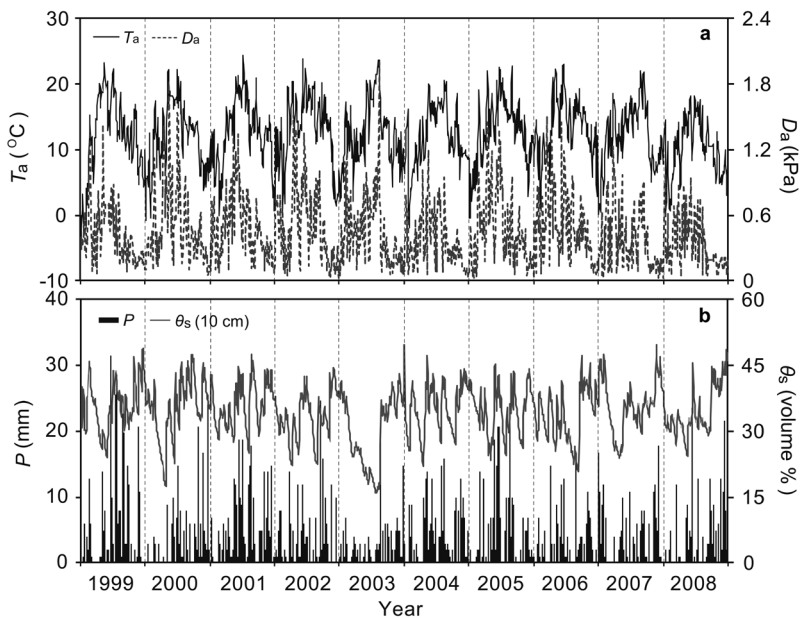
Moreover, previous studies have demonstrated that the FinnFor model is capable of simulating the total photosynthetic production (or GPP) of a Scots pine forest under different climatic conditions (Wang *et al.* 2004b, Ge *et al.* 2011a) based on leaf-to-canopy photosynthetic processes. In the present study, the model was tested in advance for the estimation of daily GPP values for 1999–2008 using the measured climatic variables. The modelling results showed that the day-to-day variation in GPP calculated as the sum of NEE and TER agreed closely ($r^2 = 0.94$) with the day-to-day variation in total photosynthetic production.

Statistical analyses

Before the analysis, the years were divided into two parts according to the amount of rainfall. Due to lower precipitation ($< 250 \text{ mm}$) in 2000, 2003 and 2006 (Table 1), these years were regarded as “low-rainfall” years in the subsequent data analyses, and the other years were regarded as “abundant-rainfall” years. With daily sums of GPP, ETP and WUE over the growing seasons of 1999–2008, we worked out the weekly averages of fluxes during the six months (April–September) for each low-rainfall year of 2000, 2003 and 2006 (*see* Appendix) and the abundant-rainfall years (average over 1999, 2001, 2002, 2004, 2005, 2007 and 2008).

First of all, the non-parametric Kruskal-Wallis one-way analysis of variance was used to test the differences in GPP, ETP and WUE, in four groups: (1) abundant-rainfall years, (2) year 2000, (3) year 2003 and (4) year 2006. If the test result was significant ($p < 0.05$), then we used the Wilcoxon rank-sum test to determine which of the sample pairs are significantly dif-

Fig. 1. Average daily meteorological and soil conditions during the 1999–2008 growing seasons. (a) Air temperature (T_a) and vapour-pressure deficit (D_a). (b) Precipitation (P) and soil moisture (θ_s , 10-cm depth).



ferent (low-rainfall year vs. abundant-rainfall year) for each of the variables (GPP, ETP and WUE). Relationships between the fluxes and environmental variables were evaluated by the best curve-fitting model with the highest r^2 value (Motulsky and Christopoulos 2002). All statistical analyses were made with SPSS (SPSS 16.0 for Windows, SPSS Ltd., USA).

Results

Climatic conditions and carbon and water budgets

The seasonal variability of the climatic and edaphic variables during the 1999–2008 growing seasons (April–September) is illustrated in Fig. 1.

Table 1. Daily mean temperature (T_a) above the canopy, daily mean vapour-pressure deficit (D_a), daily mean soil temperature (T_s , 10-cm depth), daily mean solar radiation (R_o), daily mean soil water content (θ_s), total photosynthetically active radiation absorbed by the canopy (APAR), total precipitation amount (P) and days with precipitation (P_{day}) during the 1999–2008 growing seasons at the Huhus site.

Year	T_a (°C)	D_a (kPa)	T_s (°C)	R_o (W m ⁻²)	θ_s (%)	APAR (mol m ⁻²)	P (mm)	P_{day} (days)
1999	11.9	0.46	7.9	246	36.32	4364	432	57
2000 ^a	12.4	0.48	8.7	235	30.80	4158	249	44
2001	12.1	0.46	8.5	230	36.06	3978	436	77
2002	11.9	0.48	8.8	239	33.02	4342	329	61
2003 ^a	12.5	0.49	8.0	258	28.78	4498	205	48
2004	9.7	0.34	7.8	228	35.16	3900	365	63
2005	11.2	0.37	8.3	234	34.70	4718	300	57
2006 ^a	11.5	0.41	8.1	240	31.20	4689	243	63
2007	11.5	0.36	8.2	239	33.65	4165	301	68
2008	11.6	0.43	7.6	238	32.98	4262	321	59
CV (%)	7.0	13.5	4.7	3.6	3.8	6.4	23.9	15.5

^a defined as “low-rainfall” years based on P .

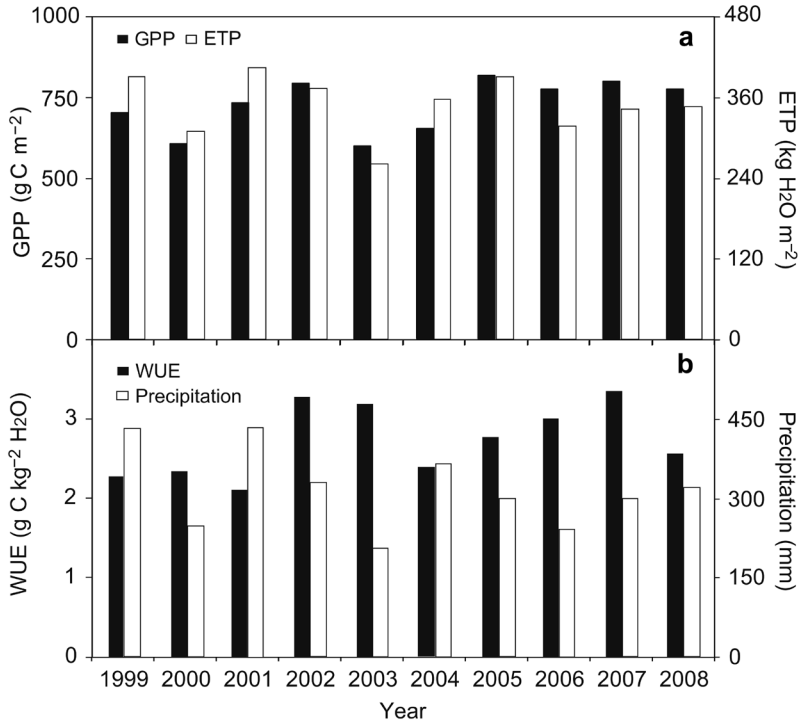


Fig. 2. (a) Total gross primary production (GPP) and evapotranspiration (ETP), and (b) mean daily water-use efficiency (WUE) and precipitation in the studied Scots pine forest during the growing seasons (April–September) of 1999–2008.

The discrepancies in the daily means of T_a , D_a , APAR, P and P_{day} were clear ($CV > 5\%$; Table 1). During the study period, 2004 was colder than average by 2 °C and less incident radiation was recorded during that year. The hottest years with the largest vapour-pressure deficits were 2000 and 2003. The mean daily soil moisture (at a depth of 10 cm) during the growing seasons was the lowest (less than 32% volumetric water content) in the low-rainfall years of 2000, 2003 and 2006. The daily total incident solar radiation was similar in all of the growing seasons ($R_0 = 215\text{--}265 \text{ W m}^{-2}$) and was strongly correlated with APAR (Pearson's correlation: $r^2 = 0.68$).

During the ten growing seasons, the GPP ranged from 592 to 794 g C m⁻², with the lowest values occurring in the low-rainfall years of 2000 and 2003 and in the coldest year, 2004 (Fig. 2a). The total values of ETP ranged from 264 to 415 kg H₂O m⁻² during the growing seasons, with the lowest values occurring in the three low-rainfall years. Daily GPP increased with increasing ETP, and a power-function relationship was found for both abundant- and low-rainfall years (Fig. 3a). When the ETP was less

than approximately 3 kg m⁻² day⁻¹, the GPP increased relatively rapidly, thereafter, the rate of increase was reduced. During the growing seasons of low-rainfall years, the fluxes of GPP and ETP were significantly (Kruskal-Wallis test: $\chi^2 = 8.09$, $df = 3$, $p = 0.045$ and $\chi^2 = 7.80$, $df = 3$, $p = 0.050$, respectively) lower than in the abundant-rainfall years (Table 2 and Fig. 3a), and the decreases in the water fluxes (20.3% on average) were higher than those of the carbon fluxes (12.2% on average).

During the period 1999–2008, the mean daily WUE values of the growing seasons ranged from 2.1 to 3.4 g C kg⁻¹ H₂O (Fig. 2b), with the highest values occurring in 2002 and 2007 (together with high GPP values). The next-largest WUE values (greater than the average for 1999–2008) were measured in the low-rainfall year of 2003, and the lowest WUE values were measured in 2001 and 2004 (less than the average for 1999–2008). The daily ecosystem WUE decreased with increasing ETP in both abundant- and low-rainfall years and was consistently low when ETP was higher than 3 kg H₂O m⁻² day⁻¹ (Fig. 3b).

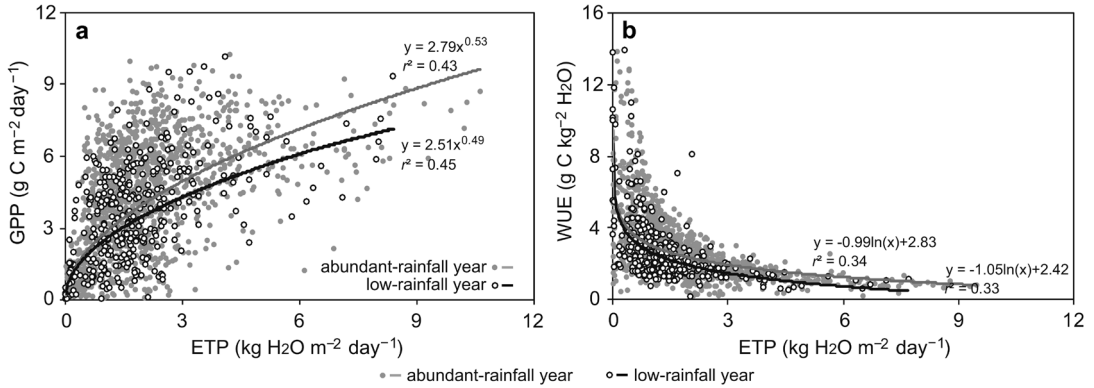


Fig. 3. (a) Daily gross primary production (GPP), and (b) water-use efficiency (WUE) as functions of evapotranspiration (ETP) during the growing seasons of abundant-rainfall and low-rainfall years during the 1999–2008 study period. The lines are the fitted curves and only significant ($p < 0.05$) regression equations are shown.

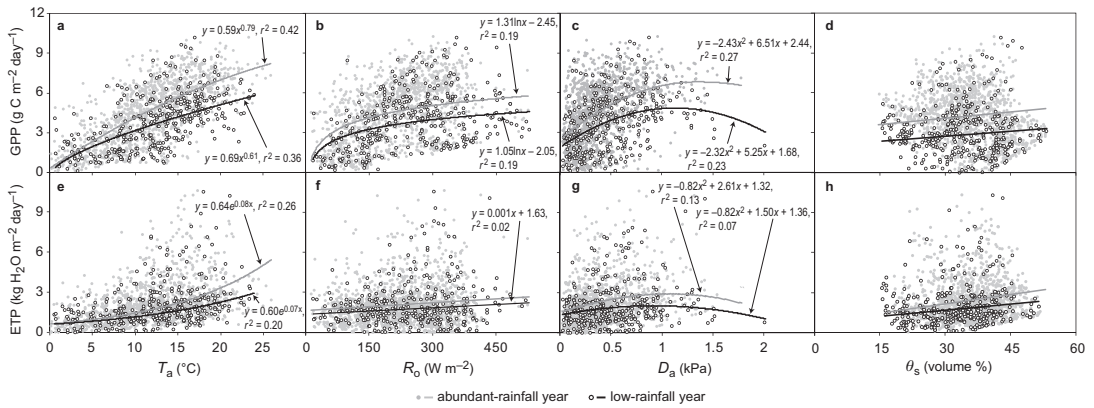


Fig. 4. (a–d) Relationships of daily gross primary production (GPP), and (e–h) evapotranspiration (ETP) to (a, e) temperature (T_a), (b, f) solar radiation (R_o), (c, g) vapour-pressure deficit (D_a), and (d, h) soil water content (θ_s) during the 1999–2008 growing seasons. The relationships are shown separately for abundant-rainfall and low-rainfall years. The lines are the fitted curves and only significant ($p < 0.05$) regression equations are shown.

Responses of GPP, ETP and WUE to environmental factors

During the studied period daily GPP or ETP correlated only weakly with any single environmental variable apart from soil water content (θ_s). T_a affected positively daily GPP (Fig. 4a), but the temperature sensitivity of GPP decreased in the low-rainfall years at higher values of T_a . Radiation and vapor pressure deficit explained only about one fifth to quarter of the daily variation in GPP, and temperature about the same share of the variation in ETP (Fig. 4b, c and e). As expected, the weak relationship was saturating for T_a , R_o and GPP and for D_a and GPP and ETP; and exponential for T_a and ETP.

Daily ecosystem WUE decreased with increasing D_a during both abundant- and low-rainfall years and was consistently low when D_a was greater than 0.5 kPa (Fig. 5a). However, there was no relationship between WUE and θ_s (Fig. 5b).

Table 2. Kruskal-Wallis test results for each of the variables (GPP, ETP and WUE) in four groups: (1) abundant-rainfall years, (2) year 2000, (3) year 2003 and (4) year 2006. Samples (weekly averages) are given in Appendix.

	GPP	ETP	WUE
χ^2	8.09	7.80	8.22
df	3	3	3
p	0.045	0.050	0.042

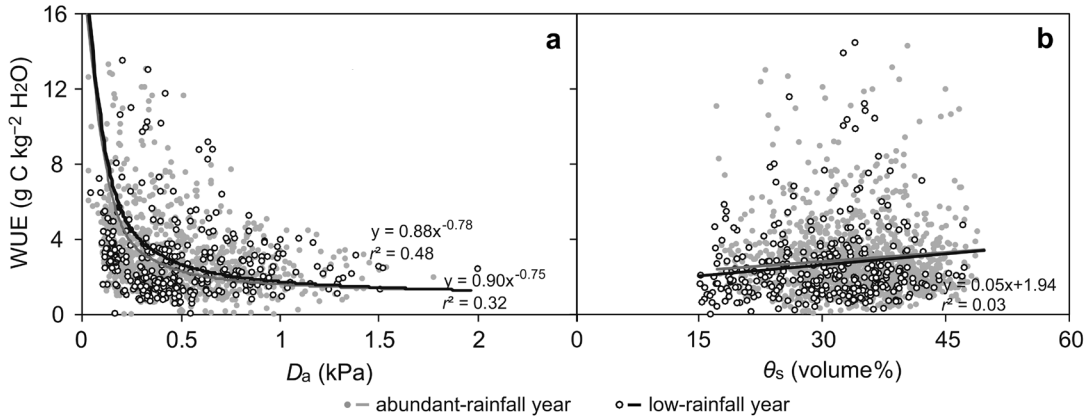


Fig. 5. Relationships between daily water-use efficiency (WUE) and (a) vapour-pressure deficit (D_a) and (b) soil moisture (θ_s) during the 1999–2008 growing seasons. The lines are fitted curves and only significant ($p < 0.05$) regression equations are shown.

Effects of seasonal precipitation variability on carbon and water budgets

The seasonal distribution of precipitation varied by year (Fig. 6): the number of days with precipitation was lowest in 2000 and 2003, when long-lasting droughts occurred, whereas 63 rainy days (exceeding the ten-year average) were measured in 2006 (Table 1).

During the growing seasons of 1999–2008, GPP was significantly lower in 2000 (Wilcoxon rank-sum test: $Z = -3.92$, $p < 0.001$; Table 3) and 2003 (Wilcoxon rank-sum test: $Z = -4.28$, $p < 0.001$; Table 3) than during the abundant-rainfall

years due to lower peak values of GPP from June to August in low-rainfall years (Fig. 6a). However, GPP was not significantly (Wilcoxon rank-sum test: $Z = -1.38$, $p = 0.17$) lower during the growing season of 2006, and the value was similar to that in the abundant-rainfall years. High WUE values ($> 3 \text{ g C kg}^{-1} \text{ H}_2\text{O}$) were frequently measured in the abundant-rainfall years of 2002 and 2007 (Fig. 6b). There were no statistical significant differences in WUE between the abundant- and low-rainfall years of 2003 and 2006 (Table 3). However, WUE was significantly (Wilcoxon rank-sum test: $Z = -2.40$, $p = 0.016$) lower in 2000 than in the abundant-rainfall years.

Table 3. Wilcoxon rank-sum test for each of the variables (GPP, ETP and WUE) between sample pairs of low-rainfall and abundant-rainfall years. Samples (weekly averages) are given in Appendix.

Variables	Z	p
2000 vs. abundant-rainfall years		
GPP	-3.92	<0.001
ETP	-2.25	0.025
WUE	-2.40	0.016
2003 vs. abundant-rainfall years		
GPP	-4.28	<0.001
ETP	-3.44	0.001
WUE	-0.368	0.71 ^{ns}
2006 vs. abundant-rainfall years		
GPP	-1.38	0.17 ^{ns}
ETP	-2.07	0.038
WUE	-0.140	0.89 ^{ns}

Discussion

GPP and ETP under climatic variability

The growth of boreal forests in northern Europe is mainly restricted by the relatively low summer temperatures and the short growing season (Jarvis and Linder 2000). The increase in temperatures over the years has lengthened the growing season and increased total photosynthesis (Ge et al. 2011a). However, the response of carbon uptake to temperature is primarily dependent on the availability of growth resources such as water. Our result showed that in low-rainfall years, the sensitivity of GPP to temperature

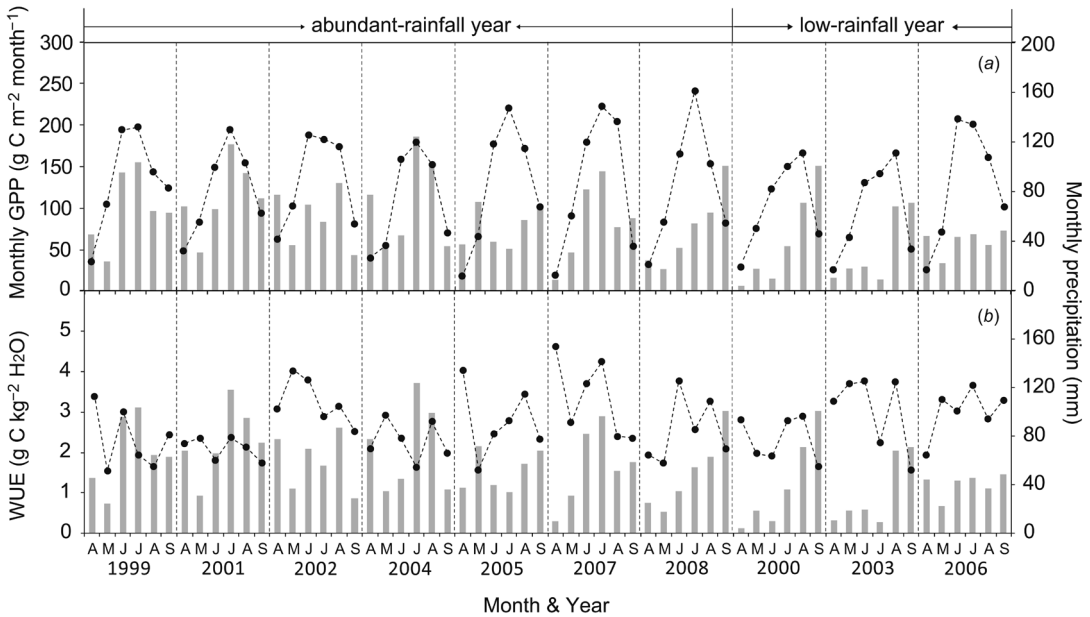


Fig. 6. (a) Variations in monthly gross primary production (GPP), and (b) water-use efficiency (WUE) during the 1999–2008 growing seasons. The bars show monthly precipitation. Note that the abundant-rainfall years (1999, 2001, 2002, 2004, 2005, 2007 and 2008) are shown first.

decreases at higher temperatures more than in abundant-rainfall years (Fig. 4a). Based on the previous EC measurements and model simulations (Ge *et al.* 2011b, 2011c), high temperatures increase the vapour-pressure deficit and soil water stress, resulting in the stomatal enclosure of Scots pine and a consequent lower carbon uptake. Another probable explanation is that the photosynthetic apparatus is impaired through photoinhibition or direct mesophyll-level effects on conductance or carboxylation under water stress (Bota *et al.* 2004, Kitao *et al.* 2007, Ge *et al.* 2012). The range of measured GPP values fit the results in laboratory conditions (Kellomäki and Wang 1997) for Scots pine but the saturating response of GPP to photosynthetically active radiation was weaker than expected. The majority of leaves in the canopy are subject to low light levels and responses at low light levels are more important than the light-saturated capacity to assimilate CO₂ (Duursma *et al.* 2009). As presented in our previous report (Wang *et al.* 2004b), the shaded foliage fraction of boreal Scots pine contributes more to gross ecosystem carbon uptake than the sunlit fraction during the growing season.

The amounts of ETP were much lower in low-rainfall years than in abundant-rainfall years, indicating the interaction between climatic variations and water consumption in the forest ecosystem. Tree transpiration was the dominant component of ETP flux (approximately 60%–73%, see Ge *et al.* 2011c), which is mainly controlled by the environmental factors of vapour-pressure deficit and soil moisture (Kellomäki and Wang 2000, Wang *et al.* 2004a). High vapour-pressure deficits in low-rainfall years resulted from higher temperature and lower relative humidity, reduced leaf-to-canopy stomatal conductance and the consequent transpiration flux in the Scots pine stand (Ge *et al.* 2011c). As Kellomäki and Wang (2000) reported, canopy stomatal behaviour and transpiration is also greatly depressed when the soil moisture content is less than 22%. On the other hand, low amount of precipitation generally led to less evaporation from ground surface and rainfall interception by the canopy in the drought years (Ge *et al.* 2011c).

The daily GPP was positively correlated with ETP in both abundant- and low-rainfall years, which indicates that the carbon and water fluxes in the forest ecosystem are intrinsically linked

(Law *et al.* 2002). During the studied period, responses of daily GPP and ETP to changes in environmental variables were systematically weaker in the low-rainfall years than in the abundant-rainfall years, but due to the very low explanation power of the regressions no conclusion can be drawn from these differences. However, that type of pattern could be expected due to the down regulation of tree physiology during drought as noted above. Against expectations, no correlation between GPP and ETP and soil water content (θ_s) was found in this study. As reported by Barr *et al.* (2007) and Kljun *et al.* (2007), water availability at a depth of rooting zone actually controls GPP and ETP. At the Huhus site, soil is a haplic podzol dominated by fine sand with low water-holding capacity. The rooting zone of mature Scots pine at a depth of about 30 cm, while the soil measurements were conducted at a depth of 10 cm that could distort the results.

With respect to the seasonality of precipitation during the low-rainfall years, long-lasting droughts occurred from April to July in 2000 (with a mean soil moisture of 28.4%) and 2003 (with a mean soil moisture of 25.2%) because of reduced rainfall and few precipitation events. Our findings indicate that in the low-rainfall years 2000 and 2003, GPP was significantly lower than in the abundant-rainfall years. During the former, particularly the early-summer rainfall levels were low (Fig. 6), and this period is essential for the carbon-sequestration capacity of the vegetation (Kolari *et al.* 2009). In contrast, the amount of carbon uptake in 2006 was similar to that measured in the abundant-rainfall years. In 2006 (with a mean soil moisture of 34.5% during the growing season) the seasonal distribution of precipitation was relatively even and more rainy days occurred, thus preventing early drought and extended periods of stress.

WUE under climatic variability

The variations in WUE reflected the difference in the coupling between GPP and ETP. In this study, 85% of the daily ecosystem WUE ranged from 1.0 to 6.0 g C kg⁻¹ H₂O. These values are consistent with the results obtained in other

boreal forests (Coursolle *et al.* 2006, Kljun *et al.* 2007, Reichstein *et al.* 2007). A similar annual mean value of daily WUE during the growing season was measured in a boreal jack pine (*Pinus banksiana*) stand with a density of 1190 trees ha⁻¹ (Arain *et al.* 2002, Kljun *et al.* 2007).

We found that daily ecosystem WUE was sensitive to increases in ETP and was consistently low when ETP was high in both abundant- and low-rainfall years (Fig. 3b). Thus, excessive water consumption did not cause a corresponding increase in the total photosynthetic productivity of the forest. The correlation between WUE and the vapour-pressure deficit is consistent with results reported by Law *et al.* (2002) and Ponton *et al.* (2006). These results indicate that the variation in WUE is primarily driven by changes in ETP because these changes can also control carbon uptake to match leaf water potential (Rascher *et al.* 2004).

There was no effect of soil moisture on WUE. Reichstein *et al.* (2007) reported that for many European EC sites, carbon and water fluxes were correlated and year-to-year changes in WUE were small in non-drought and drought years. No consensus has been reached concerning the response of WUE at either the leaf or canopy level to the soil water content (Law *et al.* 2002, Ponton *et al.* 2006, Reichstein *et al.* 2007, Granier *et al.* 2008). Yang *et al.* (2010) reported that the response of WUE to the soil water content was dependent on the vapour-pressure deficit, i.e., that WUE increases with increasing soil moisture at high vapour-pressure deficits but decreases at low vapour-pressure deficits. The asynchronous response of carbon and water fluxes to climatic variables determines the coupling and decoupling between GPP and ETP for WUE. Higher vapour-pressure deficits during low-rainfall period tend to lower the photosynthetic rate and transpiration with relatively consistent WUE, indicating a coupled interaction between GPP and ETP in boreal forests. This process might also reflect a cooperative adjusting mechanism of the water-use strategies of plants under drought conditions (Bacelar *et al.* 2012).

High monthly WUE was measured frequently in the abundant-rainfall years of 2002 and 2007 and in the low-rainfall year of 2003. In 2002 and 2007, the WUE was enhanced by favour-

able climatic conditions, which resulted in higher GPP. In 2003, lower water consumption resulted in a higher WUE. Drought-induced increases in WUE detected through flux-tower monitoring (Krishnan *et al.* 2006, Ponton *et al.* 2006, Granier *et al.* 2008) and stable-isotope measurements (Ponton *et al.* 2006) have often been reported. In 2006, when precipitation was evenly distributed throughout the growing season, higher GPP also led to higher WUE (Fig. 6). In contrast, the lower WUE in 2000 and 2001 was caused by less and excessive precipitation, which resulted in lower GPP and higher ETP, respectively.

Implications for climate-change impacts

EC measurements of year-to-year variations in carbon and water fluxes, as well as climatic conditions, have been used extensively to calibrate and validate ecosystem models and weather models for predicting the potential impacts of climate change on carbon and water balances in forests (Davi *et al.* 2006, Luo *et al.* 2008).

Our results show that higher daily mean temperatures markedly promote carbon uptake by forest vegetation. A moderate increase in temperature is likely to extend the growing season, thus increasing the potential carbon stocks and growth of boreal coniferous forests (Bergh *et al.* 2003). Higher temperatures should also increase ETP as a result of stimulated water evaporation. Higher rates of water loss reduce water availability in the ecosystem, especially in drought years, leading to limited GPP. As simulated by the FinnFor model under the climate-change scenarios (Ge *et al.* 2013), elevated temperatures (with unchanged precipitation) should increase ETP and reduce water infiltration into the soil profile, resulting in an increased occurrence of drought and reduced GPP in boreal forests in southern Finland. In contrast, a continuous increase in temperature should offset the increase in gross photosynthesis by stimulating ecosystem respiration, and this effect will be exacerbated by water deficits (Hanson *et al.* 2005).

The variations in the monthly distribution of precipitation and in the severity and frequency of drought events during the study period were found to be highly important in determining

the response of GPP. Forest productivity was less limited in 2006, which was a low-rainfall year with evenly distributed seasonal precipitation and more rainy days, than in other low-rainfall years (2000 and 2003). Therefore, the frequency and distribution of precipitation during the growing season may be meaningful variables in describing the nature of climate change relative to the amount of precipitation input. Many modelling studies have predicted that decreased summer rainfall would reduce primary production in forest ecosystems (Davi *et al.* 2006, Gerten *et al.* 2008). Some simulations have indicated that net ecosystem productivity would respond negatively to altered precipitation seasonality (Gerten *et al.* 2008, Luo *et al.* 2008).

In the current study, the difference between the response of WUE to vapour-pressure deficit and soil moisture in abundant-rainfall years and low-rainfall years was not found to be significant (*see* curves in Fig. 5). This finding indicates that to a certain extent, trees are able to regulate their stomatal behaviour and resulting water consumption, mainly through transpiration, to adapt to environmental change or stress.

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Appendix. Weekly means \pm SE of GPP, ETP and WUE for the six months (April–September) of the growing season in abundant-rainfall years (average over 1999, 2001, 2002, 2004, 2005, 2007 and 2008) and each low-rainfall year of 2000, 2003 and 2006.

Month	Week	Abundant-rainfall years						Low-rainfall years											
		GPP	ETP	WUE	GPP	ETP	WUE	GPP	ETP	WUE	GPP	ETP	WUE						
		2000						2003						2006					
April	1	0.8 ± 0.4	0.4 ± 0.3	3.1 ± 1.9	0.4 ± 0.3	0.1 ± 0.1	2.7 ± 1.5	0.8 ± 0.4	0.3 ± 0.3	3.6 ± 1.5	0.6 ± 0.3	0.4 ± 0.4	2.3 ± 2.0						
	2	1.3 ± 0.7	0.6 ± 0.4	3.3 ± 1.8	1.0 ± 0.8	0.5 ± 0.5	2.8 ± 1.9	0.9 ± 0.4	0.3 ± 0.3	4.1 ± 2.2	0.9 ± 0.4	0.6 ± 0.4	1.9 ± 1.4						
	3	1.7 ± 0.5	0.6 ± 0.4	3.6 ± 2.0	1.5 ± 0.7	0.8 ± 0.4	3.1 ± 2.2	0.8 ± 0.3	0.3 ± 0.3	4.7 ± 2.6	1.2 ± 0.2	0.8 ± 0.3	1.6 ± 0.4						
May	4	1.8 ± 0.6	1.4 ± 0.5	1.7 ± 0.7	0.8 ± 0.4	1.3 ± 0.6	0.7 ± 0.3	2.3 ± 1.0	0.6 ± 0.2	3.2 ± 1.1	1.8 ± 0.8	0.3 ± 0.2	6.5 ± 2.3						
	5	2.4 ± 0.6	1.5 ± 0.8	2.7 ± 2.5	2.0 ± 0.4	1.3 ± 0.3	1.6 ± 0.4	1.9 ± 1.0	0.1 ± 0.1	1.4 ± 1.5	2.7 ± 0.5	1.4 ± 0.9	3.1 ± 2.5						
	6	2.6 ± 0.8	1.7 ± 0.6	2.0 ± 0.9	2.8 ± 0.5	1.1 ± 0.2	2.6 ± 0.4	1.4 ± 0.2	1.2 ± 0.3	1.3 ± 0.4	1.7 ± 0.3	1.7 ± 0.7	1.2 ± 0.5						
June	7	3.9 ± 0.7	2.1 ± 0.6	2.5 ± 1.7	3.2 ± 0.6	1.4 ± 0.2	2.3 ± 0.4	2.3 ± 1.4	0.9 ± 0.3	2.6 ± 1.3	3.0 ± 1.5	1.1 ± 0.3	3.5 ± 1.7						
	8	4.6 ± 1.0	2.0 ± 0.6	3.1 ± 1.8	3.6 ± 0.9	1.4 ± 0.4	2.9 ± 0.8	3.1 ± 0.9	1.2 ± 0.4	2.9 ± 1.0	4.3 ± 1.9	1.4 ± 0.4	3.3 ± 1.0						
	9	5.7 ± 1.0	2.3 ± 0.8	2.8 ± 0.7	3.8 ± 1.0	1.8 ± 0.7	2.3 ± 0.3	3.9 ± 1.5	0.9 ± 0.1	4.3 ± 1.3	6.1 ± 0.5	1.8 ± 0.5	3.6 ± 0.6						
July	10	6.3 ± 0.8	2.2 ± 0.6	3.4 ± 1.2	4.2 ± 0.7	2.2 ± 0.8	2.1 ± 0.6	3.8 ± 0.5	1.6 ± 0.7	3.2 ± 1.7	6.7 ± 1.6	3.1 ± 1.1	2.3 ± 0.5						
	11	6.8 ± 1.0	3.2 ± 1.3	2.9 ± 1.0	4.1 ± 0.7	2.7 ± 1.4	1.8 ± 0.6	4.7 ± 1.4	1.5 ± 0.5	3.7 ± 1.6	8.8 ± 1.2	3.3 ± 1.2	3.0 ± 0.7						
	12	6.7 ± 1.0	3.0 ± 1.0	3.0 ± 1.6	4.1 ± 0.4	4.6 ± 1.6	1.0 ± 0.2	4.9 ± 0.5	1.7 ± 0.7	3.5 ± 1.2	6.9 ± 0.6	2.2 ± 0.4	3.2 ± 0.6						
August	13	7.5 ± 0.8	4.3 ± 1.7	2.3 ± 0.9	5.3 ± 0.3	1.5 ± 0.7	4.5 ± 1.4	5.6 ± 0.8	2.0 ± 0.6	3.0 ± 0.7	7.0 ± 0.9	2.2 ± 0.9	3.8 ± 1.4						
	14	7.7 ± 0.8	4.1 ± 1.3	2.4 ± 0.9	5.9 ± 0.7	3.6 ± 1.4	2.0 ± 0.7	5.3 ± 1.4	2.6 ± 0.9	2.4 ± 1.2	7.4 ± 1.2	1.7 ± 0.9	6.1 ± 2.7						
	15	7.3 ± 1.0	2.7 ± 1.0	3.6 ± 1.7	5.1 ± 1.1	2.1 ± 1.2	3.0 ± 1.0	6.5 ± 1.5	4.3 ± 1.3	1.6 ± 0.3	6.6 ± 1.4	2.7 ± 0.9	2.8 ± 0.9						
September	16	6.7 ± 0.8	3.4 ± 1.3	2.6 ± 1.7	6.4 ± 1.5	3.6 ± 1.5	2.1 ± 0.8	5.5 ± 1.2	3.2 ± 0.8	1.8 ± 0.5	6.8 ± 1.0	3.4 ± 1.3	2.6 ± 1.2						
	17	6.6 ± 1.1	3.4 ± 1.2	2.3 ± 0.5	5.9 ± 0.4	2.2 ± 0.5	2.9 ± 0.7	5.0 ± 1.0	1.8 ± 0.4	2.9 ± 0.9	5.6 ± 1.5	3.7 ± 1.9	2.2 ± 1.2						
	18	6.0 ± 1.1	2.9 ± 0.9	2.6 ± 0.8	5.0 ± 0.3	1.4 ± 0.4	3.8 ± 0.9	4.1 ± 0.7	1.3 ± 0.6	4.0 ± 2.1	6.1 ± 0.3	1.8 ± 0.2	3.4 ± 0.4						
September	19	5.9 ± 0.8	2.8 ± 0.8	3.2 ± 1.0	3.9 ± 1.3	2.6 ± 1.2	2.1 ± 1.1	4.1 ± 1.0	2.0 ± 0.7	2.4 ± 0.9	5.2 ± 1.0	1.8 ± 0.4	3.0 ± 0.6						
	20	5.6 ± 0.7	2.0 ± 0.5	3.4 ± 1.5	4.4 ± 0.4	2.8 ± 1.1	1.9 ± 0.6	4.2 ± 1.0	1.1 ± 0.6	5.8 ± 3.2	4.9 ± 1.1	2.6 ± 0.6	2.0 ± 0.4						
	21	4.9 ± 0.7	1.7 ± 0.6	3.9 ± 1.5	3.1 ± 1.3	1.2 ± 0.7	3.2 ± 1.8	3.6 ± 0.7	1.4 ± 0.6	3.0 ± 0.9	5.1 ± 0.6	2.0 ± 0.9	3.2 ± 1.2						
September	22	4.1 ± 0.6	1.4 ± 0.5	3.6 ± 1.7	2.5 ± 0.6	1.8 ± 0.2	1.5 ± 0.3	2.9 ± 0.7	1.3 ± 0.5	2.8 ± 1.4	4.5 ± 0.5	1.7 ± 0.6	3.0 ± 0.9						
	23	3.3 ± 0.7	1.9 ± 0.7	2.2 ± 0.8	2.8 ± 0.2	2.1 ± 0.4	1.3 ± 0.2	1.7 ± 0.6	1.3 ± 0.6	1.9 ± 1.2	3.7 ± 0.5	1.9 ± 0.4	2.0 ± 0.3						
	24	2.7 ± 0.5	1.9 ± 0.7	1.7 ± 0.8	2.2 ± 0.3	1.7 ± 0.5	1.4 ± 0.4	0.9 ± 0.4	1.7 ± 0.5	0.6 ± 0.2	2.9 ± 1.1	0.7 ± 0.2	4.6 ± 2.6						
September	25	1.9 ± 0.5	1.2 ± 0.5	2.0 ± 1.1	1.7 ± 0.4	0.9 ± 0.4	2.7 ± 1.7	0.9 ± 0.3	1.5 ± 0.6	0.7 ± 0.2	2.3 ± 1.0	1.0 ± 0.6	3.5 ± 2.4						
	26	1.9 ± 0.7	1.0 ± 0.8	3.1 ± 0.9	1.3 ± 0.4	1.0 ± 0.6	1.4 ± 1.4	0.7 ± 0.4	0.6 ± 0.6	1.1 ± 0.2	0.8 ± 0.9	0.5 ± 0.5	1.5 ± 2.0						