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Forest ecosystem as a source of CO_2 during growing season: relation to weather conditions**

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A b s t r a c t. Net ecosystem production reflects the potential of the ecosystem to sequestrate atmospheric CO_2. Daily net ecosystem production of a mountain Norway spruce forest of the temperate zone (Czech Republic) was determined using the eddy covariance method. Growing season days when the ecosystem was a CO_2 source were examined with respect to current weather conditions. During the 2005, 2006, and 2007 growing seasons, there were 44, 65, and 39 days, respectively, when the forest was a net CO_2 source. The current weather conditions associated with CO_2 release during the growing seasons were: cool and overcast conditions at the beginning or end of the growing seasons characterized by a 3-year mean net ecosystem production of -7.2 kg C ha^{-1} day^{-1}; overcast or/and rainy days (-23.1 kg C ha^{-1} day^{-1}); partly cloudy and hot days (-11.8 kg C ha^{-1} day^{-1}); and overcast and hot days (-13.5 kg C ha^{-1} day^{-1}). CO_2 release was the highest during the overcast or/and rainy conditions (84%, average from all years), which had the greatest impact during the major production periods. As forests are important CO_2 sinks and more frequent weather extremes are expected due to climate change, it is important to predict future forest carbon balances to study the influence of heightened variability in climatic variables.

K e y w o r d s: net ecosystem production, CO_2 source days, eddy covariance, weather conditions, Norway spruce

INTRODUCTION

The net carbon budget of ecosystems consists in a fine balance between processes of carbon acquisition (such as photosynthesis, tree and plant growth, and carbon accumulation in soils) and carbon release (such as respiration of living biomass, tree mortality, microbial decomposition of dead biomass, oxidation of soil carbon, degradation and disturbance) (Malhi *et al*., 1999). The carbon budget expresses the ability of ecosystems to sequestrate atmospheric CO_2. If acquisition prevails, ecosystems are considered carbon sinks. The differences among various types of ecosystems in their CO_2 sequestration potentials are large (Litton *et al*., 2007; Marek *et al*., 2011), as the aforementioned processes operate on a variety of time scales and are influenced by a number of factors. These factors include climate and meteorological parameters (amount and quality of radiation, temperature, and humidity); physiological state of the ecosystem (its age, structure, species composition, and history); water, nutrient, and substrate availability; and such ecosystem disturbances as diseases, insects, and thinning (Dore *et al*., 2012; Xenakis *et al*., 2012).

Some ecosystem responses to environmental variations are immediate and direct, such as that of photosynthesis responding to light, temperature, soil moisture, and saturation deficit (Baldocchi *et al*., 1997; Chen *et al*., 1999) and respiration to temperature, soil moisture (Chen *et al*., 1999), and organic substrate availability (Kuzyakov and Gavrichkova, 2010). Others are indirect, mediated through such associated biophysical factors as leaf phenology and canopy structure (Barr *et al*., 2007). There are also transient responses that involve physiological adaptations, such as acclimation of assimilatory and respiratory processes to temperature (Tjoelker *et al*., 1999; Valentini *et al*., 2000) or changes in soil nutrient availability (Jarvis and Linder, 2000).

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Most studies concerning ecosystem carbon balance deal with seasonal and annual productions and their variability (Anthoni *et al*., 2002; Aubinet *et al*., 2002; Kljun *et al*., 2007; Piao *et al*., 2008; Reichstein *et al*., 2007; Vesala *et al*., 2010). They often demonstrate the impact of anomalies, such as drought (Schwalm *et al*., 2012), flood (Dušek *et al*., 2009), and volcanic eruption (Gu *et al*., 2003). Other studies have analysed responses of CO_2 uptake to different types of radiation (Knohl and Baldocchi, 2008; Niyogi *et al*., 2004; Oliphant *et al*., 2011; Urban *et al*., 2007, 2012), vapour pressure deficit, and temperature (Dewar *et al*., 1999; Pingintha *et al*., 2010). There are a few studies based on year-round data sets obtained on a daily basis (Dore *et al*., 2012). Some authors intentionally do not assess daily net ecosystem production (NEP) and its dependence on environmental factors because the overall impact of such short-term events on the monthly or yearly ecosystem carbon budget is negligible (Allard *et al*., 2008). However, ecosystems that are overall CO_2 sinks usually have days during the growing season during which carbon release prevails over its accumulation. Kuzyakov and Gavrichkova (2010) have pointed out that these short-term events have stronger impacts on carbon fluxes compared with long-term trends because of their higher frequency. Analysis of these days is important for understanding the physiological processes that will finally determine the reaction of the ecosystem as a whole.

Due to global climate change, extreme weather events and altered fluctuation of climate variables are expected in future (Allan and Soden, 2008; Easterling *et al*., 2000; Reyer *et al*., 2013) and changes in the distribution of climate anomalies are believed to have a stronger impact on carbon balance than changes in average climate do (Wu *et al*., 2012). This may lead to greater occurrence of CO_2 source days and hence to lower carbon sequestration into the ecosystem.

This study presents the carbon balance of a Norway spruce forest measured by the eddy covariance method during 2005-2007 and characterizes growing seasons with respect to their length and weather conditions. The main aims were to: investigate days within the growing seasons when CO_2 release prevails over its uptake in relation to actual weather conditions; and determine weather parameters leading to these days and quantify the carbon loss.

We believe that the results of this study may support the community of modellers dealing with future ecosystem changes in atmospheric CO_2 sequestration.

MATERIALS AND METHODS

Measurements were conducted in a young Norway spruce forest at the Bílý Kříž Experimental Ecological Study Site (EESS) during 2005-2007. The locality is situated within a cool and humid area having high precipitation in the Moravian-Silesian Beskydy Mountains (Czech Republic, 49°30´N, 18°32´E, 800-900 m a.s.l.; for detailed description of the site, Urban *et al*., 2012). The investigated forest was planted in 1981 with four-year-old *Picea abies* (L.) Karst. seedlings on a 12.5° slope with southern exposure. The main meteorological and forest characteristics are listed in Table 1.

Except for a snowbreak during the winter 2005/2006, the examined forest was subject to no forest disturbances affecting physiological processes. The aforementioned snowbreak reduced stand tree density and leaf area index (LAI) by approximately 30% (Table 1). Fallen tree trunks were left in the forest, but no insect or pathogen outbreaks were observed.

Eddy covariance CO_2 flux data and data from micrometeorological sensors were used. The eddy covariance system was in continuous operation using the following

T a b l e 1. Description of the Bílý Kříž Experimental Ecological Study Site (mean and standard deviation)

Environmental parameters		1998-2007	
Mean annual air temperature (°C)		6.7 ± 1.2	
Annual sum of precipitation (mm)		1374 ± 186	
Mean annual relative air humidity (%)		82 ± 4	
Average number of days with snow cover		160	
Prevailing winds		South	
Soil type		Haplic podsol (according to FAO)	
Forest characteristics (by year)	2005	2006	2007
Stand density (trees ha^{-1})	2076	1552	1552
Mean tree height (m)	9.8 ± 0.1	10.4 ± 0.1	11.2 ± 0.2
Stem diameter at breast height (cm)	13.5 ± 0.3	14.1 ± 0.3	15.0 ± 0.3
Leaf area index – seasonal maximum ($m^2 m^{-2}$)	11.8 ± 0.1	8.0 ± 0.1	8.5 ± 0.2

equipment: a Licor 7000 closed path infrared gas analyzer (Li-Cor, USA), an R3 ultrasonic anemometer (Gill Instruments, Hampshire, UK), and EcoFlux software (InSituFlux, Sweden). The system was installed at 13 and 15 m (2005-2006 and 2007, respectively) above ground level and had a footprint of 200-300 m in the up-wind direction. After data post-processing (Aubinet *et al*., 2000), half-hourly averages were available. Missing and poor-quality data were gap-filled according to interconnected models of the light response curve (Prioul and Chartier, 1977) and Arrhenius type respiration function (Hikosaka, 1997; Johnson and Thornley, 1985). For this study, days with more than 4 h of missing measurements were excluded from the analysis.

The micrometeorological measurements data for air temperature (HMP45D Vaisala, Finland; placed in thermometer screen), global radiation (CM6B, Kipp-Zonen, Netherlands), and precipitation (Envitech, CZ) were included into the investigation. Data were collected as half-hourly averages (from 30 s readings). For further details on the eddy covariance system and micrometeorological measurements (Urban *et al*., 2012).

We determined the length of the growing seasons by counting the number of days between spring and fall sign change in net ecosystem exchange (NEE; Falge *et al*., 2002). A control measure was included by:

– counting all days where the ratio of gross primary production and respiration exceeded 1 (GPP/Re>1; Falge *et al*., 2002), and
– counting all days from the time when the 5-day running mean of NEE fell below (spring) and exceeded (autumn) zero (Piao *et al*., 2008).

According to the ecological view of signs (Chapin III *et al*., 2006), CO_2 source days were defined as days with a negative daily sum of NEP (*ie* the daily sum of ecosystem respiration exceeded the daily sum of gross ecosystem production). *Vice versa*, days with a positive daily sum of NEP were considered CO_2 sink days. The following meteorological characteristics were examined, daily:

– sums of global radiation,
– averages of air temperature (T_a),
– sums of precipitation.

To categorize the CO_2 source days, time series of the aforementioned meteorological characteristics were first inspected visually and comparison was made between source periods and 10 adjacent days. Next, meteorological characteristics considerably different on the source days compared to the adjacent days were identified and combined into weather categories into which the days were then assigned. Using daily sums of global radiation (GR), the days were characterized as sunny, overcast, or partly cloudy, respectively, by the clearness index (CI, ratio of daily sums of global to extraterrestrial solar radiation) values of >0.7, <0.4 and 0.4-0.7 (Sánchez *et al*., 2012). As temperature extremes limit photosynthesis (Špunda *et al*., 1997; Wu *et al*., 2011), the cool conditions at the beginnings and ends of the growing seasons ($T_a < 4$°C) and the hot periods during summers (T_a of 18°C and more) were especially identified using daily average air temperature. The daily precipitation (P) sums were inspected in terms of their occurrence and amounts.

Source day categorization was refined by inspecting the aforementioned value intervals of meteorological characteristics. Days not meeting these criteria were removed from the categorization and regarded as unclassified.

RESULTS AND DISCUSSION

The studied period (2005-2007) was characterized by comparing selected meteorological characteristics to a ten-year (1995-2004) average and checking them for climate extremes. The comparison was conducted by examining T_a and P during March-November and GR during May-October (corresponding meteorological measurements were conducted only then). First, mean values for each parameter in each month were calculated to characterize the months as is customary from a meteorological viewpoint. The non-parametric Kruskal-Wallis test (α=0.05) was then applied to data sets that were not normally distributed. It is important to note that this test compares the distribution functions of the selected data sets, not their mean values (Table 2).

Among the investigated meteorological characteristics, monthly T_a exhibited the largest differences between the years studied and the reference decade. During 2005-2007, it was often higher compared to 1995-2004, with July and September 2006 being the months that differed most. Except for five months (drier September and October 2005, July 2006 and April 2007; rainier August 2006), the differences in P were not statistically significant, although the Augusts 2005-2007 were generally rainier and Julys drier than in the reference period. Compared to the reference period, GR was generally higher during May-July (all years; significant differences occurred in July 2006) and lower in August (all years, significant differences occurred in August 2005 and 2006). Temporal courses of the investigated meteorological characteristics are shown in Fig. 1.

There is no consensus in the scientific literature as to a universally valid method for determining the beginning and end of growing seasons. Similar results were obtained by determining sign change in NEE, GPP/Re>1, and the sign change of five-day running mean of NEP. The length of the growing season is, respectively, for 2005: 250, 249, 248 days; for 2006: 245, 246, 238; and for 2007: 226, 227, 227 days. The lengths of the 2005 and 2006 growing seasons were similar. Both began around mid-March and ended in mid-November. The 2007 growing season started earlier (at the beginning of March) and ended much earlier (mid-October) compared to both previous seasons. It was thus much shorter due to the occurrence of overcast and/or rainy days in the second half of October and a subsequent temperature decline.

Table 2. Comparison of selected meteorological characteristics (averages) during the studied period 2005-2007 with a reference decade (1995-2004). Differences are calculated between the monthly averages of each particular year studied and the reference decade. Plus and minus signs indicate an increase and decrease, respectively, in the studied parameter values. Grey denotes a statistically significant difference (α=0.05) between the distribution functions of the highlighted investigated month data set and those of the corresponding reference month

Parameter	March	April	May	June	July	August	September	October	November
					Daily average air temperature, T_a (°C)				
1995-2004	-0.49	4.69	10.99	13.79	15.20	15.76	10.13	6.23	0.88
2005	-0.61	6.92	12.65	14.97	17.62	15.26	13.71	9.36	1.73
difference	0.12-	2.23+	1.66+	1.18+	2.42+	0.50-	3.58+	3.13+	0.85+
2006	-3.04	5.17	9.35	14.72	19.72	13.35	15.25	8.10	2.84
difference	2.55-	0.48+	1.64-	0.93+	4.52+	2.41-	5.12+	1.87+	1.96+
2007	2.65	7.86	13.24	16.18	16.79	16.10	9.48	5.52	-1.51
difference	3.14+	3.17+	2.25+	2.39+	1.59+	0.34+	0.65-	0.71-	2.39-
					Daily sum of precipitation, P (mm day^{-1})				
1995-2004	3.86	3.52	3.84	5.23	7.08	3.72	4.85	3.31	3.32
2005	3.46	1.68	4.65	3.98	4.92	6.85	1.33	0.47	3.09
difference	0.40-	1.84-	0.81+	1.25-	2.16-	3.13+	3.52-	2.84-	0.23-
2006	5.74	4.62	4.30	5.23	2.52	12.41	3.45	0.91	3.53
difference	1.88+	1.10+	0.46+	0.00	4.56-	8.69+	1.40-	2.40-	0.20+
2007	4.62	0.39	2.68	5.18	3.48	5.24	9.18	3.44	3.53
difference	0.76+	3.13-	1.16-	0.05-	3.60-	1.52+	4.33+	0.13+	0.21+
					Daily sum of global radiation, GR (MJ m^{-2} day^{-1})				
1995-2004	NA	NA	17.37	17.51	16.36	16.32	10.23	5.98	NA
2005	NA	NA	17.80	17.76	16.73	12.52	11.66	8.67	NA
difference			0.43+	0.25+	0.37+	3.80-	1.43+	2.69+	
2006	NA	NA	15.79	19.34	22.67	11.42	13.78	8.28	NA
difference			1.58-	1.83+	6.31+	4.90-	3.55+	2.30+	
2007	NA	NA	17.93	18.14	18.68	15.74	9.42	5.67	NA
difference			0.56+	0.63+	2.32+	0.58-	0.81-	0.31-	

NA – indicates not applicable. Comparison was not possible in these months due to an absence of GR measurements in March, April and November for the reference decade.

During the 2005, 2006, and 2007 growing seasons, there were 43, 65 and 39 source days, respectively (Table 3). The selected weather conditions considered to have an important impact on source day occurrence were the following: cool and overcast conditions at the beginning or end of growing seasons (CO), overcast and/or rainy days (OR), partly cloudy and hot days (PCH), and overcast and hot days (OH). Four CO_2 source days were not assigned to a weather category (*ie* left unclassified).

The range of meteorological parameter values in each weather category compared to the situation for CO_2 sink days is depicted in Fig. 2. The aim was to show and compare the different ranges of meteorological parameters among source and sink days. The biggest difference is seen in precipitation. At least mild precipitation occurred almost every CO_2 source day except for those in category (PCH). A temperature limitation is seen in category (CO). Category (OR) has a precipitation range similar to (CO), but it is characterized by higher temperature not limiting physiological processes and a low amount of incident global radiation. Both categories (PCH) and (OH) are limited by high temperatures. Category (PCH) is, moreover, characterized by drought, while category (OH) combines high temperatures, precipitation, and a lower amount of radiation. Among the

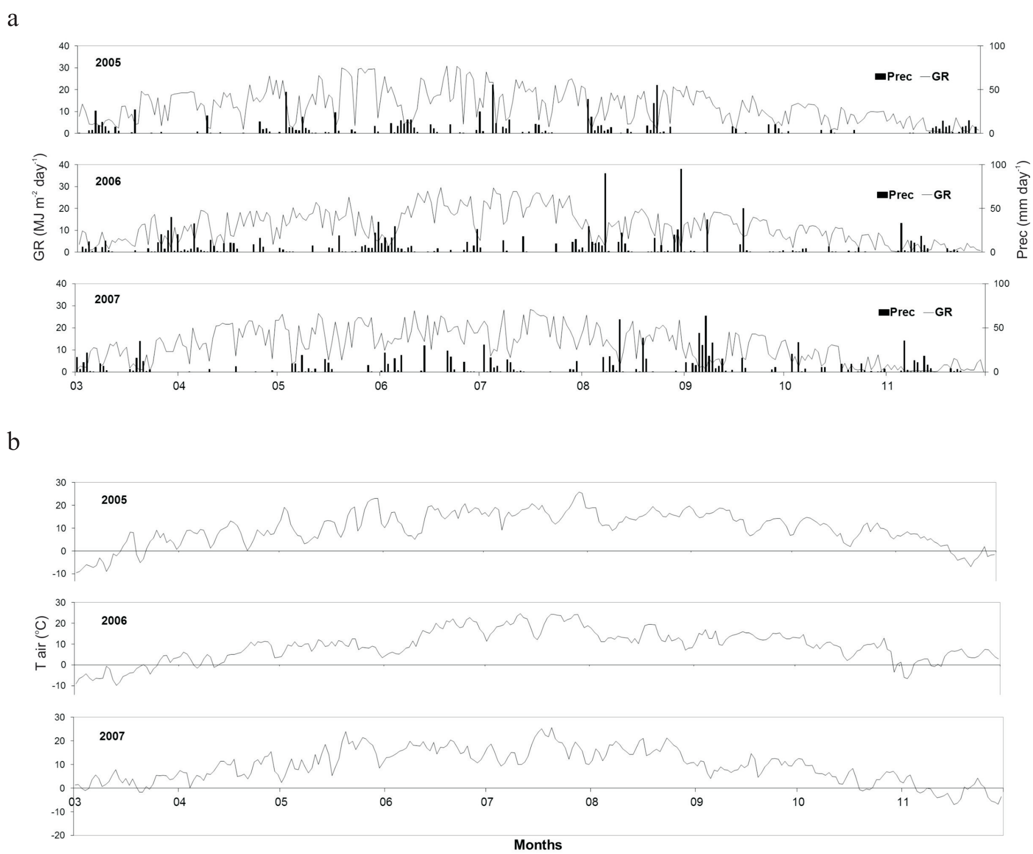

Fig. 1. Seasonal variation in: a – daily sum of global radiation and daily sum of precipitation, and b – daily average air temperature. March-November 2005-2007.

T a b l e 3. Characterization of CO_2 sink and source days of a Norway spruce forest during 3 years with focus on the growing season (GS). Total net ecosystem production (NEP) values are expressed in kg C ha^{-1} per particular period (*ie* number of days)

Parameter	2005		2006		2007	
	Growing season beginning-end*					
	14 March – 16 November		12 March – 12 November		6 March – 17 October	
	No. of days	Total NEP	No. of days	Total NEP	No. of days	Total NEP
Full year	365	4971	365	3869	365	4735
Growing season (GS)	250*	5515	245*	4515	226*	5606
CO_2 sink	207	6095	180	5423	187	6232
CO_2 source	43	-580	65	-908	39	-626
Cool and overcast at beginning/ end of GS	0	0	11	-52	5	-28
Overcast or/and rainy	35	-492	37	-676	30	-590
Partly cloudy and hot	4	-35	12	-143	2	-2
Overcast and hot	2	-44	4	-34	2	-6
Unclassified source days	3	-9	1	-3	0	0

*Determined according to NEP sign change.

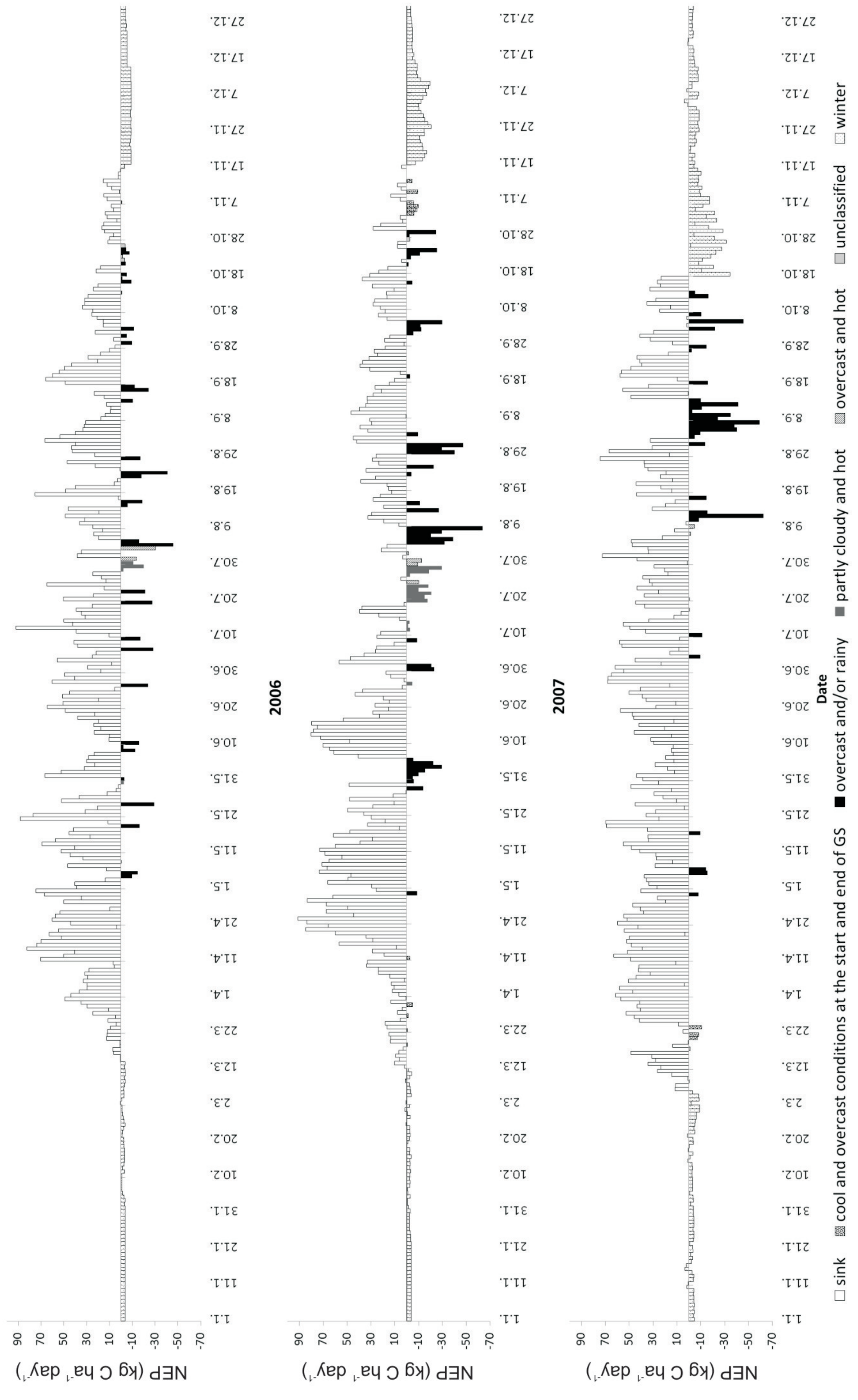

Fig. 2. Seasonal courses of net ecosystem production (NEP) in Norway spruce forest during March-November 2005-2007. Daily NEP values are plotted. Values >0 represent CO_2 sink; values <0 indicate CO_2 loss. Weather condition categories are assigned to CO_2 source days.

sink days, a period (12-17 March 2006) was observed with clear sunny days (mean daily GR sum 5.7 MJ m^{-2}) and average white day T_a below zero (-5.6°C). It is presumed that needles became heated and CO_2 uptake slightly prevailed (average daily sum 6.2 kg C ha^{-1}) over its release. Such a phenomenon had been observed and described by Sevanto *et al*. (2006).

Source days were primarily connected with overcast and/or rainy weather (81, 57, and 77% of total source days in 2005, 2006, and 2007, respectively), followed by partly cloudy and hot weather (7, 19, and 5% of source days), cool and overcast conditions at the beginning and end of the growing season (no occurrence, 17 and 13%), and overcast and hot conditions (5, 6, and 5%) (Table 3). The 2005 and 2007 growing seasons were very similar regarding the occurrence of specific weather conditions connected with CO_2 source days in that overcast and/or rainy days clearly dominated over the few days characterized by the other weather conditions (Table 3). The authors are aware of the fact that statistics for weather categories connected with only a few days should be viewed with caution due to the small sample size.

Total yearly NEP (Table 3) was the lowest in 2006, while 2005 and 2007 were by this measure similar to one another. The same pattern is observable when comparing total NEP values for growing seasons.

The contributions of CO_2 source days by the specified weather categories to the total NEP of each growing season are shown in Table 3. The median NEP for CO_2 source days was similar in all three years (-11.1, -9.6, and -10.5 kg C ha^{-1} day^{-1} during the 2005, 2006, and 2007 growing seasons, respectively). The highest CO_2 release (*ie* the lowest 3-year median NEP) took place on overcast and/or rainy days (-13.1 kg C ha^{-1} day^{-1}). Lower values were obtained for partly cloudy and hot (-7.4 kg C ha^{-1} day^{-1}) and overcast and hot weather (-9.7 kg C ha^{-1} day^{-1}). The lowest CO_2 losses occurred during cool and overcast weather at the beginning and end of the growing seasons (-5.6 kg C ha^{-1} day^{-1}). Medians are calculated here instead of means, as the distribution of the NEP data set is not normal.

Bílý Kříž is a wet locality with frequent occurrence of clouds and rains. Although the efficiency of photosynthetic light use increases when overcast (Urban *et al*., 2012), total daily amounts of fixed CO_2 are reduced. An overcast sky and regular moderate rain slow down photosynthesis, whereas the soil temperature (and thus soil respiration, as a major source of CO_2 in our forest) remains the same. This results in lowering the assimilation/respiration ratio.

Hot weather, accompanied with high irradiances and high vapour pressure deficit, is not frequent in Bílý Kříž. When it occurs, however, such weather slows photosynthesis by way of stomatal closure, temperature-stimulated photorespiration, and/or photoinhibition at the highest irradiances (Urban *et al*., 2012). Dry periods, and especially in summer, affect physiological processes and thus change photosynthesis and respiration rates (Carrara *et al*., 2004; Wu *et al*., 2011). Photosynthesis is also slowed when new snow occurs and temperatures decrease (freeze) after the beginning of the growing season (Gu *et al*., 2008).

The year 2005 was characterized by the longest growing season and the highest number of days when the forest was a sink for CO_2. Source days were distributed regularly over

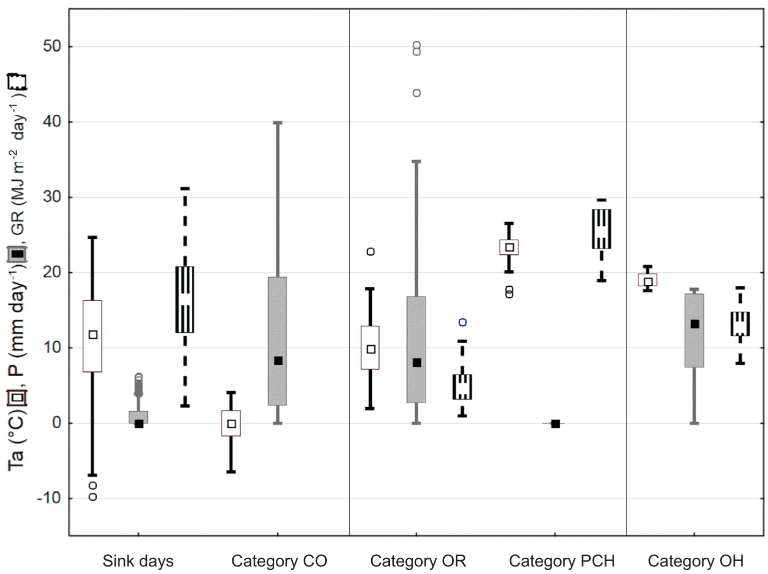

Fig. 3. Range of meteorological parameter values in each weather category compared to the situation on CO_2 sink days. Category CO refers to cool and overcast CO_2 source days at the beginning or end of the growing season, category OR to overcast and/or rainy CO_2 source days, category PCH to partly cloudy and hot CO_2 source days, and category OH to overcast and hot CO_2 source days. Squares denote medians, boxes 25 and 75% quantiles, whiskers non-outlier minima and maxima, and circles outliers. In order to keep the y-axis within a reasonable scale, extreme values are not depicted.

the entire growing season (Fig. 3). A vast majority of CO_2 source days were connected with overcast and/or rainy weather. July was significantly warmer (+2.4°C) than the reference period and had several source days connected with hot weather and a partly cloudy or overcast sky. No dry period lasting several days occurred among the CO_2 source days of this growing season. There were no cool conditions at the beginning or end of the growing season. Detailed descriptive statistics of NEP values and weather conditions for the years 2005-2007 are presented in Table 4.

The 2006 growing season was characterized by the highest number of CO_2 source days and, at the same time, by the greatest CO_2 loss and lowest CO_2 sink among the studied growing seasons (Table 3). The season was characterized by considerably different weather conditions in comparison to the 2005 and 2007 growing seasons, *ie* a longer period with high ecosystem temperature, drought and high irradiance in July (+4.5°C, -4.6 mm day^{-1}, +6.3 MJ m^{-2} day^{-1} compared to the reference period), and overcast and/or rainy weather in August (-2.4°C, +8.7 mm day^{-1}, -4.9 MJ m^{-2} day^{-1} compared to the reference period). Moreover, a snowbreak occurred during the winter 2005/2006 and reduced tree density from 2 076 to 1 552 trees ha^{-1}. Fallen tree trunks remained in the forest.

Slightly more than half (57%) of CO_2 source days were connected with overcast and/or rainy weather occurring particularly during two periods (May/June and the beginning and end of August, Fig. 3), where the latter was characterized by two outstanding precipitation events connected with the two greatest daily losses of CO_2 in this weather category (August 8th: 90 mm day^{-1}, -63.7 kg C ha^{-1} day^{-1}; August 31st: 100 mm day^{-1}, -47.4 kg C ha^{-1} day^{-1}). The weather in July led to a period of source days connected with hot weather. Although this period was followed by rain, the forest did not recover to the same sink strength as it had been before the drought.

Contrary to 2005, moderately wet and cool conditions at the beginning and end of the 2006 growing season did contribute to CO_2 loss from the forest. That, however, had only a limited impact on overall carbon balance, especially because CO_2 fluxes are generally low at the beginning and end of the growing season (Fig. 3).

In contrast to reports in the literature relating to thinning intensity comparable to that of a snowbreak (Dore *et al.*, 2012; Grote *et al.*, 2011; Misson *et al.*, 2005), the aforementioned winter snowbreak did not turn out to be a carbon source in the forest studied for the first one or two years.

Table 4. Characterization of source day categories (median (min, max)) for the analyzed periods according to net ecosystem production (NEP), clearness index (CI), daily precipitation (P), and air temperature (T_a)

Year	Category	No. days	NEP (kg C ha^{-1} day^{-1})	CI	P (mm day^{-1})	T_a (°C)
			median (min, max)			
2005	Cool and overcast at GS beginning or end of GS	0	–	–	–	–
	Overcast or/and rainy	35	-12.2 (-45.9, -0.2)	0.13 (0.05, 0.26)	6.4 (0.3, 55.3)	10.7 (1.9, 17.3)
	Partly cloudy and hot	4	-6.7 (-20.0, -2.0)	0.62 (0.54, 0.71)	0.0 (0.0, 8.3)	24.8 (23.0, 25.9)
	Overcast and hot	2	-21.8 (-30.1, -13.6)	0.26 (0.20, 0.32)	19.5 (0.0, 39.0)	18.9 (18.9, 19.0)
2006	Cool and overcast at GS beginning or end of GS	11	-4.8 (-9.8, -0.1)	0.04 (0.00, 0.11)	7.1 (0.0, 39.9)	0.4 (-6.5, 2.8)
	Overcast and/or rainy	37	-12.1 (-63.7, -1.6)	0.17 (0.03, 0.35)	8.12 (0.0, 100.0)	9.9 (3.5, 22.8)
	Partly cloudy and hot	12	-12.5 (-29.5, -1.1)	0.58 (0.50, 0.66)	0.0 (0.0, 2.4)	23.5 (22.0, 24.2)
	Overcast and hot	4	-9.7 (-12.6, -1.7)	0.35 (0.27, 0.43)	10.6 (5.0, 15.0)	19.8 (17.6, 20.7)
2007	Cool and overcast at GS beginning or end of GS	5	7.2 (-10.6, -0.4)	0.05 (0.02, 0.13)	9.7 (2.7, 35.0)	-0.57 (-1.7, 4.1)
	Overcast or/and rainy	30	-14.5 (-62.3, -2.5)	0.17 (0.04, 0.28)	9.8 (0.4, 62.5)	8.8 (1.9, 15.9)
	Partly cloudy and hot	2	-0.9 (-1.0, -0.9)	0.66 (0.63, 0.69)	0.0 (0.0, 0.0)	26.1 (25.6, 26.6)
	Overcast and hot	2	-3.2 (-4.8, -1.6)	0.33 (0.32, 0.35)	17.1 (16.6, 17.7)	18.6 (18.5, 18.8)

GS – growing season.

Even though overall CO_2 loss was the highest in 2006, the median daily loss was the least negative across all three years (-11.1, -9.6 and -10.6 kg C ha^{-1} day^{-1} for 2005, 2006, and 2007, respectively). As the weather extremes during 2006 were the greatest among the three years, the effects of unfavourable weather, low LAI values, and decomposition of fallen tree trunks cannot be easily separated. The high CO_2 uptake during the growing season in 2007 would suggest the influence of favourable weather, and forest recovery (LAI increase to 8.5 m m^{-2}) was more important than was the influence from decomposition of fallen tree trunks.

The 2007 growing season was the shortest but with highest total NEP (Table 3). The high uptake can be explained by CO rapid recovery of the forest after tree removal accompanied by an LAI increase (Table 1) leading to higher CO_2 assimilation, and OR favourable weather conditions. There was the lowest number of weather extremes (Table 2) and early start of warm spring with the highest CO_2 uptake of all the years (Fig. 2). The growing season included 39 days when the forest was a source of CO_2 and the mean carbon release per source day was the highest. The vast majority of CO_2 source days were connected with overcast and/or rainy weather occurring mainly from mid-August until the end of the growing season (Fig. 2). The short period of moderately wet and cool conditions in the 3rd decade of March also contributed to CO_2 loss from the forest. Both June and July were warmer (+2.39 and +1.59°C, respectively) than the reference period, but there were just two source days with insignificant CO_2 loss connected with hot weather in July. Meteorological characteristics in August did not differ significantly from those of the reference period, and two hot source days during that time were also insignificant as to their values.

CONCLUSIONS

1. Within the Bílý Kříž Norway spruce forest ecosystem, generally, the highest CO_2 loss occurred during overcast and/or rainy weather. The major reasons for this were cool and overcast conditions at the beginning or end of growing seasons a fairly low median net ecosystem production, and overcast and/or rainy days frequent occurrence of this weather category. As overcast or/and rainy weather is typical for the investigated locality, it is generally associated with the majority of CO_2 source days at this site. Partly cloudy and hot weather and the exceptionally occurring overcast and hot days were associated with much less CO_2 release from the forest. Lower median net ecosystem production during the partly cloudy and hot days in the 2006 versus 2005 growing season may suggest a dependence of CO_2 release intensity during this weather condition on its duration. Net ecosystem production is generally low at the beginning and end of the growing season, and CO_2 loss during these periods was also found to be small.

2. Most of the CO_2 source days and at the same time the highest CO_2 loss occurred during the 2006 growing season, which was characterized by a long period of sunny and hot weather in July and an exceptionally rainy August. Furthermore, this growing season was the first following a snowbreak in the winter 2005/2006 that had reduced the tree density as well as leaf area index in the investigated forest by approximately 30%. It was difficult to differentiate the influences of unfavourable weather conditions from those of snowbreak on the forest carbon balance.

3. The lowest number of CO_2 source days occurred during the 2007 growing season, which was characterized by the highest mean net ecosystem production among those growing seasons studied. We suggest that the beginning of the forest recovery after the snowbreak enhanced CO_2 assimilation.

REFERENCES

Allan R.P. and Soden B.J., 2008. Atmospheric warming and the amplification of precipitation extremes. Science, 321, 1481-1484.

Allard V., Ourcival J.M., Rambal S., Joffre R., and Rocheteau A., 2008. Seasonal and annual variation of carbon exchange in an evergreen Mediterranean forest in southern France. Glob. Chang. Biol., 14, 714-725.

Anthoni P.M., Unsworth M.H., Law B.E., Irvine J., Baldocchi D.D., Van Tuyl S., and Moore D., 2002. Seasonal differences in carbon and water vapor exchange in young and old-growth ponderosa pine ecosystems. Agric. For. Meteorol., 111, 203-222.

Aubinet M., Grelle A., Ibrom A., Rannik U., Moncrieff J., Foken T., Kowalski A.S., Martin P.H., Berbigier P., Bernhofer C., Clement R., Elbers J., Granier A., Grunwald T., Morgenstern K., Pilegaard K., Rebmann C., Snijders W., Valentini R., and Vesala T., 2000. Estimates of the annual net carbon and water exchange of forests: The EUROFLUX methodology. Adv. Ecol. Res., 30, 113-117.

Aubinet M., Heinesch B., and Longdoz B., 2002. Estimation of the carbon sequestration by a heterogeneous forest: night flux corrections, heterogeneity of the site and inter-annual variability. Glob. Chang. Biol., 8, 1053-1071.

Baldocchi D.D., Vogel C.A., and Hall B., 1997. Seasonal variation of carbon dioxide exchange rates above and below a boreal jack pine forest. Agric. For. Meteorol., 83, 147-170.

Barr A.G., Black T.A., Hogg E.H., Griffis T.J., Morgenstern K., Kljun N., Theede A., and Nesic Z., 2007. Climatic controls on the carbon and water balances of a boreal aspen forest, 1994-2003. Glob. Chang. Biol., 13, 561-576.

Carrara A., Janssens I.A., Yuste J.C., and Ceulemans R., 2004. Seasonal changes in photosynthesis, respiration and NEE of a mixed temperate forest. Agric. For. Meteorol., 126, 15-31.

**Chapin III F.S., Woodwell G.M., Randerson J.T., Rastetter E.B., Lovett G.M., Baldocchi D.D., Clark D.A., Harmon M.E., Schimel D.S., Valentini R.,Wirth C., Aber J.D., Cole J.J., Goulden M.L., Harden J.W., Heimann M., Howarth R.W., Matson P.A., McGuire A.D., Melillo J.M., Mooney H.A.,

Neff J.C., Houghton R.A., Pace M.L., Ryan M.G., Running S.W., Sala O.E., Schlesinger W.H., and Schulze E.D., 2006. Reconciling carbon-cycle concepts, terminology, and methods. Ecosystems, 9, 1041-1050.

Chen W.J., Black T.A., Yang P.C., Barr A.G., Neumann H.H., Nesic Z., Blanken P.D., Novak M.D., Eley J., Ketler R.J., and Cuenca A., 1999. Effects of climatic variability on the annual carbon sequestration by a boreal aspen forest. Glob. Chang. Biol., 5, 41-53.

Dewar R.C., Medlyn B.E., and McMurtrie R.E., 1999. Acclimation of the respiration photosynthesis ratio to temperature: insights from a model. Glob. Chang. Biol., 5, 615-622.

Dore S., Montes-Helu M., Hart S.C., Hungate B.A., Koch G.W., Moon J.B., Finkral A.J., and Kolb T.E., 2012. Recovery of ponderosa pine ecosystem carbon and water fluxes from thinning and stand-replacing fire. Glob. Chang. Biol., 18, 3171-3185.

Dušek J., Čížková H., Czerný R., Taufarová K., Šmídová M., and Janouš D., 2009. Influence of summer flood on the net ecosystem exchange of CO_2 in a temperate sedge-grass marsh. Agric. For. Meteorol., 149, 1524-1530.

Easterling D.R., Meehl G.A., Parmesan C., Changnon S.A., Karl T.R., and Mearns L.O., 2000. Climate extremes: Observations, modeling, and impacts. Science, 289, 2068-2074.

Falge E., Baldocchi D., Tenhunen J., Aubinet M., Bakwin P., Berbigier P., Bernhofer C., Burba G., Clement R., Davis K.J., Elbers J.A., Goldstein A.H., Grelle A., Granier A., Gudmundsson J., Hollinger D., Kowalski A.S., Katul G., Law B.E., Malhi Y., Meyers T., Monson R.K., Munger J.W., Oechtel W., U K.T.P., Pilegaard K., Rannik Ü., Rebmann C., Suyker A., Valentini R., Wilson K., and Wofsy S., 2002. Seasonality of ecosystem respiration and gross primary production as derived from FLUXNET measurements. Agric. For. Meteorol., 113, 53-74.

Grote R., Kiese R., Grünwald T., Ourcival J.M., and Granier A., 2011. Modelling forest carbon balances considering tree mortality and removal. Agric. For. Meteorol., 151, 179-190.

Gu L., Baldocchi D.D., Wofsy S.C., Munger J.W., Michalsky J.J., Urbanski S.P., and Boden T.A., 2003. Response of a deciduous forest to the Mount Pinatubo eruption: Enhanced Photosynthesis. Science, 299, 2035-2038.

Gu L., Hanson P.J., Mac Post W., Kaiser D.P., Yang B., Nemani R., Pallardy S.G., and Meyers T., 2008. The 2007 eastern US spring freeze: Increased cold damage in a warming world? Biosci., 58, 253-262.

Hikosaka K., 1997. Modelling optimal temperature acclimation of the photosynthetic apparatus in C_3 plants with respect to nitrogen use. Ann. Bot., 80, 721-730.

Jarvis P. and Linder S., 2000. Botany: constraints to growth of boreal forests. Nature, 405, 904-905.

Johnson I.R. and Thornley J.H.M., 1985. Temperature dependence of plant and crop processes. Ann. Bot., 55, 1-24.

Kljun N., Black T.A., Griffis T.J., Barr A.G., Gaumont-Guay D., Morgenstern K., McCaughey J.H., and Nesic Z., 2007. Response of net ecosystem productivity of three boreal forest stands to drought. Ecosystems, 9, 1128-1144.

Knohl A. and Baldocchi D.D., 2008. Effects of diffuse radiation on canopy gas exchange processes in a forest ecosystem. J. Geophys. Res.: Biogeosciences, 113(G2), G02023.

Kuzyakov Y. and Gavrichkova O., 2010. Time lag between photosynthesis and carbon dioxide efflux from soil: a review of mechanisms and controls. Glob. Chang. Biol., 16, 3386-3406.

Litton C.M., Raich J.W., and Ryan M.G., 2007. Carbon allocation in forest ecosystems. Glob. Chang. Biol., 13, 2089-2109.

Malhi Y., Baldocchi D.D., and Jarvis P.G., 1999. The carbon balance of tropical, temperate and boreal forests. Plant Cell Environ., 22, 715-740.

Marek M.V., Janouš D., Taufarová K., Havránková K., Pavelka M., Kaplan V., and Marková I., 2011. Carbon exchange between ecosystems and atmosphere in the Czech Republic is affected by climate factors. Environ. Pollut., 159, 1035-1039.

Misson L., Tang J., Xu M., McKay M., and Goldstein A., 2005. Influences of recovery from clear-cut, climate variability and thinning on the carbon balance of a young ponderosa pine plantation. Agric. For. Meteorol., 130, 207-222.

Niyogi D., Chang H.I., Saxena V.K., Holt T., Alapaty K., Booker F., Chen F., Davis K.J., Holben B., Matsui T., Meyers T., Oechel W.C., Pielke Sr R.A., Wells R., Wilson K., and Xue Y., 2004. Direct observations of the effects of aerosol loading on net ecosystem CO_2 exchanges over different landscapes. Geophys. Res. Lett., 31(20), L20606.

Oliphant A.J., Dragoni D., Deng B., Grimmond C.S.B., Schmid H-P., and Scott S.L., 2011. The role of sky conditions on gross primary production in a mixed deciduous forest. Agric. For. Meteorol., 151, 781-791.

Piao S., Ciais P., Friedlingstein P., Peylin P., Reichstein M., Luyssaert S., Margolis H., Fang J., Barr A., Chen A., Grelle A., Hollinger D.Y., Laurila T., Lindroth A., Richardson A.D., and Vesala T., 2008. Net carbon dioxide losses of northern ecosystems in response to autumn warming. Nature, 451, 49-52.

Pingintha N.., Leclerc M.Y., Beasley J. P., Durden D., Zhang G., Senthong C., and Rowland D., 2010. Hysteresis response of daytime net ecosystem exchange during drought. Biogeosciences, 7, 1159-1170.

Prioul J.L. and Chartier P., 1977. Partitioning of transfer and carboxylation components of intracellular resistance to photosynthetic CO_2 fixation: A critical analysis of the methods used. Ann. Bot., 41, 789-800.

Reichstein M., Ciais P., Papale D., Valentini R., Running S., Viovy N., Cramer W., Granier A., Ogee J., Allard V., Aubinet M., Bernhofer C., Buchmann N., Carrara A., Grunwald T., Heimann M., Heinesch B., Knohl A., Kutsch W., Loustau D., Manca G., Matteucci G., Miglietta F., Ourcival J.M., Pilegaard K., Pumpanen J., Rambal S., Schaphoff S., Seufert G., Soussana J.F., Sanz M.J., Vesala T., and Zhao M., 2007. Reduction of ecosystem productivity and respiration during the European summer 2003 climate anomaly: a joint flux tower, remote sensing and modelling analysis. Glob. Chang. Biol., 13, 634-651.

Reyer C.P.O., Leuzinger S., Rammig A., Wolf A., Bartholomeus R.P., Bonfante A., Lorenzi de F., Dury M., Gloning P., Jaoudé R.A., Klein T., Kuster T.M., Martins M., Niedrist G., Riccardi M., Wohlfahrt G., Angelis de P., Dato de G., François L., Menzel A., and Pereira M., 2013. A plant's perspective of extremes: terrestrial plant responses to changing climatic variability. Glob. Chang. Biol., 19, 75-89.

Sánchez G., Serrano A., and Cancillo M.L., 2012. Effect of cloudiness on solar global, solar diffuse and terrestrial downward radiation at Badajoz (Southwestern Spain). Opt. Pura Apl., 45, 33-38.

Schwalm C.R., Williams C.A., Schaefer K., Baldocchi D.D., Black T.A., Goldstein A.H., Law B.E., Oechel W.C., Kyaw Tha Paw U, and Scott R.L., 2012. Reduction in carbon uptake during turn of the century drought in western North America. Nat. Geosci., 5, 551-556.

Sevanto S., Suni T., Pumpanen J., Grönholm T., Kolari P., Nikinmaa E., Hari P., and Vesala T., 2006. Wintertime photosynthesis and water uptake in a boreal forest. Tree Physiol., 26, 749-757.

Špunda V., Kalina J., Marek M.V., and Nauš J., 1997. Regulation of photochemical efficiency of photosystem 2 in Norway spruce at the beginning of winter and in the following spring. Photosynthetica, 33, 91-102.

Tjoelker M.G., Oleksyn J., and Reich P.B., 1999. Acclimation of respiration to temperature and CO_2 in seedlings of boreal tree species in relation to plant size and relative growth rate. Glob. Chang. Biol., 5, 679-691.

Urban O., Janouš D., Acosta M., Czerný R., Marková I., Navrátil M., Pavelka M., Pokorný R., Šprtová M., Zhang R., Špunda V.R., Grace J., and Marek M.V., 2007. Ecophysiological controls over the net ecosystem exchange of mountain spruce stand. Comparison of the response in direct vs. diffuse solar radiation. Glob. Chang. Biol., 13, 157-168.

Urban O., Klem K., Ač A., Havránková K., Holišová P., Navrátil M., Zitová M., Kozlová K., Pokorný R., Šprtová M., Tomášková I., Špunda V., and Grace J., 2012. Impact of clear and cloudy sky conditions on the vertical distribution of photosynthetic CO_2 uptake within a spruce canopy. Funct. Ecol., 26, 46-55.

Valentini R., Matteucci G., Dolman A.J., Schulze E-D., Rebmann C., Moors E.J., Granier A., Gross P., Jensen N.O., Pilegaard K., Lindroth A., Grelle A., Bernhofer C., Grünwald T., Aubinet M., Ceulemans R., Kowalski A.S., Vesala T., Rannik Ü., Berbigier P., Loustau D., Gudmundsson J., Thorgeirsson H., Ibrom A., Morgenstern K., Clement R., Moncrieff J., Montagnani L., Minerbi S., and Jarvis P.G., 2000. Respiration as the main determinant of carbon balance in European forests. Nature, 404, 961-865.

Vesala T., Launiainen S., Kolari P., Pumpanen J., Sevanto S., Hari P., Nikinmaa E., Kaski P., Mannila H., Ukkonen E., Piao S.L., and Ciais P., 2010. Autumn temperature and carbon balance of a boreal Scots pine forest in Southern Finland. Biogeosci., 7, 163-176.

Wu Z.T., Dijkstra P., Koch G.W., Penuelas J., and Hungate B.A., 2011. Responses of terrestrial ecosystems to temperature and precipitation change: a meta-analysis of experimental manipulation. Glob. Chang. Biol., 17, 927-942.

Wu J., Linden van der L., Lasslop G., Carvalhais N., Pilegaard K., Beier C., and Ibrom A., 2012. Effects of climate variability and functional changes on the interannual variation of the carbon balance in a temperate deciduous forest. Biogeosci., 9, 13-28.

Xenakis G., Ray D., and Mnecuccini M., 2012. Effects of climate and site characteristics on Scots pine growth. Eur. J. For. Res., 131, 427-439.