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CO_2 efflux in different types of ecosystems

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Podpis

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Eva Dařenová
CO_2 efflux in different types of ecosystems
Tok CO_2 v různých typech ekosystémů

Abstrakt

Ve třech různých ekosystémech byl sledován tok CO_2 z půdy (smrkový les, bukový les a mokřad) a na jednom stanovišti tok CO_2 z celého ekosystému (louka). Manuální a automatická kontinuální měření byla prováděna během růstové sezóny v letech 2008 – 2012. Byly sledovány faktory ovlivňující prostorovou variabilitu a časovou dynamiku toku CO_2. Časová dynamika byla řízena především teplotou půdy, dále také vlhkosti půdy, která měla i vliv na prostorovou variabilitu toku CO_2. Tato prostorová variabilita závisela také například na množství nadzemní biomasy nebo tloušťce opadu. Dále byl sledován rozdíl závislosti toku CO_2 z půdy na teplotě v závislosti na denní době, kdy byla měření toku CO_2 prováděna. Tyto rozdíly pak následně ovlivňovaly i stanovení množství CO_2 uvolněného z půdy za celou sezonu. V poslední části práce byl sledován okamžitý i dlouhodobý vliv změny distribuce srážek a vliv sucha simulovaného v první polovině růstové sezony na tok CO_2 z lučního ekosystému.

Klíčová slova: Tok CO_2 z půdy, komorová metoda, dynamika v čase, prostorová variabilita, manuální měřeni, automatická měření, sucho, smrkový les, bukový les, louka, mokřad.

Abstract

CO_2 efflux from soil at three different ecosystems (spruce forest, beech forest, wetland) and from the whole ecosystem at one site (grassland) was measured during campaigns of manual measurements or automated continuous measurements during growing seasons 2008 – 2012. There were determined factors driving spatial variability and temporal dynamics of CO_2 efflux. Soil temperature was mostly the driving factor responsible for temporal dynamics and soil water content contributed to both temporal dynamic and spatial variability. Also the amount of grass or litter affected the variability. We also determined that time of the day when the measurements of soil CO_2 efflux are done can influence estimation of seasonal sum of released carbon from soil. Finally, it was determined that changing precipitation pattern with simulated drought in the first half of the growing season has both immediate and long-term impact on CO_2 efflux from the grassland ecosystem.

Key words: Soil CO_2 efflux, chamber method, temporal dynamics, spatial variability, manual measurements, automated measurements, drought, spruce forest, beech forest, grassland, wetland

Content

List of used abbreviations and symbols

C	carbon
CH_4	methane
CO_2	carbon dioxide
CV	coefficient of variation
D_{WT}	water table level (cm)
GPP	gross primary production
NEP	net ecosystem production
NPP	net primary production
Q_{10}	the proportional change in CO_2 efflux from 10 °C increase in temperature
R	CO_2 efflux (µmol $m^{-2}s^{-1}$)
R^2	coefficient of determination
R_{10}	CO_2 efflux normalized for the temperature of 10 °C (µmol $m^{-2}s^{-1}$)
R_m	modeled soil CO_2 efflux (µmol $m^{-2}s^{-1}$)
SAMTOC	automated system for measurement of CO_2 efflux (in the forest)
SAMTOL	automated system for measurement of CO_2 efflux (in the grassland)
SD	standard deviation
T_s	soil temperature (°C)

1 Introduction

Recently, a great attention has been paid to the concentration of greenhouse gases in the atmosphere. The greenhouse gases permit incoming solar radiation to reach the surface of the earth but restrict the outward flux of infrared radiation. They absorb and reradiate the outgoing infrared radiation, effectively storing some of the heat in the atmosphere. In this way, greenhouse gases hold heat within the atmosphere, resulting in climate warming near the earth surface. The enhanced concentration of greenhouse gases in the atmosphere enhances the absorption and emission of infrared radiation. This warming together with changes in precipitations, wind speed and other components of the atmosphere are generally called as Global Climate Change. One of the greenhouse gases is carbon dioxide (CO_2) which concentration in the atmosphere has rapidly increased (source NOAA, www.esrl.noaa.gov), therefore, a lot of effort has been focused on the carbon cycle for the last decades.

CO_2 is bound from the atmosphere by the autotrophic organisms through the photosynthesis and incorporated to their tissues. The amount of carbon assimilated by the photosynthesis is called gross primary production (GPP). A big portion of the assimilated carbon is returned to the atmosphere by the autotrophs through respiration process. The gross primary production minus the reparation results in so called net primary production, which represents the total available energy in an ecosystem the form of dry plant biomass. If the heterotrophic respiration of soil organisms is taken account, it is then talked about net ecosystem production (difference between GPP and total ecosystem respiration) (Chapin et al. 2006). Soil respiration, therefore, affects the amount of carbon bound in the ecosystem.

Different ecosystems can become a sink or on the contrary source of the carbon and significantly contribute to changes in CO_2 in the atmosphere. Forests represent the large terrestrial carbon stock. Forest become sources of greenhouse gases especially when they are disturbed or converted into another land-use type (Amiro and Barr 2006), because the carbon reservoir of the forest will be partly or totally released into atmosphere during this process. Grasslands are mostly sink of the carbon but it depends on their conditions and management (grazing, mowing etc.) (Schönbach et al. 2012). Wetlands or peatlands has formed a significant sink for atmospheric CO_2 because of very slow decomposition rate of by organic matter (Šantrůčková et al. 2004) which has been accumulated in these ecosystems. Due to the generally wet soil conditions, they are also significant emitters of the strong greenhouse gas methane (CH_4) (Knorr et al. 2008). Their disturbance or drainage can turn them into the source of the large amount of CO_2 released into atmosphere (Lund et al. 2012).

After the photosynthesis, CO_2 flux from soil is the second largest carbon flux in most of ecosystems and is a big source of CO_2 released into the atmosphere. Climatic changes, such as for example increasing temperature and changes in the intensity and distribution of precipitations, have an impact on soil respiration (Bond-Lamberty and Thompson 2010, Harper et al. 2005) and they can cause a significant increase in the amount of CO_2 released from terrestrial ecosystems into the atmosphere (Bond-Lamberty and Thompson 2010) and therefore increase the concentration of atmospheric greenhouse gases.

To estimate correctly the impact of climate changes on CO_2 flux from soil in different ecosystems in the future, it is necessary to well understand courses of soil CO_2 efflux through the year and its response to the changing factors. The aim of this study is focused on measurements of soil (or ecosystem) CO_2 efflux in four ecosystems and on its temporal dynamics and spatial heterogeneity.

2 Aims

The aims of the study are as follows.

- to describe temporal variability of CO_2 efflux from spruce forest soil and grassland ecosystem, and to determine factors that affect the CO_2 efflux and can help in its modeling
- to determine spatial heterogeneity of soil (ecosystem) CO_2 efflux in four ecosystems within the footprint of eddy-covariance measurements, to try to determine factors driving the variability and to suggest suitable CO_2 efflux measurement protocol at these sites.
- to determine the influence of the time of the day of the soil CO_2 measurements on calculation of seasonal cumulative carbon efflux from the forest soil.
- to determine impact of the change of precipitation distribution and induced drought on the grassland ecosystem respiration.

The solving of the problems was based on testing of these hypotheses:

- Can soil moisture and other parameters, like phenological phases, influence the parameters of soil/ecosystem CO_2 efflux dependence on soil temperature (the main factor driving CO_2 efflux) during the growing season?
- Do the factors responsible for the spatial heterogeneity of CO_2 efflux and the heterogeneity itself differ among ecosystems, and, moreover, do the variability and the impact of the factors change during the year?
- Is the dependency of soil CO_2 efflux on soil temperature and thus models of the seasonal release of carbon from soil based on soil temperature biased by the time of day and night when the measurements of soil CO_2 efflux and temperature are done?
- Will the expected change in precipitation pattern (IPCC 2001), especially spring drought and extreme rain events, have an impact on carbon budget of mountain grassland?

3 Background

3.1 Respiration

Respiration is a series of metabolic processes that catabolize organic molecules to liberate energy, water and carbon dioxide (CO_2) in a cell. Most of the living organisms – plants, animals, microorganisms – share similar pathways of respiration to obtain the energy while releasing CO_2. The energy is then used for growth, maintenance of existing structures and functions, transport of metabolites and ions, protein regeneration and repair processes. The respiration can be studied in relation to energy supply at the biochemical and cellular levels, or in relation to CO_2 and O_2 exchanges.

Respiration on the ecosystem level can be divided into respiration of above-ground respiration and below-ground (or soil) respiration. In many ecosystems the soil respiration accounts over 50 % of total ecosystem respiration in dependence on ecosystem type, age and external factors. Technically, the rate of CO_2 production in the soil is difficult to be directly measured in the field. Measurements are often made at the soil surface to quantify a rate of CO_2 efflux from the soil into the atmosphere (Pumpanen et al. 2004).

3.2 Processes and sources of CO_2 production in soil

The three carbon pools that can be recognized as sources of CO_2 efflux from soil Kuzyakov 2006):

1) the soil organic matter (SOM),
2) above and below ground dead plant residues,
3) organic substances released by living roots (rhizodeposits or exudates).

The pools have no sharp boundaries, e.g. are many dead plant residues in the soil that are partly humified, thus part of SOM.

There are two main groups of organisms in the soil: heterotrophic and autotrophic. Most CO_2 evolved by heterotrophic soil organisms is respired by microorganisms (bacteria, fungi, and actinomycetes). Contribution of soil macrofauna is small. Autotrophic organisms are mostly represented by plant roots. Root respiration also represents a major source of CO_2 loss in plants, with 8 – 52 % of the CO_2 fixed by photosynthesis being released back into the atmosphere by root respiration (Lambers et al., 1996).

Kuzyakov (2006) described five processes of soil CO_2 production:

- microbial decomposition of SOM in root free soil without undecomposed plant remains (basal respiration),
- microbial decomposition of SOM in root affected or plant residue affected soil (priming effect),
- microbial decomposition of dead plant remains,
- microbial decomposition of organic substances released from living roots (rhizodeposits) (rhizomicrobial respiration),
- root respiration.

Only the first process contributes to the CO_2 efflux from all soils containing organic matter. The contribution of the four other sources depends on the presence of vegetation in the study year and/or in the previous few years.

In some cases, when the method does not allow separation of the respiration by rhizosphere microorganisms from the respiration by microorganisms decomposing SOM, the term microbial respiration is used (e.g. Larionova et lal. 2003). In this case, microbial respiration includes rhizomicrobial respiration. The “rhizosphere respiration” is frequently used in literature to refer to the sum of root respiration and rhizomicrobial respiration (e.g. Sulzman et la. 2005), referring to the location of CO_2 production.

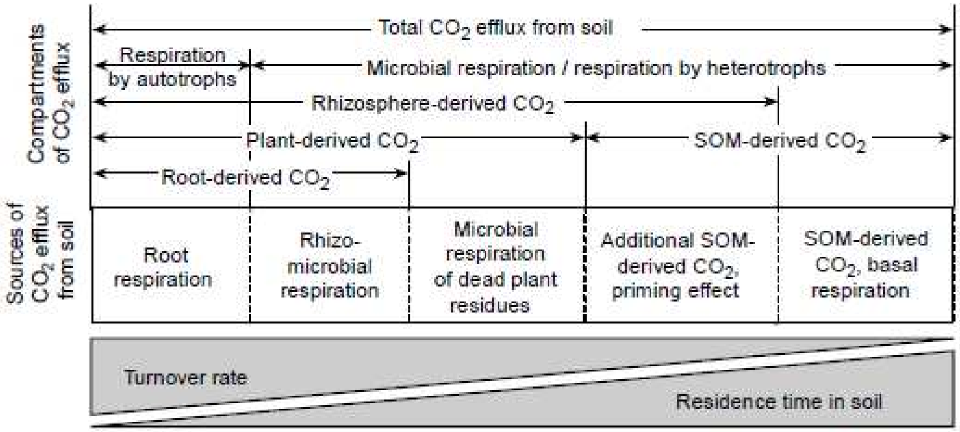

Fig. 1: The main processes of soil CO_2 production, ordered according to the turnover rate and mean resistance tome of carbon in soil, and components of soil CO_2 efflux (Kuzyakov 2006).

A very important difference between the five processes of CO_2 efflux is the turnover rate (TR) of the carbon pools. The turnover rate means the rate of cycling of carbon in a pool or a system. Different turnover rates result in largely different mean residence times (MRT) of carbon in the SOM pools. The mean residence time is inverse of TR (MRT=1/TR) and denotes the mean period of residence of C in the soil or in the SOM pool (Kuzyakov 2006) (Fig. 1).

As soil is a complex system, it is difficult to investigate individual processes of soil CO_2 production. However, several methods have been developed. The most used are:

- comparison of planted and unplanted soil – different soil CO_2 efflux of soil influenced by roots and soil without roots (Kocyigit and Rice 2006),
- "trenching" – this method involves cutting of roots in soil around the investigated area. Therefore, the transport of assimilates to roots is stopped (Jassal et Black 2006, Wang et Yang 2007).
- shading and clipping of above-ground biomass – they are based on stopping leaf photosynthesis and thus excluding new assimilate transport to the roots (Craine et al. 1999, Wan et Luo 2003).
- tree girdling - girdling of phloem interrupts the flow of assimilates from leaves to the roots (Andersen et al. 2005, Binkley et al. 2006).
- regression technique - is based on the assumed linear relationship between root biomass and the amount of CO_2 respired by roots and rhizosphere microorganisms (Kucera et Kirgham 1971, Zhang et al. 2009).
- respiration by excised roots – measurement of respiration of living roots incubated after separation from soil (Bekku et al. 2009)
- Isotope methods – using isotope tracers stable carbon-13 (^{13}C) (Kuzyakov 2005) or radioactive carbon-14 (^{14}C) (Trumbore 2000)

Each method has its advantages and disadvantages. Any of them can not avoid to some degree of disturbance of the investigated ecosystem, which can influence the results

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3.3 Methods of soil CO_2 efflux measurement

Soil CO_2 efflux is presently measured *in situ* mainly using chamber techniques. Currently three major chamber techniques are used (Livingston and Hutchinstone, 1995):

- Closed static chamber method

  Chambers are closed without air flow except CO_2 release from soil. The chambers contain a chemical absorbent inside to absorb CO_2 molecules within a certain time. The chemical absorbents for CO_2 mostly include soda lime, which consists of NaOH and $Ca(OH)_2$. The amount of CO_2 absorbed by soda lime in the chamber over the soil surface is determined by the gain in soda lime dry weight during the sampling period.

  This method is also called as non-steady-state or non-through-flow method.

- Open dynamic chamber method

  Ambient air flows from an inlet through the chamber to an outlet and the air leaving the chamber is enriched in CO_2 concentration relative to the air of known CO_2 concentration entering the chamber due to CO_2 release from respiration of the soil.

  This method is also called as steady-state through-flow method.

- Closed dynamic chamber method

  The air circulates in a loop between the chamber and a CO_2-detecting sensor during measurement. When the closed chamber cover the soil surface, CO_2 concentration in the chamber rises due to release CO_2 efflux from soil. The rate of CO_2 concentration increase is proportional to the soil CO_2 efflux.

  This method is also called as non-steady-state through-flow method.

The chamber systems can be further divided into manual and automated systems. Both methods have advantages and disadvantages.

Automated systems

+ measure continuously for long periods
+ measure regardless of the weather and time of day
- require permanent energy supply
- have a limited number of measurement positions

Manual systems

+ can be easily implemented on a large number of positions. That narrows the standard deviation from the CO_2 efflux mean, thus increasing confidence in the site estimation of CO_2 efflux with respect to its spatial heterogeneity
+ can measure at sites without the possibility of energy supply
- are usually carried out during daytime and non-rainy periods, therefore, the immediate response to changing factors can be missed

The choice of the measurement technique depends on the site conditions and what is to be investigated (e.g. spatial heterogeneity, temporal dynamics, influence of environmental factors).

3.4 Factors influencing soil CO_2 efflux

Temperature is the key factor influencing soil CO_2 efflux in most of studied ecosystems. Positive correlation between soil CO_2 efflux and soil temperature has been observed in many studies. Actually, soil CO_2 increases up to its maximum at a temperature of about 40 °C and then declines (Atkin and and Tjoelker 2003, Lellei-Kovacs et al. 2011) (Fig. 2). Low temperatures have mostly effect on enzymes activity (Atkin et al. 2002), while under high temperatures, soil respiration is influenced by substrate supply (Atkin and and Tjoelker 2003).

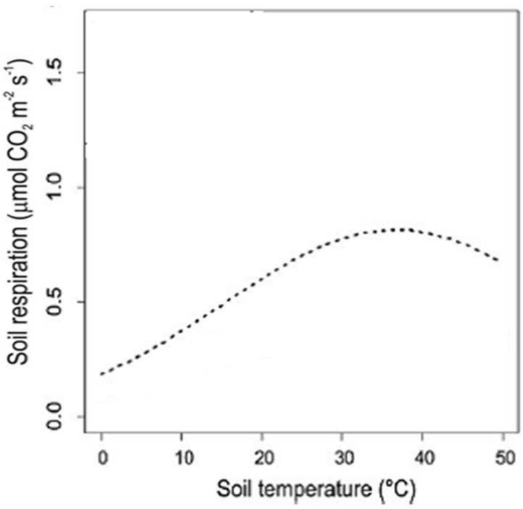

Fig. 2: Soil CO_2 efflux response to soil temperature (Lellei-Kovacs et al. 2011).

The sensitivity of soil CO_2 efflux to temperature is often described by an exponential relationship, expressed as Q_{10} (proportional change in CO_2 efflux when temperature changes by 10 °C), or Arrhenius type relationship (Lloyd and Taylor 1994). The first is more frequently used but it has often been criticized because the Q_{10} itself decreases with increasing temperature and depends on soil moisture conditions (Davidson et al. 2006a). The Arrhenius relationship is based on activation energy which decreases with increasing soil temperature (Lloyd and Taylor 1994).

Soil moisture is another important factor influencing soil respiration. Soil respiration is low in dry conditions and increases to a maximum at intermediate moisture levels (Xu et al. 2004). Under high moisture condition, the soil CO_2 efflux begins to decrease because of limitation of oxygen availability due to reduced air diffusion for decomposition and root maintenance and growth. The studies have shown that soil moisture limits respiration at the lowest and highest conditions. The dependence of soil CO_2 efflux can be described by the curve according to Janssens et al. (1999) (Fig. 3). The shape of the moisture response curve depends on site specific factors such as soil texture and structure, amount and type of organic matter, and soil temperature (Howard and Howard, 1993).

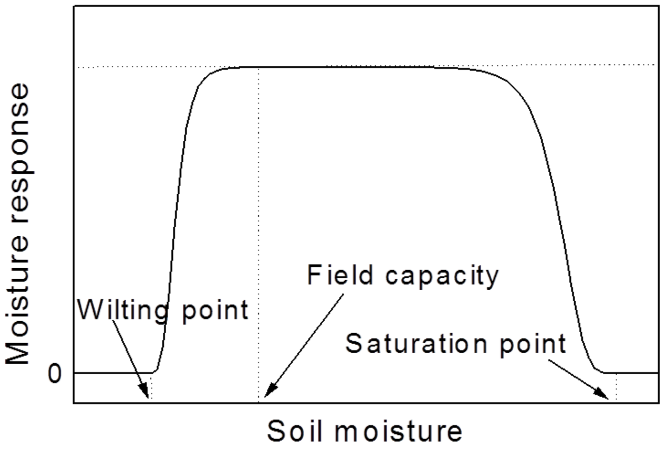

Fig. 3: Soil moisture response of soil CO_2 efflux (Janssens et al. 1999)

Soil temperature and moisture change rapidly in time, therefore they are key factors responsible for temporal changes in soil CO_2 efflux. Sometimes it can be difficult to separate these two factors. For example, high soil temperature often coincides with low moisture availability, therefore soil moisture becomes a driving factor of soil CO_2 efflux rate and that can become even independent of soil temperature (Yuste et al. 2003).

Furthermore, soil respiration is influenced by nitrogen content in soil. Respiration generates energy to support root nitrogen uptake and assimilation (Bloom et al. 1992). High nitrogen content is also usually associated with high growth rates, leading to high growth respiration, and with litter decomposition rates and thus microbial respiration in a complex pattern (Saiya-Cork et al. 2002).

Moreover soil CO_2 efflux can be affected by e. g. pH (Xu et Qi 2001a), the amount of above- and below-ground biomass (Craine and Wedin 2002), soil type (Arrouays et al. 2001), phenology (Byrne and Kiely 2006) etc.

3.5 Soil and climate change

Soil respiration becomes relevant to climate change because the CO_2 released from soil respiration is one of the greenhouse gases. As described above, rising CO_2 concentration in the atmosphere enhances greenhouse effect, resulting in global warming. The global warming could substantially stimulate soil respiration (Bond-Lamberty and Thompson 2010), resulting in release of more CO_2 to the atmosphere to hold the heat. Thus, the climate system and the carbon cycle form a positive feedback loop to reinforce each other (Friedlingstein et al. 2003). The magnitude of the response of soil respiration to soil warming is expected to be greater in cold, high-latitude ecosystems than in the warm areas, and recent climatic warming has likely caused a great loss of carbon from tundra and boreal soils (Goulden et al. 1998).

The global change is also related to the change in rainfall patterns – precipitation intensity, frequency and timing. A reduction of rainfall or prolonged water deficits between the periods of rainfall reduce soil CO_2 efflux in many ecosystems as a result of increased plant and microbial stress (Harper et al. 2005). However, in ecosystems with very high soil water content, such as wetlands or peatlands, the reduction of precipitation and consequently soil water contents increases soil aeration and stimulates respiration rates by releasing oxygen limitation to soil microorganisms (Couwenberg et al. 2010), therefore the high amount of organic matter, which accumulated in the soil over years, could be decomposed and the high amount of CO_2 released into the atmosphere.

Also elevated concentration of CO_2 in the atmosphere usually increases soil respiration. That is mainly result of stimulation of plant photosynthesis and growth, and subsequent delivery of more carbon substrate stimulates root and soil carbon processes, such as root biomass (King et al. 2001), root respiration (Thomas et al. 2000), litter production and decomposition (Finzi et al. 2001), etc.

In conclusion we can say that global change can have a great impact on soil CO_2 efflux in dependence on the character of the change and the ecosystem characters and condition. Therefore, more investigations of this impact on different ecosystems are needed.

3.6 Grasslands

Grasslands cover about 30 % of the global terrestrial ice-free surface. Whether grasslands act as a source or a sink of CO_2 depends on external conditions (Flanagan et al. 2005) and also on the management. Abandoning, grazing or mowing has different impact on grassland carbon balance (Bahn et al. 2006, Rich et al. 2007).

Highest emissions from grasslands come from soil (Rich and Frank 2007). Due to grassland structure and thick biomass, it is, however, very difficult to separate CO_2 efflux from soil and respiration from the above-ground biomass. Methods when the above-ground biomass is cut and removed have effect on radiation at the soil surface, soil temperature and moisture, increases plant stress and disrupts the assimilate supply to roots and rhizospheric microbes (Bremer et al.1998, Bahn et al. 2006).

The impact of climatic change and management on grassland ecosystems could have a considerable impact on the global carbon cycle. Therefore, it is important to have a good knowledge of different grassland types on changing conditions.

4 General materials and methods

4.1 Study sites

4.1.1 Spruce forest

The Norway spruce (*Picea abies*) forest is a part of Ecological Experimental Study Site (EESS) Bily Kriz in Moravian-Silesian Beskydy Mts (49°30´ N, 18°32´ E) (Fig.4). It is situated in the altitude of 890 m a. s. l. (meteorological tower position) on a slope of 12.5° with a south exposure. The site is characterized by mean annual air temperature of 6.8 °C and annual precipitation of 1 318 mm (for the period 1998-2011) (Marková et al. 2014). The spruce stand was planted in 1981, using four-year-old seedlings. The stand characteristics are summarized in Tab. 1. In the winter in the beginning of 2012 there was a severe damage of the forest and the stand density decreased from 1488 tree ha^{-1} to 1270 tree ha^{-1}. The understory is dominated by *Vaccinium myrtillus*. The soil type is Haplic Podzol (FAO classification). The depth of soil profile is 60 – 80 cm, the highest root density is in the depth of 3 – 13 cm, pH of soil without litter is 4.3 and the amount of soil carbon and nitrogen is summarized in Tab. 2.

Fig. 4: Experimental spruce stand in Bily Kriz, Moravian-Silesian Beskydy Mts.

Tab. 1: Tree density, mean stand height, tree diameter at breast height (DBH) and leaf area index in the spruce forest in four years (Marková et al. 2014).

	2009	**2010**	**2011**	**2012**
Tree density (tree ha^{-1})	1492	1488	1488	1270
Stand height (m)	13.3	13.9	14.6	15.5
DBH (cm)	15.9	16.4	16.9	17.9
LAI (m^{2}m^{-2})	9.6	10.1	10.2	7.5

Tab. 2: Amount of total soil organic carbon (C%) and nitrogen (N%) at the spruce forest in 2011 (Formanek, personal communication).

Depth (cm)	**Horizon**	**C%**	**N%**
0 - 1	L	47.19	1.47
1 - 3	F	40.50	1.74
3 - 12	H	29.47	1.38
12 - 15	Ae/Ep	3.49	0.16
15 - 23	Bhs	4.31	0.20
23 - 70	Bs	2.08	0.08
70 - 90	B/C	1.09	0.08

4.1.2 Grassland

The grassland is also a part of the EESS Bily Kriz. It is situated in the altitude of 855 m a. s. l. (meteorological tower position) on a slope of 8.5° with south-east exposure (49°30´ N, 18°32´ E) (Fig. 5). The site is characterized by mean annual air temperature of 6.8 °C and annual precipitation of 1 318 mm (for the period 1998-2011) (Marková et al. 2014). The grassland used to be divided into two parts – mown grassland (mowing was done once during the growing season) and non-mown grassland. Since 2009, both parts of the grassland have been mowed once a year at the same time (in that time grass was cut also on measurement positions of CO_2 efflux measurement system SAMTOL (chapter 4.2.2) (Tab. 3). The originnnally mown grassland is dominated by red fescue (*Festuca rubra* agg.), moor matgrass (*Nardus stricta*), common speedwell (*Veronica officinalis*), smooth hawkweed (*Hieracium laevigatum*) and common tormentil (*Potentilla erecta*). The originally non-mown grassland was formed by common sorrel (*Rumex acetosa*), imperforate St John's-wort (*Hypericum maculatum*), creeping soft grass (*Holcus mollis*) and common yarrow (*Achillea millefolium*).

Fig. 5: Experimental grasland in Bily Kriz, Moravian-Silesian Beskydy Mts.

The soil type is Gleyic Luvisol (FAO classification). The depth of soil profile is about 80 cm, the highest root density is in the depth of 2 – 8 cm, pH of soil without litter is 4.9 and the amounts of soil carbon and nitrogen are summarized in Tab. 4.

Tab. 3: Dates of mowing of the grassland and cutting of the grass on positions on CO_2 efflux measurements of the system SAMTOL.

	2009	**2010**	**2011**	**2012**
Mowing	23 July	14 July	12 July	24 July
Cutting	25 July	15 July	13 July	30 July

Tab. 4: Amount of total soil organic carbon (C%) and nitrogen (N%) at the grassland site in 2004 (Formanek, personal communication).

Depth (cm)	**Horizon**	**C%**	**N%**
0 - 2	L	31.10	1.72
2 - 6	F	26.32	1.67
6 - 8	H	22.03	1.44
8 - 21	Ah	4.85	0.29
21 - 28	Ae	2.54	0.15
28 - 42	Btg	2.29	0.12
42 - 78	Bt	1.60	0.07

4.1.3 Beech forest

The beech (*Fagus sylvatica*) forest is situated in Bílé Karpaty near Štítná nad Vláří (49°02´ N, 17°58´ E), in the altitude 559 m a, s. l. (meteorological tower position) on a slope of 8° with a south-west exposure (Fig. 6). The site is characterized by mean annual air temperature of 7.5 °C and annual precipitation of 800 mm. The age of the stand was 108 years in 2011. The stand characteristics are summarized in

Fig. 6: Experimental beech stand in Bílé

Tab. 5. The understory is dominated in the spring aspect by *Dentaria bulbifera*, sweet woodruff (*Galium odoratum*), early dog-violet (*Viola* reichenbachiana), wood sorrel (*Oxalis acetosella*), and the by perennial *Carex pilosa*, Carex *brizoides*) a false brome (*Brachypodium sylvaticum*) (Markova et al. 2014).

The soil type is Eutric Cambisol (FAO classification). There is an increased degree of presence of roots with a diameter less than 10 mm in about 50 cm deep, pH of soil without litter is 7.0 and the amounts of soil carbon and nitrogen are summarized in Tab. 6.

Tab. 5: Tree density, mean stand height, tree diameter at breast height (DBH) and leaf area index in the beech forest in two years (Marková et al. 2014).

	2010	**2011**
Tree density (tree ha^{-1})	285	283
Stand height (m)	32.0	32.2
DBH (cm)	35.1	35.5
LAI (m^{2}m^{-2})	-	11.6

Tab. 6: Amount of total soil organic carbon (C%) and nitrogen (N%) at the beech forest in 2011 (Formanek, personal communication).

Depth (cm)	**Horizon**	**C%**	**N%**
0 - 2	L	42.40	1.20
2 - 3	F+H	22.62	1.07
3 - 14	Ah	6.30	0.46
14 - 26	Bvt	2.35	0.15
26 - 52	Bv1	1.61	0.21
52 - 70	Bv2	1.53	0.14
70 - 88	BC	1.53	0.14
88<	C	2.20	0.18

4.1.4 Wetland

The monitored sedge-grass marsh is a 1.5 ha part of the large „Wet Meadows“ wetland complex situated near the town Třeboň, South Bohemia, Czech Republic, close to an ancient man-made lake Rožmberk. It is a flat area at an altitude 426.5 m a. s. l. (49°01´ N, 14°46´ E) (Fig. 7). The water level fluctuates mostly between 0.2 m below and 0.2 m above the soil surface. During extreme floods, the water table can reach up to 1 m. Most frequently, the water level is situated at about 0.1 m below the soil surface. In some years, spring or summer floods occurred. The site is characterized by mean annual air temperature of 7.6 °C and annual precipitation of 614 mm for the 35-year period (1977 to 2011) (Dušek et al. 2012). During the last 50 years, after cessation of mowing, a distinct stand pattern of hummocks and hollows has developed. The hummocks are formed by tussocks of *Carex acuta*. The soil is classified as histosoil (Reddy and DeLaune 2008) with the high amount of organic matter in upper soil layers, pH of soil without litter is 4.8 and the amount of soil carbon is summarized in Tab. 7

Fig. 7: Experimental wetland in South Bohemia.

Tab. 7: Amount of total soil organic carbon (C%) at the wetland site in 2009 (Dušek, personal communication).

Depth (cm)	**C%**
0 - 30	14.65
30 - 50	28.51
60 - 80	18.72

4.2 Measurement instrumentation

4.2.1 SAMTOC

SAMTOC is an automated modified closed gasometrical (non-steady-state through-flow) system for measurements of CO_2 efflux from soil. The system was developed at Global Change Research Centre AS CR (former Institute of Systems Biology and Ecology AS CR) (Pavelka et al. 2004). It consisted of eight chambers (Fig. 8) and control units for chamber closing, infrared gas analyzer (Li-840, Li-Cor, Inc., USA) and a personal computer with a control software (INRIS, CR) and an additional hardware (Fig. 9). The chambers had a cylindrical shape of 30 cm in diameter and 20 cm in height and were inserted about 3 cm into the soil.

Fig. 8: Chamber for continuous measurement of soil CO_2 efflux in the spruce forest.

The system measured soil CO_2 efflux sequentially in all eight chambers in 10-minute intervals. Therefore, value of CO_2 efflux rate for each chamber was available every 80 minutes. After closing the chamber measurement started after 20s delay during which the air sample got from the chamber into the analyzer. The measurement took 200 seconds during which twenty values of CO_2 concentration were obtained. From these values, the control program calculated soil CO_2 efflux and saved it to file. Then the chamber opened. The chambers were closed for 4 min.

Furthermore, the system involved also eight thermometers PT-100 (Treston a.s., CR) which measured soil temperature in the depth of 1.5 cm (Pavelka et al. 2007) within each chamber simultaneously with soil CO_2 efflux.

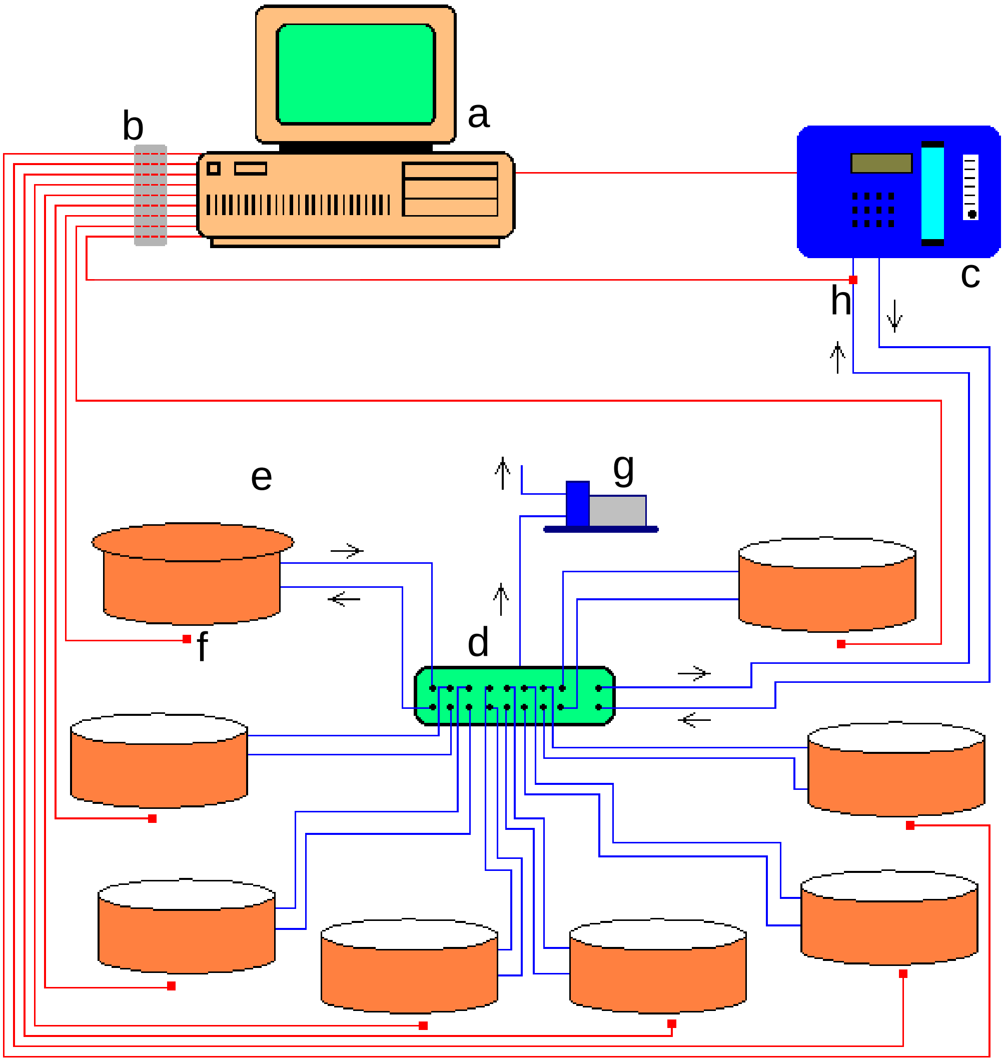

Fig. 9: Simplified scheme of the system for measuring of soil CO_2 efflux – SAMTOC: a - computer with control software, b - signal transducers, c - infrared gas analyzer, d - switching valves, e - set of soil chambers, f - set of sensors to measure soil temperature, g - pump for hose ventilation, h - a sensor for measuring temperature of air incoming to the analyzer (Pavelka 2009).

4.2.2 SAMTOL

SAMTOL is an automated closed gasometrical system similar to SAMTOC. The main difference is in the chambers. SAMTOL has three large chambers (Fig. 10, 11) with a diameter of 60 cm and height of 60 cm. The chambers were placed on circular bases with height of 15.5 cm and provided with neoprene gasket at its top. The bases were inserted about 5 cm into the soil. Chambers were put on the base in the evening and removed in the morning to minimize the impact of shading of the above-ground biomass. During manual measurement campaigns, chambers remained put on also during the daytime to determine the CO_2 efflux dependence on temperature. The system measured ecosystem CO_2 efflux sequentially in all three chambers in 10-minute intervals. Therefore, value of CO_2 efflux rate for each chamber was available every 30 minutes. After closing the chamber measurement started after 10s delay during which the air sample got from the chamber into the analyzer. The measurement took 420 seconds during which fourteen values of CO_2 concentration were obtained. From these values, the control program calculated soil CO_2 efflux and saved it to file. Then the chamber opened. The chambers were closed for 7 min.

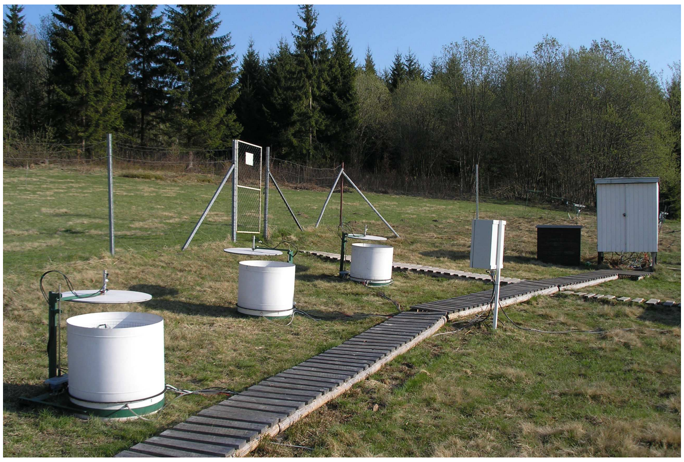

Fig. 10: Chambers for continuous measurements of ecosystem CO_2 efflux in the grassland.

Furthermore, the system involved also three thermometers PT-100 (Treston a.s., CR) which measured soil temperature in the depth of 1.5 cm within each chamber simultaneously with soil CO_2 efflux.

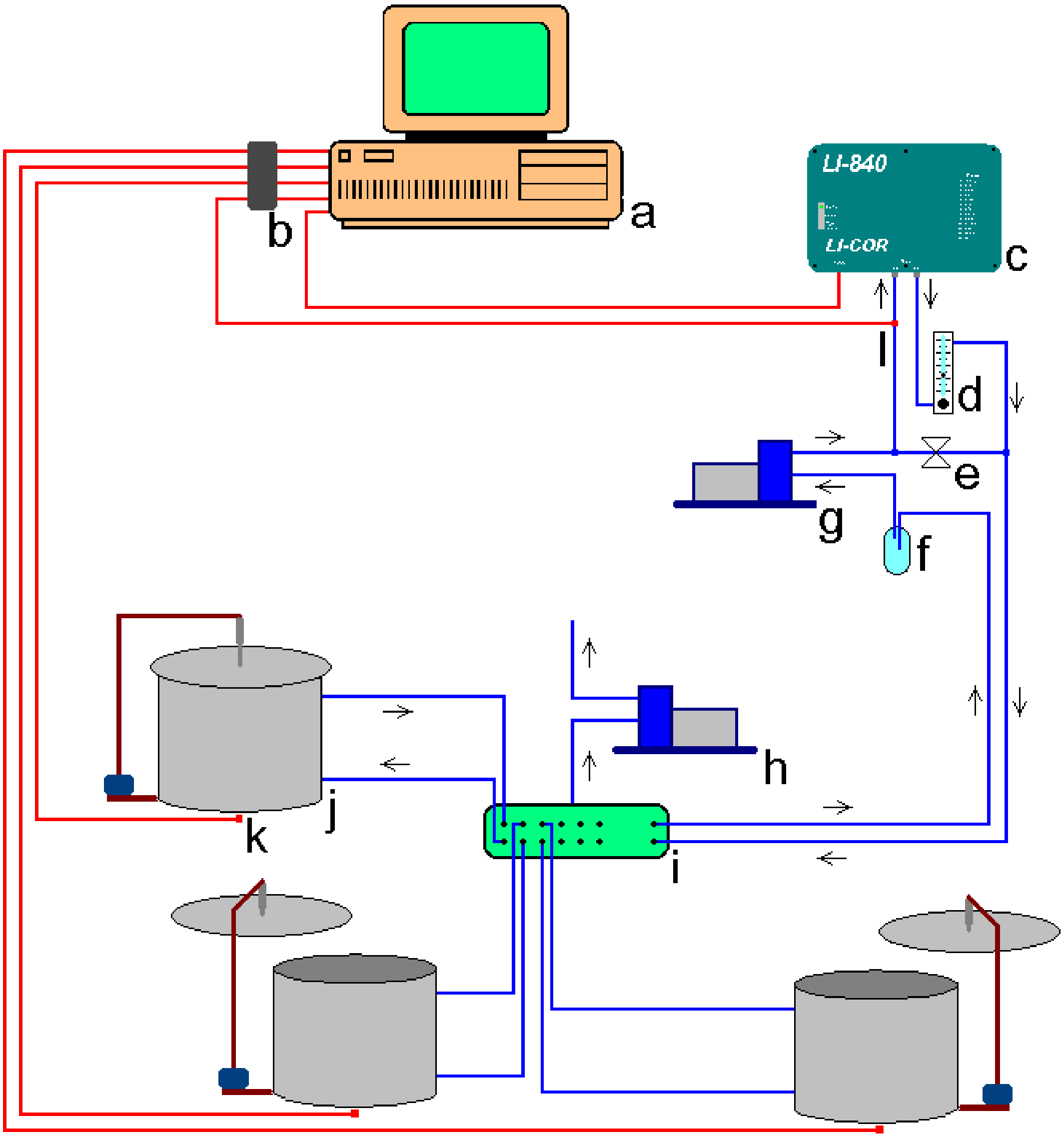

Fig. 11: Simplified scheme of the system for measuring of grassland CO_2 efflux – SAMTOL: a - computer with control software, b - signal transducers, c - infrared gas analyzer, d - flowmeter, e - throttle valve, f - water separator, g - pump, h - pump for hose ventilation, i - switching valves, j - a set of chambers, k - a set of sensors to measure soil temperature, l - a sensor for measuring temperature of air incoming to the analyzer (Pavelka 2009).

4.2.3 ACSEM

ACSEM is an automated closed gasometrical system for soil CO_2 efflux measurement (Fig. 12) developed at the Global Change Research Centre AS CR. It consisted of a chamber with automatic closing, the analyzer EGM-3 (PP-System, United Kingdom) and a battery. The chamber was controlled and data are stored in a data logger DL3000 (Delta-T Ltd, UK). Flow rate of CO_2 from the soil was measured at 15 min intervals.

Fig. 12: System ACSEM for continuous measurement of soil CO_2 efflux.

Soil temperature was measured near the chamber by the thermometer PT 1000 (HIT, Uherske Hradiste, CZ) usually in the profile 0.5, 3, 5 and 10 cm.

4.2.4 Portable system

The portable system is a system for manual measurements of CO_2 efflux (Fig. 13). It consisted of an infrared gas analyzer (Li6250, Li-Cor, USA), a control unit (Li6200, Li-Cor, USA) and soil a chamber developed at the Global Climate Change Centre AS CR. The chamber was made of white-painted PVC, it has a cylindrical shape, height 17 cm and diameter 20 cm. The chamber was applied on a set of collars. The collars were installed (inserted about 3 cm deep into the soil) at each measurement position to avoid the disturbance of the soil and to provide a

Fig. 13: Portable system Li-6200 for manual measurement of CO_2 efflux.

good tightness of the chamber during measurements. The collars were made of PVC with a diameter of 19.7 cm and a height of 8.5 cm.

Measurements began at least one day after the installation of the collars to avoid the influence of soil disturbance caused by installation. The measurement started with placing of the chamber on the collar. Then six measurements of CO_2 efflux from the soil were obtained. After the measurement, the chamber was removed and the procedure was repeated on next position.

The CO_2 analyzer calculated CO_2 efflux rate (R) according to the equation (LI-COR 1990):

$$R = \frac{\rho \cdot v \cdot \frac{\partial c_1}{\partial c_2} + c_1 u_1 - c_2 u_2}{s} \qquad [1]$$

where s is the measured area (m^2), ρ the air density (mol m^{-3}), v the total system volume, u_1 and u_2 are the velocity of air flow from the chamber and back into the chamber (mol m^{-3}), c_1 and c_2 are the CO_2 concentration (mol mol^{-1}) (see Fig. 14), t is time (s).

The volume of the system consisted of the volume of Li-6200, the volume of tubing, the volume of the chamber and the volume of the collar. Before measurement, the device saved the approximate value of the total volume of the system (with an approximate volume of rings). During the measurement campaigns, the depth of collars was measured and the total system volume for each ring was recalculated. Measured CO_2 efflux was then recalculated according to the equation :

$$R_2 = \frac{R_1}{v_1} \cdot v_2 \qquad [2]$$

where R_2 is a recalculated value of the soil CO_2 efflux, R_1 is the initial value of respiration (median of six measurements per cycle), v_1 is the approximate total volume of the system and v_2 is the exact total volume of the system for each position.

During measurement of thy e CO_2 efflux there was also manually measured soil temperature at the depth of 1.5 cm using a penetration thermometer (Roth, Germany). The manual measurements of CO_2 efflux were carried out at all above mentioned sites and during the drought experiment.

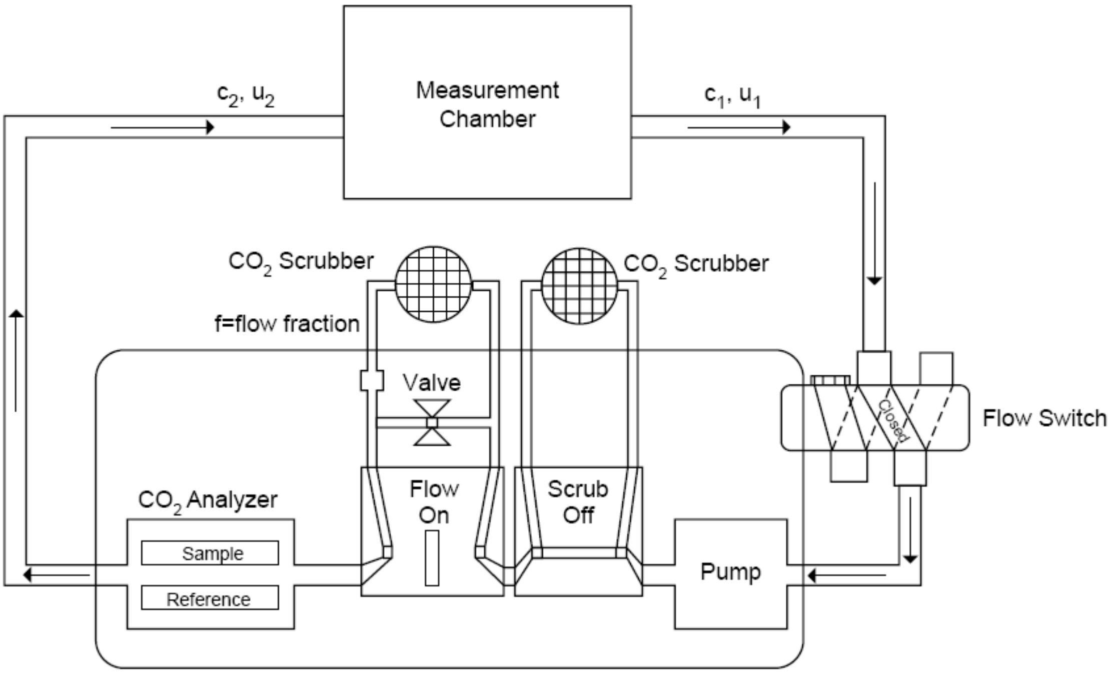

Fig. 14: Scheme of air flow in the analyzer Li-6200 (LI-COR 1990).

5 Individual experiments' design, results and discussion

5.1 Temporal dynamics of CO_2 efflux

5.1.1 Experiment design and data analyses

Long-term continuous measurements of CO_2 efflux from the spruce forest soil and the grassland ecosystem (soil and above-ground biomass) were done using the systems SAMTOC (see chapter 4.2.1) and SAMTOL (see chapter 4.2.2), respectively, during the growing seasons in 2009 – 2012 (Tab. 8).

Tab. 8: Overview of periods when long-term continuous measurements of CO_2 efflux were performed in spruce forest and grassland.

	2009	**2010**	**2011**	**2012**
Spruce forest	29.4. – 12.10.	28.4. – 25.10.	28.4. – 8.11.	1.5. – 9.11.
Grassland	22.4. – 2.11.	27.4. – 1.11.	1.5. – 8.11.	24.4. – 11.11.

Soil or ecosystem CO_2 efflux (R_S) was plotted against soil temperature (T_S) and this was fit by an exponential regression curve with the regression equation:

$$R_S = \beta \cdot e^{\alpha \cdot T_S} \qquad [3]$$

where α and β are the regression coefficients.

Q_{10} (the proportional change in CO_2 efflux from 10 °C increase in temperature) was calculated (Lloyd and Taylor 1994) using equation:

$$Q_{10} = e^{10 \cdot \alpha} \qquad [4]$$

where α is the regression coefficient obtained from the equation 3. Q_{10} was calculated for each chamber for several short periods when soil CO_2 efflux was not disturbed by external factors (e.g. rainfall).

Then, CO_2 efflux was normalized for the temperature of 10 °C (R_{10}) according to equation (van´t Hoff 1898):

$$R_{10} = \frac{R_S}{Q_{10}^{\frac{T_S - 10}{10}}} \qquad [5]$$

where R_S is the measured CO_2 efflux rate at temperature of soil (T_S). R_{10} was determined for each measurement. Mean R_{10} from all (eight in the forest, three in the grassland) chambers was calculated for each cycle.

Missing temperature data were filled on the base of temperature measured near the measurement positions. Missing values of R_{10} were filled on the base of values R_{10} before and after the gap. Missing data of CO_2 efflux (R) were filled on the base of estimated R_{10}, a value Q_{10} (calculated for the period in which the gap occurred) and soil temperature according to equation

$$R = \frac{R_{10}}{Q_{10}^{\frac{10-T_S}{10}}} \quad . \qquad [6]$$

Daily means of soil CO_2 efflux, R_{10} and temperature were performed for the whole 24-hour periods for the spruce forest. For the grassland, nighttime means were calculated for periods from 21pm to 3am.

Soil moisture was measured by ThetaProbe (Delta-T Devices, UK) installed in the depth of 5 cm in the spruce forest and in 15 cm in the grassland in the five-minute intervals. Precipitations in the spruce forest were measured by the rain gauge MetOne 386 (Met One Instruments, Inc., Oregon, USA) installed on a meteorological tower at a height of 20 m. Precipitations were recorded continuously in individual pulses corresponding to total 0.14 mm. Daily precipitation was calculated from measured values. Precipitations in the grassland were measured by the rain gauge HoBo (AMET, CR) installed on a meteorological tower at a height of 1 m. Precipitations were recorded continuously in individual pulses corresponding to total 0.385 mm. Daily precipitation was calculated from measured values.

5.1.2 Results

Spruce forest

We studied growing seasons in years 2009 – 2012 when continuous measurements of soil CO_2 efflux and other characteristics were done. The four periods of measurements were not of the same length (Tab. 7). The period when soil CO_2 efflux was measured in all four years ranged from 1 May to 12 October. The climatic and soil parameters for the different periods of four seasons are summarized in Tab. 9 and 10. From now on, I will describe data for the experimental period from 1 May to 12 October.

The mean soil temperature in 1.5 cm for the experimental period ranged between 10.9 and 12.6 °C. The warmest season was in 2012, the coldest in 2010 (Fig. 15). The lowest mean daily soil temperatures were about 5 °C and occurred at the beginning and the end of the experimental seasons. The maximum mean daily soil temperatures occurred in July and August and ranged from 15 to 20 °C (Fig. 16, 17).

The season with the highest precipitation was in 2010. The total precipitation amounted about two fold than in other years. In May there were 26 rainy days, in September during two following days fell 197 mm.

The soil moisture in the depth of 5 cm was the highest in the rainiest year 2010 and the lowest in 2012, which corresponds with the seasonal sums of precipitations (Fig. 15). The data for 2009 are not available due to malfunction of the sensor. The soil moisture steeply increased after rain and then gradually decreased till the next rain (Fig. 16, 17).

Soil CO_2 efflux followed changes in temperature. The maxima in daily mean soil CO_2 efflux also occurred in summer and they ranged between 5 and 7 µmol $m^{-2}s^{-1}$. Soil CO_2 efflux was positively correlated to soil temperature, however, the mean value of regression coefficient calculated for the whole measurement periods was 0.48 (±0.17). That indicates that there was an influence of another factor. To exclude influence of temperature, soil CO_2 efflux was normalized to 10 °C. R_{10} values ranged between 1.5 and 6.0 µmol CO_2 $m^{-2}s^{-1}$ with maxima in summer months. Soil CO_2 efflux often responded sensitively to rain events. The rain was followed by the fast increase in R_{10} which afterwards gradually decreased. This response was the most remarkable when the rain occurred after a few days with no precipitation (e.g. 19 June 2009, 17 September 2009, 26 September 2010, 7 October 2011, 1 June 2012, 16 October 2012). On the contrary, if there were more rainy days in a row or when the rain occurred when soil moisture was high, there was no response of R_{10} (e.g. the first half of May 2010, the first half of June 2012)

As mentioned above, the value of regression coefficient of the exponential relationship between soil CO_2 efflux and soil temperature was low when it was calculated for data of the entire season. Therefore, for calculation of coefficient characterizing soil CO_2 efflux sensitivity to temperature, the seasons were divided into shorter periods.

The choice of periods with different relationship of soil CO_2 efflux and temperature can cause under- or overestimation of the temperature sensitivity of soil CO_2 efflux on temperature (Fig. 18). For example, rain on 6 July 2010 increased soil CO_2 efflux but soil temperature decreased after the rain. If the temperature sensitivity of soil CO_2 efflux was determined for the whole period, there would be underestimation of the sensitivity in both periods and in this case the sensitivity was even negative (Fig 18-A). The rain on 30 June 2011 also increased soil CO_2 efflux, but in this case the range of soil temperature before and after the rain were similar. Using Q_{10} calculated from all data from the whole season would cause underestimation of temperature sensitivity of soil CO_2 efflux in the period after the rain and overestimation of that in the period before the rain (Fig 18-B). In May and June 2012, there would be overestimation of temperature sensitivity in both clearly distinguished periods if calculating Q_{10} from the entire data set (Fig 18-C).

Tab. 9: Soil and climatic characteristics at the spruce forest site for the entire seasons when the measurements of soil CO_2 efflux were carried out (29 April – 12 October 2009, 28 April – 25 October 2010, 28 April. – 8 November 2011, 1 May – 9 November. 2012).

	2009	**2010**	**2011**	**2012**
Mean soil temperature (°C)	11.6	10.3	10.7	11.6
Total precipitation (mm)	486	1034	665	603
Mean soil moisture (%)	-	25.1	22.3	20.6
Number of rainy days	65	91	75	78
Sums of released CO_2 ($t\ ha^{-2}$)	26.3	27.3	23.8	24.3
Mean daily Q_{10}	1.48	1.59	1.51	1.44
Mean daily R_{10} ($\mu molCO_2\ m^{-2}s^{-1}$)	4.00	3.93	3.16	3.11

Tab. 10: Soil and climatic characteristics at the spruce forest site for the experimental period 1 May – 12 October in 2009, 2010, 2011 and 2012.

	2009	**2010**	**2011**	**2012**
Mean soil temperature (°C)	11.7	10.9	11.7	12.6
Total precipitation (mm)	483	1021	652.2	487
Mean soil moisture (%)	-	25.2	22.5	20.9
Number of rainy days	64	87	69	64
Sums of released CO_2 ($t\ ha^{-2}$)	26.1	26.2	21.9	22.0
Mean daily Q_{10}	1.48	1.59	1.47	1.39
Mean daily R_{10} ($\mu molCO_2\ m^{-2}s^{-1}$)	4.02	4.09	3.37	3.20

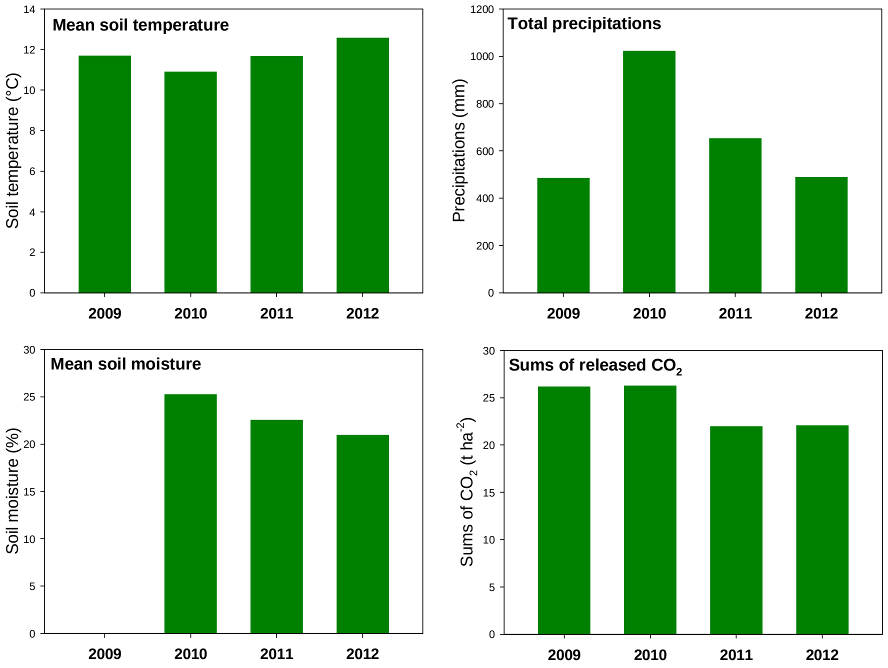

Fig. 15: Mean soil temperature, mean soil moisture, total precipitations and sums of released CO_2 from soil for the period from 1 May – 12 October in 2009, 2010, 2011 and 2012 at the spruce forest ecosystem.

The amount of CO_2 released from soil during the experimental in 2009 and 2010 was very similar and amounted by about 4 t ha^{-2} (19 %) more than in 2011 and 2012 (Tab. 10). In 2010, there was a high amount of CO_2 released from soil from July to September in spite of that the soil temperature in August and September was the lowest from all years. There was, however, the high amount of precipitation in this period. In 2011 and 2012, the seasonal sum of CO_2 released from soil was similar despite higher soil temperature in 2012 (Fig. 19). Higher soil temperature could be caused by a damage of the forest during the previous winter when many trees in the stand fell down. That caused falling of trees also near the measurement positions and exposing of some positions to higher solar radiation. This could also result in more intensive drying of the soil on these positions. That together with the lower amount of precipitation could result in reduction of the amount of CO_2 released from the soil compared to the CO_2 amount expected on the base of higher soil temperature.

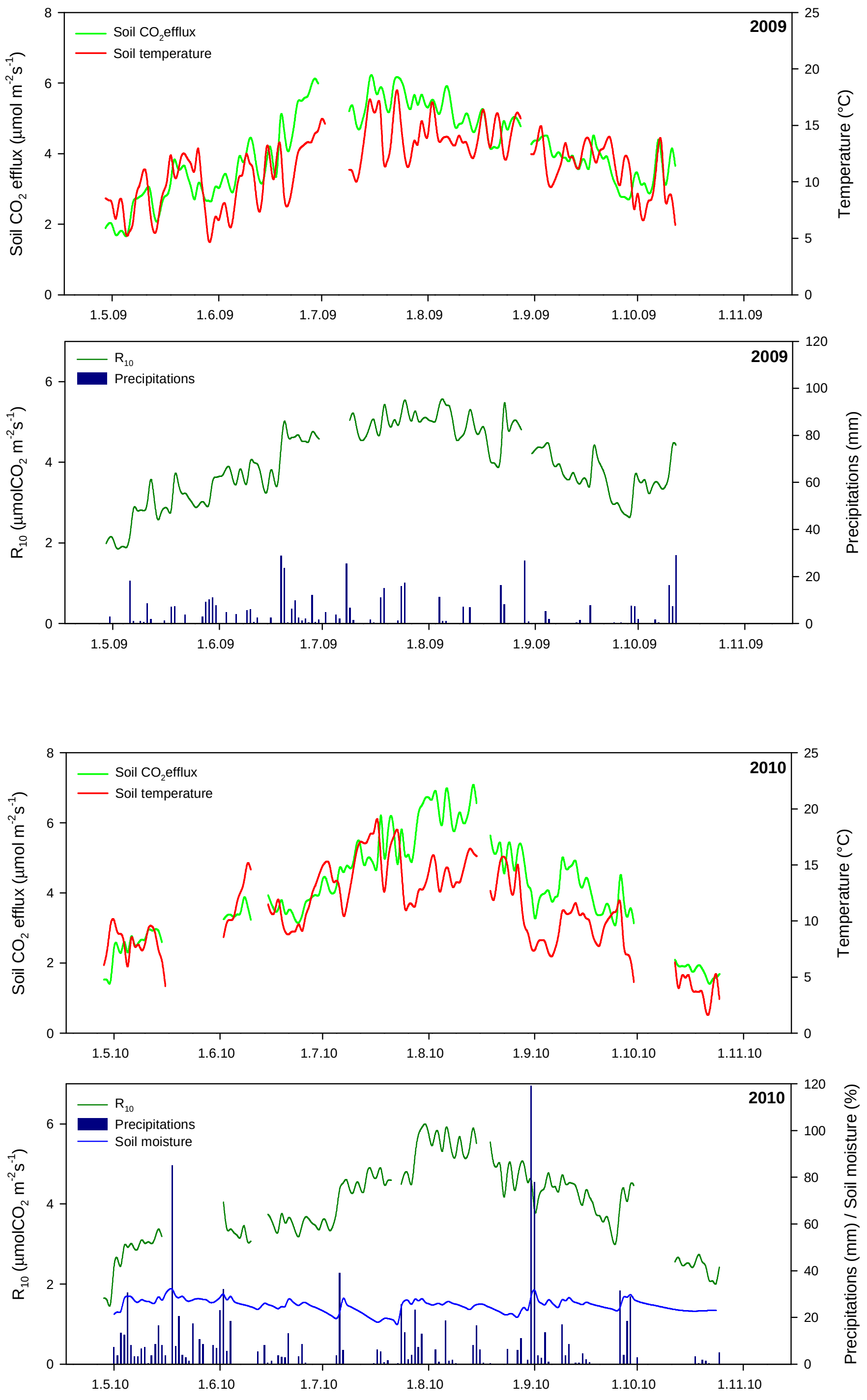

Fig. 16: Seasonal courses of daily mean soil temperature, soil CO_2 efflux, R_{10} and soil moisture, and daily sums of precipitation at the spruce forest ecosystem in the growing seasons 2009 and 2010.

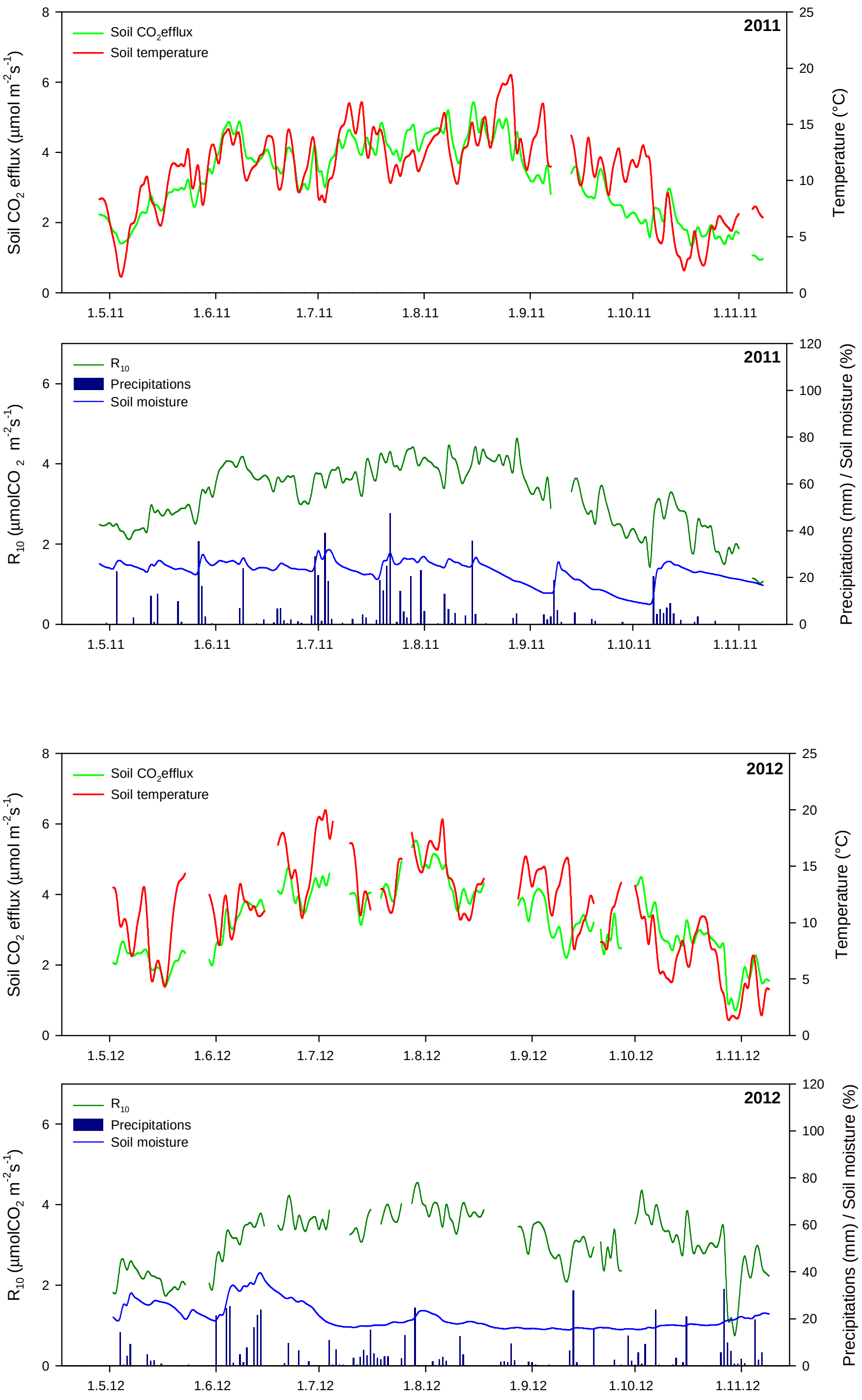

Fig. 17: Seasonal courses of daily mean soil temperature, soil CO$_2$ efflux, R$_{10}$ and soil moisture, and daily sums of precipitation at the spruce forest ecosystem in the growing seasons 2011 and 2012.

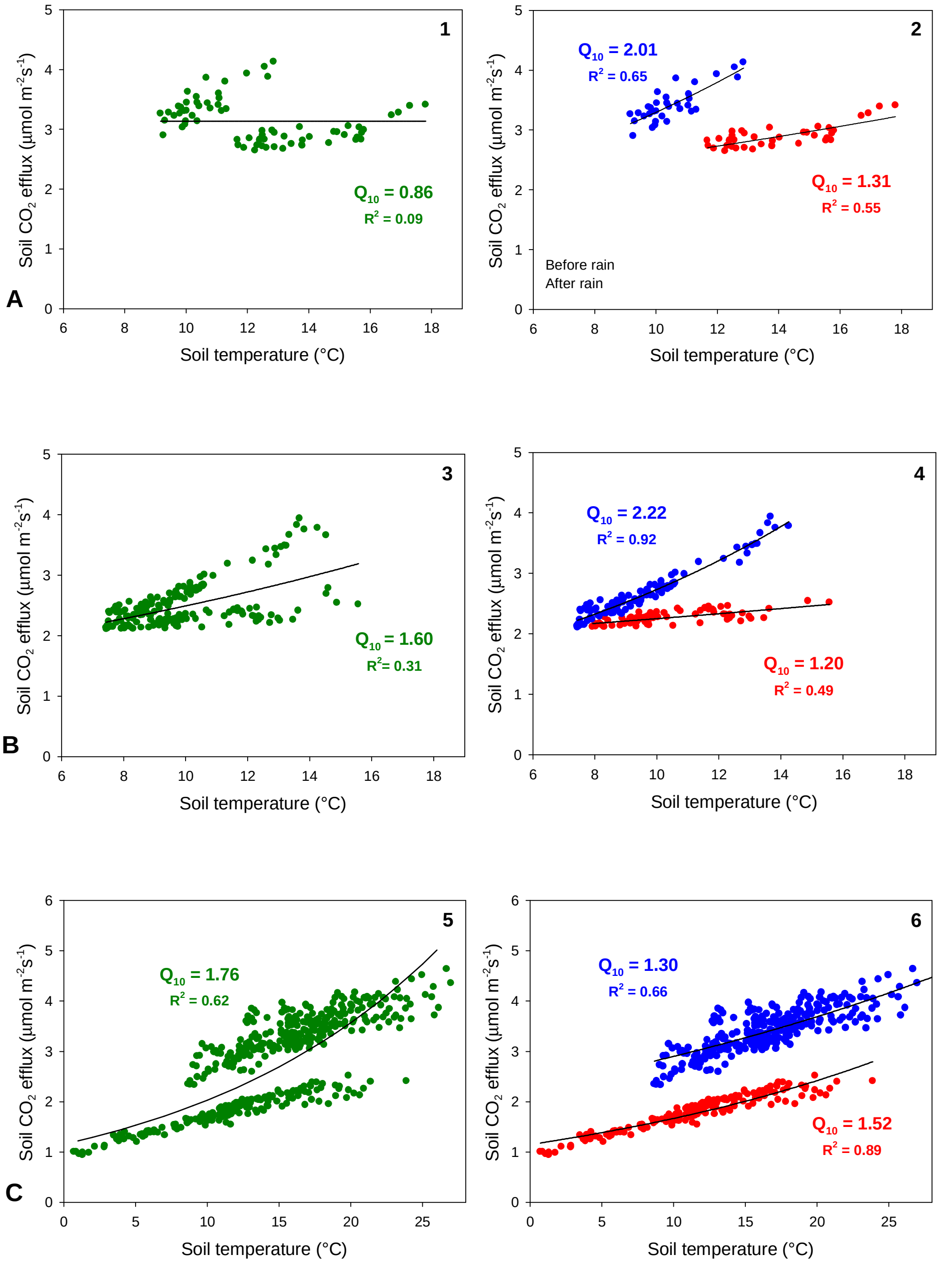

Fig. 18: Soil CO_2 efflux response to soil temperature in spruce forest in periods 25 June – 5 July 2011 (A), 3 July – 8 July 2010 (B) and 17 May – 5 July 2012 (C). Green plots (1, 3 and 5) show regression curves and Q_{10} values obtained for the whole datasets, blue and red plots (2, 4 and 6) has two regression curves and two Q_{10} values for two clearly distinguished subsets.

In 2009, the seasonal sum of released soil CO_2 was higher than in 2011 and 2012 although total precipitation and mean soil temperature were not the highest. Soil CO_2 efflux in 2009 was higher than in 2011 and 2012 during the entire experimental season (Fig. 15).

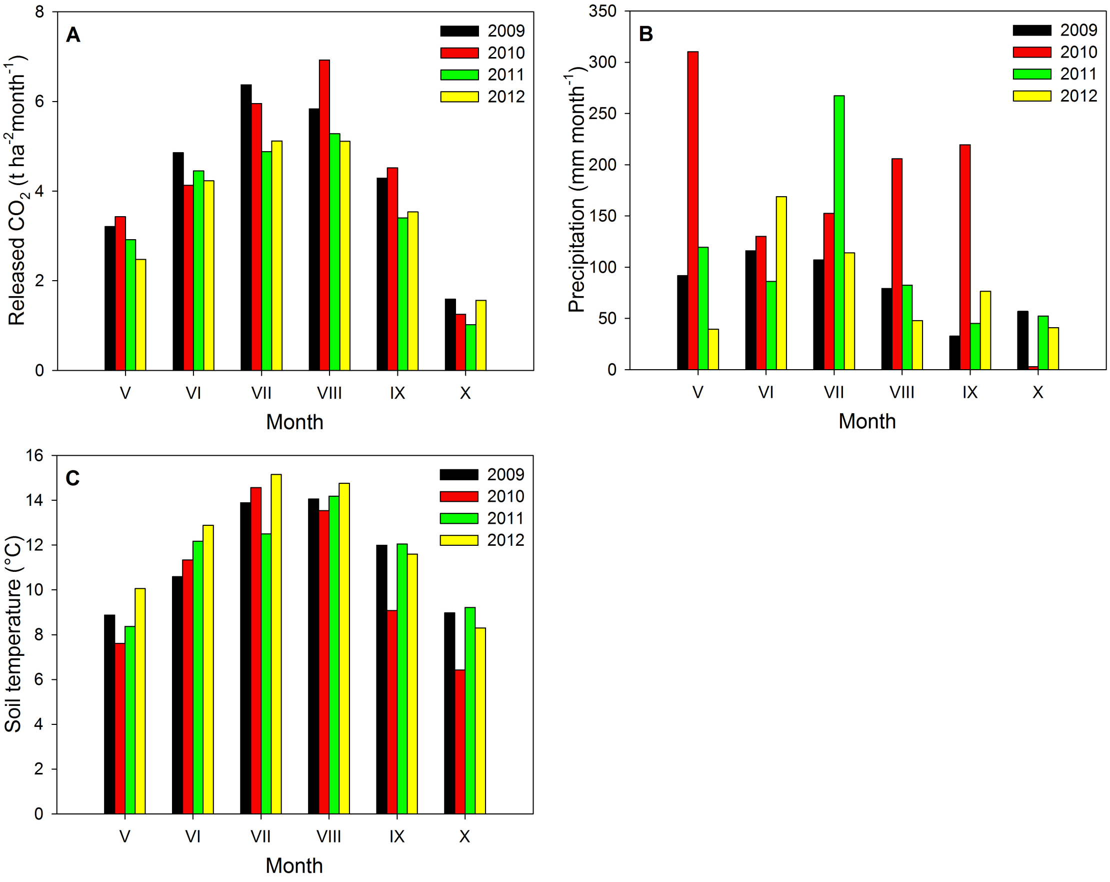

Fig. 19: Monthly sums of released CO_2 from soil (A), monthly sums of precipitations (B) and monthly mean soil temperature (C) at the spruce forest ecosystem in the period from 1 May to 12 October in 2009, 2010, 2011 and 2012.

Grassland

We studied growing seasons in years 2009 – 2012 when continuous measurements of ecosystem CO_2 efflux (soil and aboveground biomass) and other characteristics were provided during nighttime. The four periods of measurements were not of the same length (Tab. 8). The period when there were measurements in all four years was from 1 May to 31 October. The climatic parameters for the different periods of the four seasons are summarized in Tab. 11 and 12. From now on, I will describe data for the experimental period from 1 May to 31 October.

Tab. 11: Soil and climatic characteristics of the grassland ecosystem for the entire seasons when the measurements of ecosystem CO_2 efflux were carried out (22 April – 2 November 2009, 27 April – 1 November 2011, 1 May – 8 November 2011, 24 April – 11 November 2012).

	2009	2010	2011	2012
Mean soil temperature (°C)	12.1	11.8	12.8	12.6
Total precipitation (mm)	612.0	1 005	678	674
Mean soil moisture (%)	-	44	44	43
Number of rainy days	75	106	84	88
Suma CO_2 (t ha^{-2})	6.5	4.2	3.6	4.2
Mean Q_{10}	3.3	3.7	3.7	3.2
Mean R_{10} (μmolCO_2 $m^{-2}s^{-1}$)	2.5	2.4	1.9	2.2

Tab. 12: Soil and climatic characteristics of the grassland ecosystem for the experimental period 1 May – 31 October in 2009, 2010, 2011 and 2012.

	2009	2010	2011	2012
Mean soil temperature (°C)	12.4	11.8	13.0	13.2
Mean air temperature (°C)	10.7	9.6	8.9	11.0
Total precipitation (mm)	609	1 005	678	631
Mean soil moisture (%)	-	44	44	43
Number of rainy days	74	105	83	82
Suma CO_2 (t ha^{-2})	6.3	4.1	3.4	3.9
Mean Q_{10}	3.4	3.7	3.5	3.0
Mean R_{10} (μmolCO_2 $m^{-2}s^{-1}$)	2.5	2.4	1.9	2.2

The mean soil temperature in 1.5 cm for this period ranged between 11.8 and 13.2 °C. The warmest season was in 2012, the coldest in 2010 (Fig. 20). Also at this site it was observed that the lowest mean daily soil temperatures were about 5 to 10 °C and occurred at the beginning and the end of the experimental seasons. The maximum mean daily soil temperatures occurred in July and August and ranged from 15 to 20 °C. Soil temperature was the lowest at the beginning and at the end of the investigated seasons. The maxima about 18 and 20 °C occurred in July and August (Fig. 21, 22).

The season with the highest precipitation was in 2010. The total precipitation in this year amounted about two fold than in other years. The most precipitation occurred in May and September (over 300 mm in both months), when in May there were 26 rainy days and in September during two following days fell 197 mm.

Ecosystem CO_2 efflux followed changes in temperature. The maxima occurred in the second half of June and in July before cutting grass, and they ranged between 6 and 8 µmol $m^{-2}s^{-1}$. The grassland CO_2 efflux was positively correlated to soil temperature and the mean value of regression coefficient calculated for the whole measurement periods was significantly higher than in the forest soil and was equal 0.83 (±0.05). That indicates that CO_2 efflux mostly depended on changes in temperature.

Normalized CO_2 efflux (R_{10}) amounted in the range between 1.0 and 3.6 µmol CO_2 $m^{-2}s^{-1}$ and its maxima occurred in the first half of the season. After the mowing there was a steep decrease of respiration activity due to the removal of the respiring above-ground biomass. In the second half of the season, the respiration activity did not reach the values as before cutting. The decrease amounted 17.4, 18.6, 39.3 and 31.7 % of CO_2 efflux before cutting in 2009, 2010, 2011 and 2012, respectively. After the decrease, R_{10} course had a gradual increasing trend. That was most remarkable especially in 2010 when more rainy days occurred after clipping in comparison with 2009 and 2012. Any immediate increase in respiration activity was not observed as a response to rain events as was in the forest soil. On the contrary, in several cases decrease of R_{10} was observed when it was raining (e.g. 18 June 2009, 9 October 2009, 30 August 2010, 29 June 2011). However, in autumn 2011 there was a rather long period with very little precipitation and R_{10} was temporary decreasing.

The amount of CO_2 released from the grassland during period from 1 May to 31 October was 6.5, 4.2, 3.6 and 4.2 t ha^{-2}, in 2009, 2010, 2011 and 2012, respectively. The lowest differences between individual years were in May, June and October. On the contrary, the biggest difference occurred in July (Fig. 23).

In 2009, ecosystem CO_2 efflux became the highest since July despite the precipitation conditions were similar to those in 2012. In 2011 the sum of released CO_2 for July was the lowest from all four years. In this year, grass cutting was done in the earliest date (Tab. 3). Especially comparing to 2009 and 2012, there was difference of 12 and 17 days, respectively. There was also the high amount of precipitation and lower soil and air temperature in June 2011, which could cause low respiration activity of the grassland.

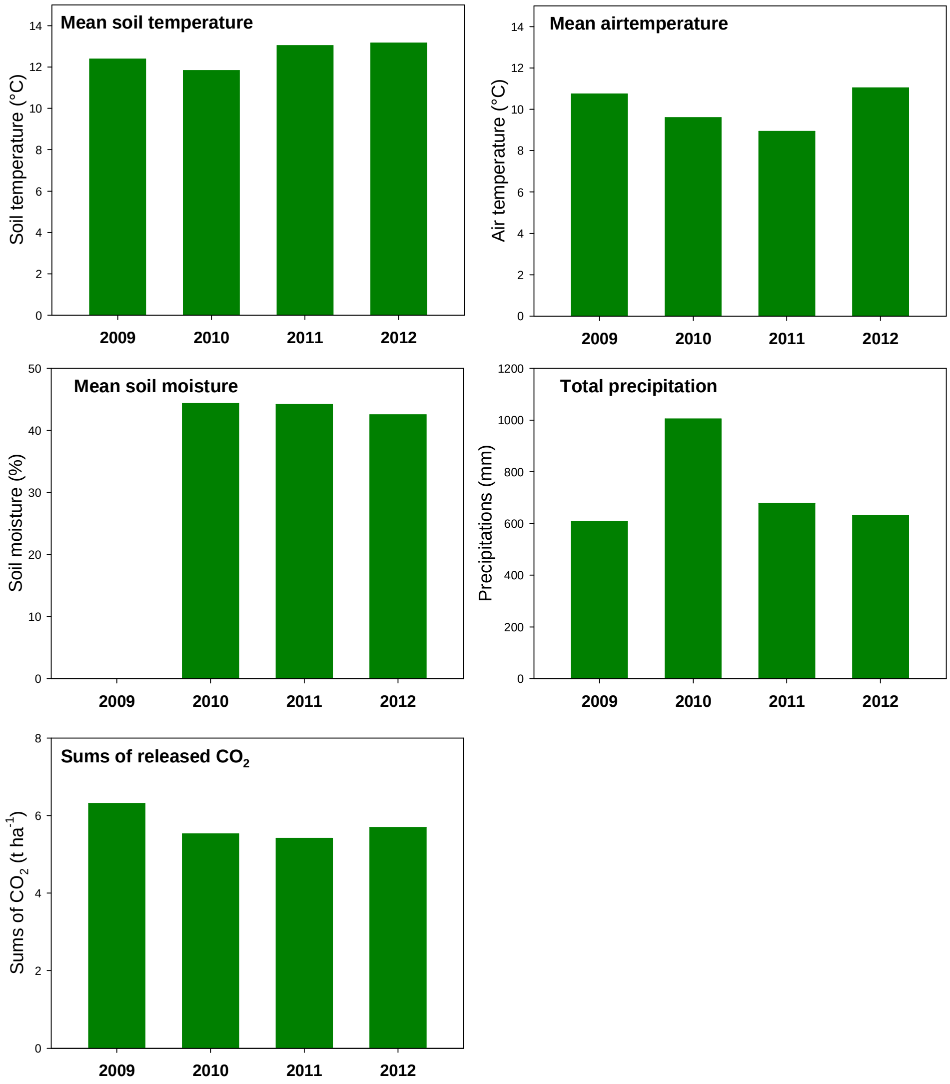

Fig. 20: Mean soil and air temperature, soil moisture, total precipitations and nighttime sums of released CO_2 from soil, mean value of R_{10} for the period from 1 May – 31 October in 2009, 2010, 2011 and 2012 at the grassland ecosystem.

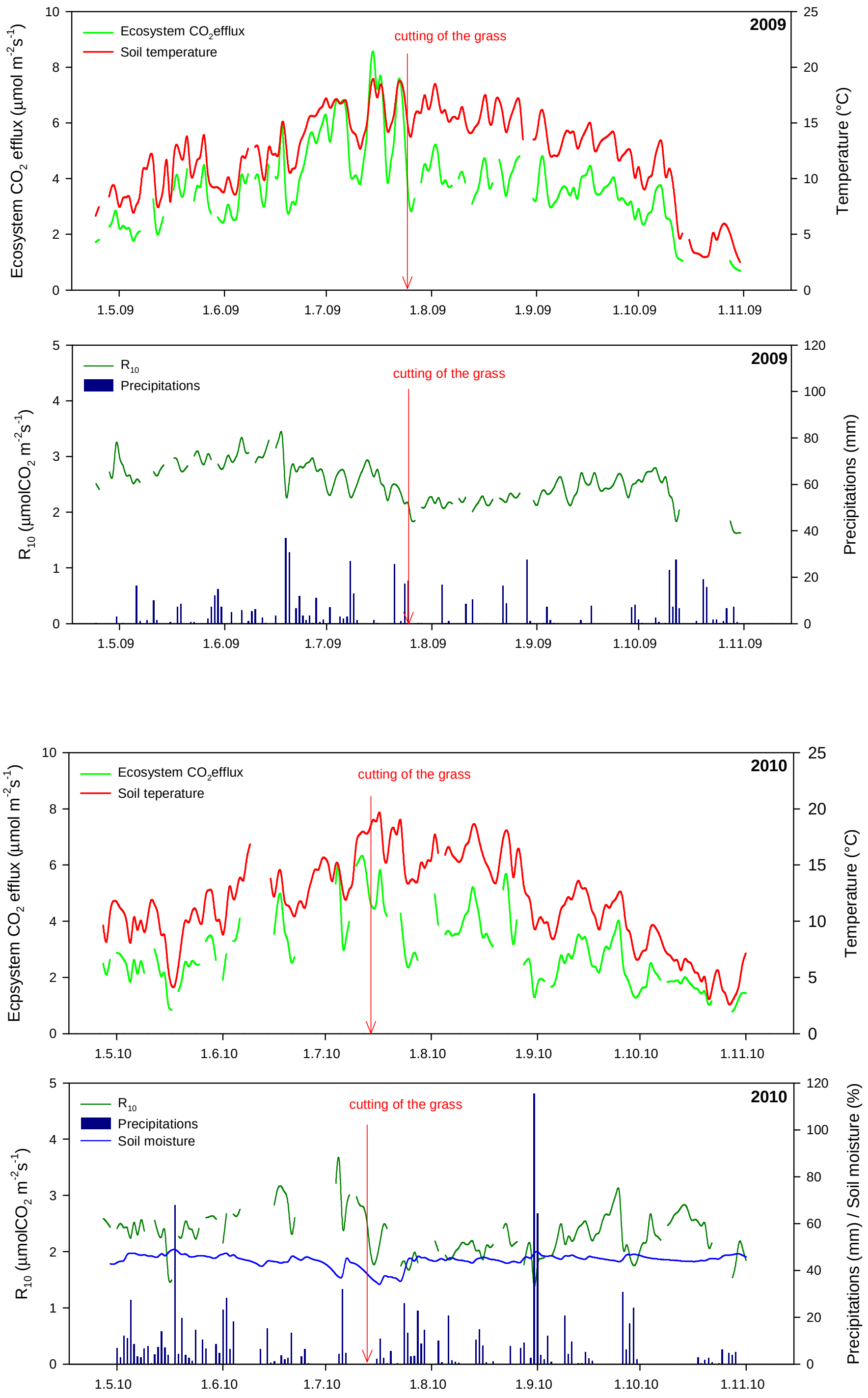

Fig. 21: Seasonal courses of nighttime mean soil temperature, ecosystem CO$_2$ efflux, R$_{10}$ and soil moisture, and daily sums of precipitation at the grassland ecosystem in the growing seasons 2009 and 2010.

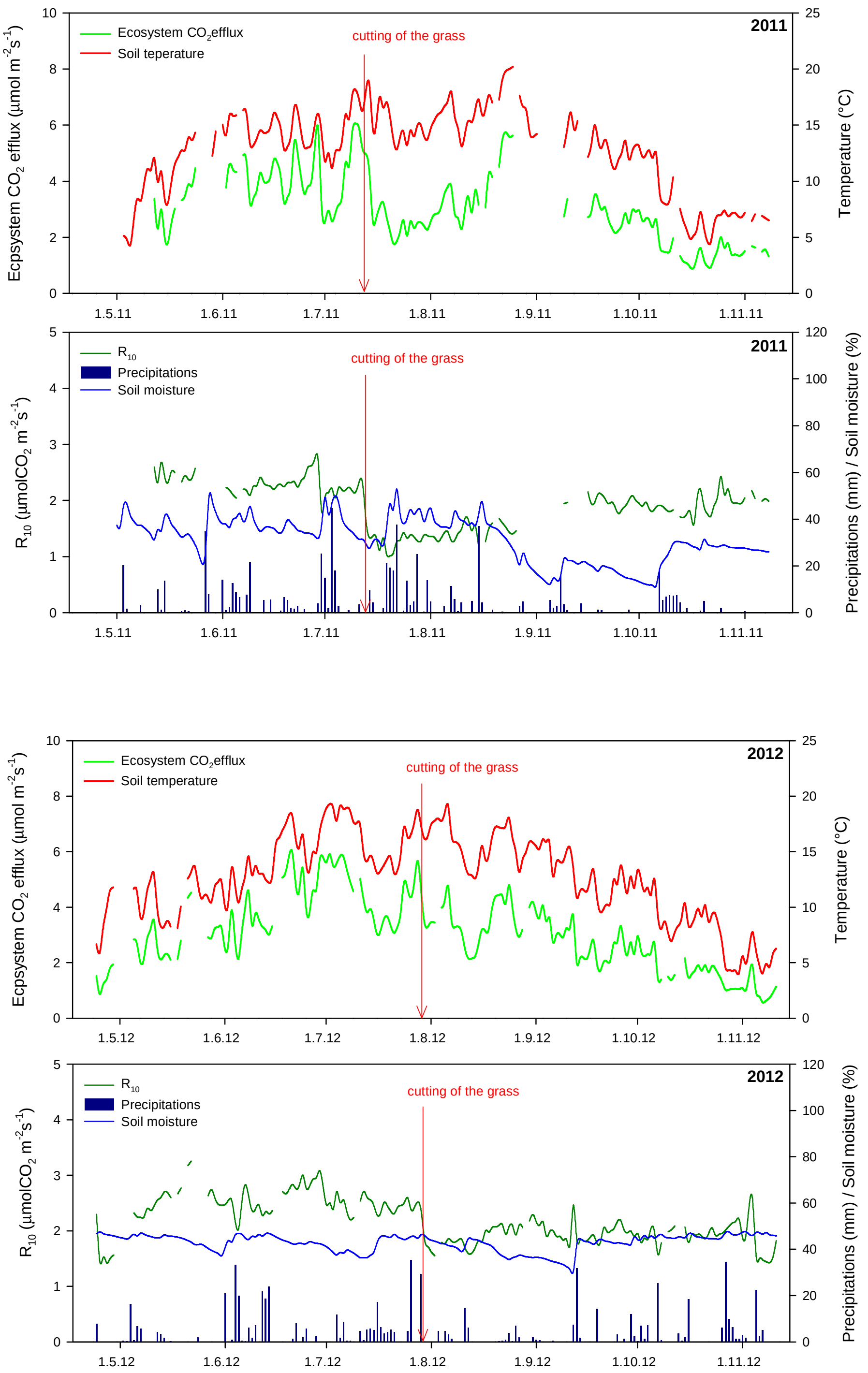

Fig. 22: Seasonal courses of nighttime mean soil temperature, ecosystem CO_2 efflux, R_{10} and soil moisture, and daily sums of precipitation at the grassland ecosystem in the growing seasons 2011 and 2012.

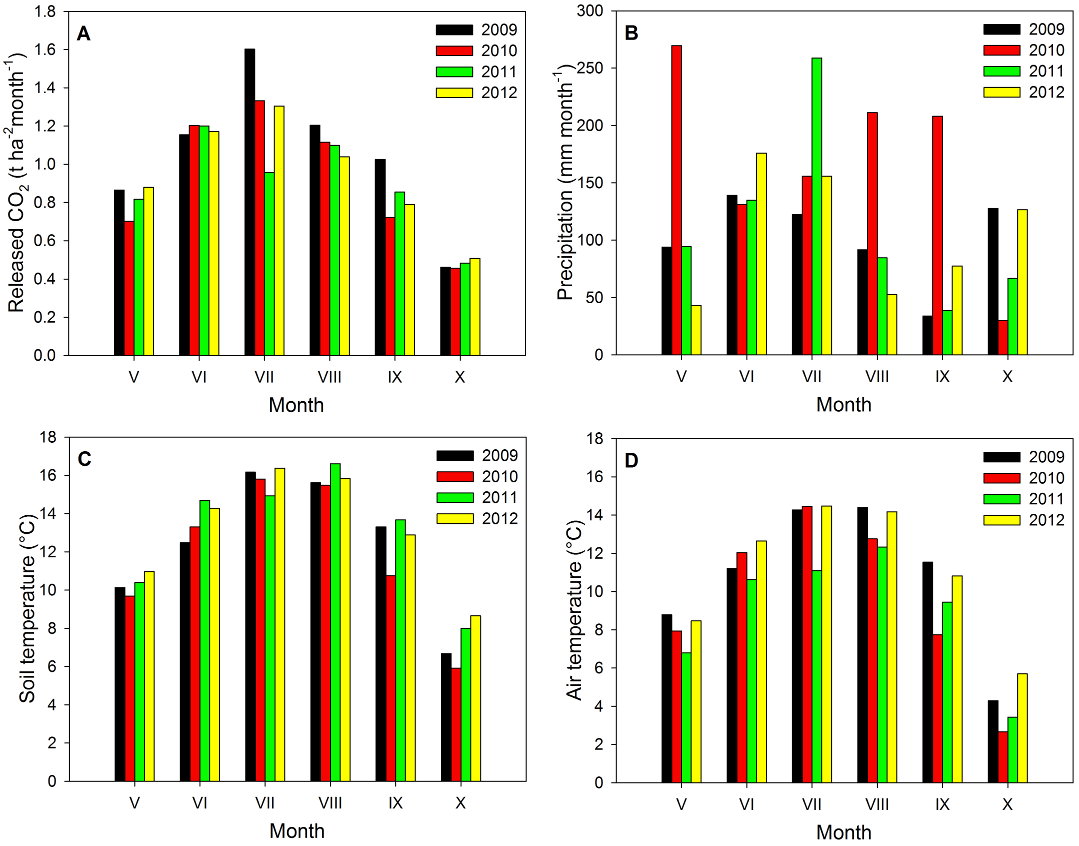

Fig. 23: Monthly nighttime sums of released CO_2 from soil (A) and monthly sums of precipitations (B), and monthly nighttime mean soil (C) and air (D) temperature at the grassland ecosystem in the period from 1 May to 31 October in 2009, 2010, 2011 and 2012.

5.1.3 Discussion

Spruce forest

Continuous measurements of soil CO_2 efflux during four growing seasons from 2009 to 2012 were analysed. Soil CO_2 efflux followed the pattern of changes in soil temperature as temperature is the driving factor of soil CO_2 efflux in many ecosystems. The sensitivity of soil CO_2 efflux on soil temperature is mostly characterised by parameter Q_{10} (proportional change in CO_2 efflux when temperature changes by 10 °C) or Arrhenius equation (Davidson et al. 2006a, Lloyd and Taylor 1994). For our analyses, parameter Q_{10} was used. This value can vary with soil moisture (Jassal et al. 2008, Qi et al. 2002) when under high or low moisture conditions, the temperature dependence of soil CO_2 efflux decreases (Xu et al. 2001, Vicca et al., 2009). Therefore, I divided the data set into several periods with similar soil moisture condition to estimate correctly the value Q_{10} and to normalize soil CO_2 efflux to 10 °C (R_{10}). The mean Q_{10} value for the forest stand was about 1.5 which is lower than in other studies in which Q_{10} reached mostly values between 2 and 4.7 (Morén and Lindroth 2000, Saiz et al. 2007). Moreover, other studies (e.g. Khomik et al. 2006, Jassal et al. 2008, Wang et al. 2010) had estimated one value of Q_{10} for the entire season, while I divided the season into shorter periods with similar soil water content conditions. Qi et al. (2002) and McCulley et al. (2007) observed an increase in the value of Q_{10} with soil moisture. According to a study by Jassal et al. (2008), however, this value can decrease under conditions of high soil water content. Furthermore, when soil moisture is too low, the relationship between soil CO_2 efflux and temperature may even decouple (Yuste et al. 2003). It can be therefore considered that estimating just single values of Q_{10} for the entire season can hide these effects.

It can be difficult to compare Q_{10} between studies as they are related to different depth of measured temperature. A few studies have described a rise in Q_{10} values with increasing depth of temperature measurement (Khomik et al. 2006, Graf et al. 2008), as the amplitude of temperature dynamics decreases in deeper soil layers. In our study, the temperature measurement depth of 1.5 cm was established on the basis of a study by Pavelka et al. (2007) in which the closest relationship between soil CO_2 efflux and temperature for this site occurred at this depth. Determination of the appropriate depth for the soil temperature measuring point depends, however, upon individual site characteristics and is crucially important.

R_{10} showed a seasonal trend (Fig. 16 and 17). It increased at the beginning of the experimental season until reaching its maximum at the end of July and in August. Then it decreased in the autumn. A similar trend with its maximum occurring in summer months was observed for example for a pine stand in a study by Law et al. (1999), and those authors attributed that trend to fine root growth. Similarly, Yan et al. (2011) determined changes in fine root biomass to be one factor influencing seasonal variation of soil CO_2 efflux in young poplar stands. Epron et al. (2001) observed a seasonal course of temperature-normalized rhizospheric respiration in young beech forest with its maximum in July when fine root growth was greatest. Fine root production was observed to be greatest during the warmest months of the growing season also in other studies (e.g. Majdi 2001, Mainiero et al. 2010). It can be, therefore, assumed that fine roots also influence seasonal course of soil CO_2 efflux at our spruce forest site.

It can be assumed that soil CO_2 efflux also responses to a current photosynthesis rate (GPP) and consequent allocation of assimilates to roots (Hogberg et al. 2001) and time lag between photosynthesis and soil CO_2 efflux can reach from hours to days (Jassal et al. 2012, Martin et al. 2012). So it can be said that during the summer, soil CO_2 efflux is enhanced not only by higher soil temperature but also by high plant photosynthetic activity (Yuste et al. 2004).

R_{10} mostly sharply increased after rain events and then it gradually decreased. When the soil is dry, the rainfall increases CO_2 efflux in different mechanisms. The first is water displacement of soil pore space gas with high CO_2 concentration. This process is very fast, and stored CO_2 from past microbial and plant respiration is released (Liu et al. 2002). The amount of released CO_2 is a function of soil texture and soil macropore structure. The second is an increase in microbial activity (Borken et al. 2003, Huxman et al 2004, Chou et al 2008), microorganism cell lysis (Halverson et al. 2000) or by destabilizing soil aggregates, making soil organic matter accessible to microbes (Denef et al. 2001). Small rain events affect only top horizons which have a high portion in soil CO_2 production (Jassal et al. 2005) and they are also more exposed to water stress than deeper horizons. With increasing rain pulse size, deeper soil layers contribute to the soil respiration and, therefore, overall CO_2 efflux from the soil surface increases with increasing size of rain pulse. However, after exceeding of a threshold rain pulse size, the CO_2 efflux pulse declines (Liu et al. 2002, Chen et al. 2008) because of decreasing of CO_2 diffusivity (Jassal et al. 2005). This phenomenon could be observed especially in 2010, which was the season with the highest total amount of precipitation and the number of rainy days comparing to other experimental seasons (Fig. 15).

The amount 23.8 – 27.3 t CO_2 ha^{-1} $season^{-1}$ was estimated for the period from 1 May to 12 October in four experimental years. These values are on the top of the range from other studies of spruce forests (Borken et al. 2002, Bergeron et al. 2009, Gaumont-Guay et al. 2009). The highest seasonal amount of CO_2 was released from soil in 2009 although it was not the season with highest temperature or precipitation, and we are not able to explain sufficiently this fact. From the remaining three years, the highest amount of CO_2 was released in 2010 (Fig. 15). Although that was the season with the lowest soil temperature, the total precipitation was the highest (even two fold than in 2012) with the high number of rainy days. Therefore, there were no long periods without precipitations, which would cause any severe water limitation of soil respiration. Several studies determined soil water content threshold of 12 – 19 % when water availability becomes a driving factor for soil respiration, exceeding effect of temperature (Yuste et al. 2003, Xu and Qi 2001b, Davidson et al. 1998). At our site soil moisture rarely decreased below 20 % in 2010.

In 2011 and 2012 the seasonal amount of released CO_2 from soil was lower than in 2012 and very similar to each other. Although there was the higher total precipitation in 2011, the number of rainy days was similar (Fig. 15). Although the quantity of precipitations is an important factor having effect on CO_2 efflux through soil water availability, the frequency of rainfalls is of the same importance (Harper et al. 2005). Pang et al. (2012) pointed out that the dry period in the spring can have effect on soil respiration in the summer. Therefore, dry periods in some parts of the season have not only the immediate but also long-term impact on soil CO_2 efflux.

Grassland

The grassland ecosystem regression coefficient (R^2) of the temperature-CO_2 efflux relationship was equal 0.83, which was higher than in the spruce forest soil. Therefore, it can be presumed that nighttime CO_2 efflux of the grassland mainly depended on temperature and other factors had a least effect. The mean ecosystem Q_{10} value was 3.4 which is about the top of the range of Q_{10} values with grassland found in other studies. (Flanegan et al. 2005, Wan and Luo 2003, Xu et al. 2004, Zhou et al. 2006). The Q_{10} value higher than for the forest soil could have been caused by counting with soil temperature which is, however, different from that of air around above-ground biomass, and has lower amplitude. Moreover, temperature sensitivity of leaves can be higher than that of soil (Loveys et al. 2003, Atkin 2005).

We observed an increasing trend of the grassland respiration activity at the beginning of the growing seasons and after the clipping of the above ground biomass, which can be explained by the growth of the above-ground biomass (Hirota et la. 2010). Together with the growing of above-ground biomass, the amount of below-ground biomass (roots) increases too. Byrne and Kiely (2006) observed that root respiration even exceeded heterotrophic respiration of the soil in summer month when the leaf area index of the grass was highest. The higher leaf area index and more intensive photosynthesis, the higher supply of photosynthesis assimilates to roots (Kuzyakov and Cheng 2001). That influences respiration of the roots themselves, but also increases release of root exudates to the soil (Kuzyakov and Cheng 2001).

The heterotrophic respiration activity of soil is, on contrary, mainly affected by water content. For instance Chen et al. (2008), Chou et al. (2008) or Harper et al. (2005) observed an increase in grassland CO_2 efflux after rain events. We, however, did not observe such an increase at our grassland site in contrast of these studies and the spruce forest soil. In several cases, there was even a decrease in the respiration activity. Soil covered by the grass is not as exposed to solar radiation as bare soil, therefore lower evaporation from soil and lower drying of the top soil can be expected. That, together with frequent precipitation, can contribute to non-limitation of respiration with drought. Therefore, further increase in water content has no or even negative effect on respiration. Moreover, it takes some time for water to infiltrate to root depth and persists for sufficient time to stimulate plant water uptake and so be available for leaf cells (Huxman et al. 2004).

Grassland ecosystem CO_2 efflux is influenced by soil and air temperature. Lower air temperature than soil temperature was observed during nighttime when CO_2 was measured. In general, soil temperature has lower amplitude of temperature fluctuation (and that still decreases with soil depth) than air temperature. Soil temperature is lower in the daytime and higher in the nighttime than air temperature thanks to slower warming and slower cooling during daytime and nighttime, respectively (Morecroft et al. 1998). This fact can contribute to explaining the lowest amount of released CO_2 in 2011. Although the mean soil temperature was the second highest, the air temperature was the lowest from all four experimental seasons. Especially, the significantly low CO_2 amount released in July compared to other years contributed to lower total CO_2 amount estimated for the whole season. In this month, both soil and especially air temperature were the lowest in comparison with July of other years, and grass cutting was done in the earliest date from the four years (Fig. 23).

The total amount of released CO_2 in 2010 and 2012 were very similar, although they were characterized by different conditions. The season 2012 was warmer than 2010 in terms of both soil and air temperature through all months. Total seasonal precipitation and number of rainy days in 2012 were, however, far less (Fig. 20). Especially, in August 2012 after removing of aboveground biomass, the amount of precipitation was very low. That could negatively affect grass regrowth (Bungener et al. 1999) and soil devoid of above-ground biomass is more sensitive to drying (Wang et al. 2011).

The season 2010 was the most wet from all seasons which could have positive effect on CO_2 losses from the ecosystem, but cutting and removal of the respiring above-ground biomass was performed 15 days sooner than in 2012.

5.2 Spatial heterogeneity of CO_2 efflux

5.2.3 Experiment design and data analyses

Soil (or ecosystem) CO_2 efflux was measured during years 2009 – 2011 using the portable system (see chapter 4.2.4) on a net of 8 x 8 positions in the grassland, 10 x 6 positions in the spruce and beach forest. The distance between the collars was 5 m. In the wetland, 15 positions situated in a line and 15 positions in three groups of five were established. This arrangement was chosen to avoid damage of the sensitive ecosystem. Dates of the measurement campaigns, a number of positions and a number of measurement cycles are summarized in Tab. 13.

At the beech forest and the wetland, the manual measurements were accompanied by the several-day-long measurement by the automated system ASCEM (see chapter 4.2.3) to estimate temperature sensitivity of soil CO_2 efflux. In the spruce forest and the grassland the data from the systems SAMTOC (see chapter 4.2.1) and SAMTOL (see chapter 4.2.2) were used, respectively.

Parameter Q_{10} was determined from the measurements during the campaign using the automated systems (ASCEM, SAMTOC, SAMTOL). Q_{10} and soil temperature measured at each position were used to calculate R_{10} for each position according to the equation [5]. Spatial heterogeneity of R_{10} was determined as coefficient of variation (CV):

$$CV = \frac{\sigma}{|\mu|} \cdot 100 \quad (\%) \qquad [7]$$

where σ is a standard deviation and $|\mu|$ is an average from measured values of R_{10}. Statistical analyses were performed in analytical software SigmaPlot 11.0 (Systat, USA). Correlation between different variables was tested by the Pearson Product Moment Correlation Test and ANOVA was used for testing of the effect of grass height on CO_2 efflux in the grassland

Tab. 13: Overview of manual measurement campaign of soil CO_2 efflux

Site	**Date of experiment**	**Number of positions**	**Number of cycles**
Spruce forest	8.-9. 6. 2010	60	3
	10.-11. 8. 2011	60	3
Grassland	13.-15. 5. 2009	64	3
	17.-19. 8. 2009	64	5
Beech forest	30. 9. 2009	60	2
	1. 10. 2009	60	2
	18.-19. 8. 2011	60	3
	25. 8. 2011	60	1
	31. 8. 2011	60	1
Wetland	21.-22. 9. 2010	30	3

As the manual measurements of soil CO_2 efflux are time consuming, I investigated the minimum number of measurement positions necessary for sufficient determination of R_{10} and its spatial variability at the individual sites. A thousand of random selections was provided for each *n*, which is a number of sampled positions from one measurement cycle at each site (n = 10, 15, 20, 25, 30, 35, 40, 45, 50, 55 from the whole data set of 60 or 64 positions in the spruce and beech forests and the grassland, n = 10, 15, 20, 25 from the whole data set of 30 position in the wetland).

Then the mean of soil CO_2 efflux, SD and descriptive statistics were calculated for each selection. As the sufficient number of positions, minimum *n*, which displayed difference of mean of R_{10} from those of the whole data set less than 5 %, was chosen. The data was processed and the statistics were run in the program *R* (R development core team 2012).

Precipitations were measured through the entire growing seasons using the rain gauge MetOne 386 (Met One Instruments, Inc., Oregon, USA) placed above the spruce forest, beech forest and wetland ecosystems and using the rain gauge HoBo (AMET, CR) placed above the grassland ecosystem.

Through the entire growing seasons, soil moisture was measured continuously by ThetaProbe (Delta-T Devices, UK) installed in the depth of 5 cm in the spruce forest, in 10 cm in the beech forest and in 15 cm in the grassland. At the wetland site, water table level was continuously measured by hydrostatic pressure sensor LP 307 (BD Sensors, Czech Republic). Negative values indicated position of water table level below the soil surface and positive values indicated position of water table level above the soil surface.

During the manual measurements of soil CO_2 efflux, soil moisture in the horizon 0-6 cm was measured at three points in a distance of about 3 cm outside the collar using ThetaProbe ML2x (Delta-T Devices, UK).

In the forest ecosystems, the distance (in cm) of the nearest tree from the center of the collar was measured using a tape measure.

As there is the thick litter layer in the beach forest which can influence soil CO_2 efflux, the distance between the top of the collar and litter surface and between the top of the collar and surface of pressed litter was measured. The litter thickness of litter was estimated as a difference of these two distances.

At the grassland site, the above-ground biomass is an important component of ecosystem CO_2 efflux, therefore grass height was measured in all collars by the type measure. The positions were divided into three groups – A (grass high maximum 5 cm), B (grass height between 5 and 10 cm) and C (grass height over 10 cm).

5.2.3 Results

<u>*Spruce forest*</u>

Measurements of soil CO_2 efflux were carried out during two campaigns in summer 2010 and 2011. Mean soil moisture measured next to the collars was 32.1 % (±6.9) during the campaign in 2010 and 37.6 % (±9.6) in 2011. To estimate the parameter Q_{10} necessary for temperature normalization of manually measured CO_2 efflux the data from the automated system SAMTOC from periods 2 – 9 June 2010 and 8 – 11 August 2011 was used. Q_{10} values were equal 1.57 and 1.77 in 2010 and 2011, respectively.

The mean value of R_{10} obtained from manual measurements on 60 positions was very similar in both campaigns in 2010 and 2011 – 3.57 (±1.02) and 3.56 (±1.43) µmolCO$_2$ m^{-2}s^{-1} (±1.43), respectively. The spatial variability was, however, lower in 2010 than in 2011 and it amounted 29 % and 40 %, respectively. In 2010, there was no correlation between R_{10} and soil moisture at individual positions. In 2011, significant negative correlation ($p<0.01$) was found (Fig. 24). Relationship between R_{10} and distance of the measurement position from the nearest tree was also studied. However, there was found no correlation.

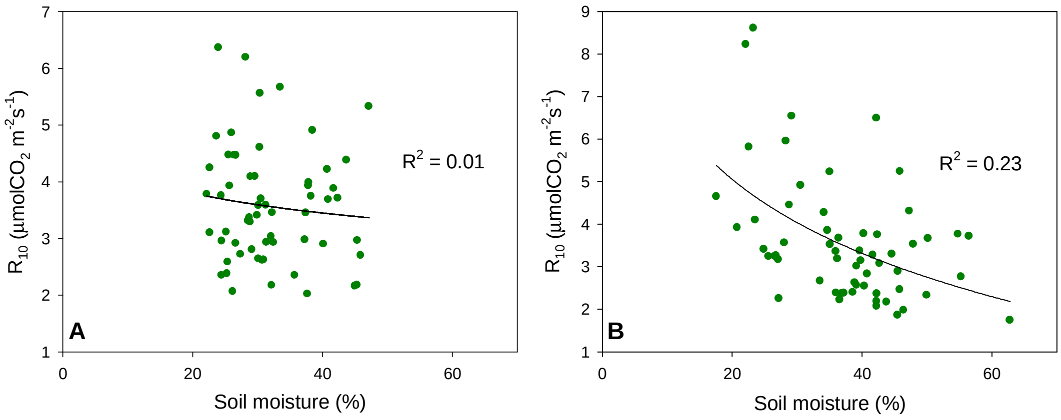

Fig. 24: R_{10} values over a range of soil moisture obtained from manual measurements on 60 positions in the spruce forest in 2010 (A) and 2011 (B).

Grassland

Measurements were carried out during periods when the grass was low, i.e. in the beginning of the growing season and shortly after mowing. Under high grass conditions it would be difficult to use the small chamber which is a part of the manual system Li-6200. Mean soil moisture measured manually was 37.6 (±9.1) % and 37.7 (±5.8) % during the first and the second campaign, respectively. The variability of the soil moisture was 24 and 15 %, respectively.

Q_{10} calculated from continuous measurements were equal 3.5 and 2.5 for the first and the second campaign, respectively. The mean R_{10} was very similar, 2.25 (±0.34) and 2.13 (±0.36) µmolCO$_2$ m^{-2}s^{-1} for the first and the second campaign. Its variability was very similar and the lowest from the investigated ecosystems, 15 and 17 % (Fig. 36).

There was an increasing trend of R_{10} in dependence on the grass height when the data from both experimental periods were evaluated (Fig. 25). There was a significant difference in R_{10} between grass height categories A (below 5 cm) and B (5 – 10 cm) and A and C (above 10 cm), and no statistically significant difference was found between categories B and C.

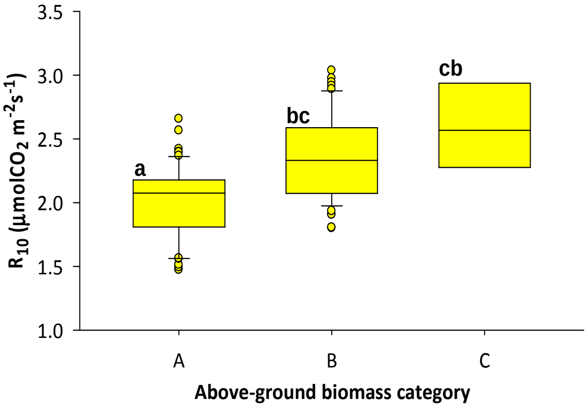

Fig. 25: R_{10} of the grassland ecosystem during two experimental periods over three above-ground biomass categories: A – bellow 5cm, B – 5 to 10 cm, C – over 10 cm. Small letters *a*, *b* and *c* express significance in difference in R_{10} between the categories.

There was no significant difference in soil moisture in dependence on the above-ground biomass height. There was, however, an increasing trend of R_{10} with soil moisture measured at the individual positions. The statistically significant correlation was observed for all measurement cycles except one on 17 August. The correlation coefficient of the significant correlations ranged from 0.27 to 0.59 (Fig. 26).

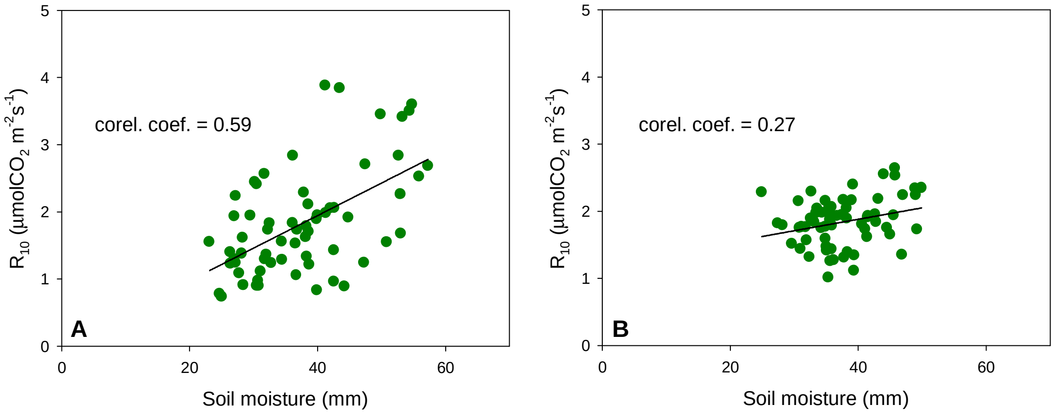

Fig. 26: Normalised CO_2 efflux from the grassland ecosystem over soil moisture during two measurement cycles on 13 May 2009 (A) and 18 August 2009 (B) (the cycles which showed the highest (A) and lowest (B) significant correlation between the variables)

Beech forest

The measurements in 2009 were done in the end of the growing season. The first day (30 September), the litter layer was wet as there was 0.3 mm of precipitation one day before measurement. The soil moisture, however, was not significantly different from that on the next day (1 October), when the litter was already dry. The mean soil moisture was 22.1 (±2.8) % and 22.4 (±2.3) %, respectively. However, there was a significantly higher ($p>0.001$) R_{10} when the litter was wet (R_{10} = 2.44 (±1.04) µmolCO$_2$ m^{-2} s^{-1}) than that when the litter was dry (R_{10} = 1.92 (±0.91) µmolCO$_2$ m^{-2} s^{-1}). The variation of R_{10} was 41 % and 46 % on 30 September and 1 October, respectively.

There was found no significant correlation between R_{10} and litter thickness. There was, however, significantly negative correlation of litter thickness and difference between R_{10} on 1 October and 30 September, expressed both in µmolCO$_2$ m^{-2}s^{-1} ($p>0.001$; correl. coefficient -0.48) and as a percentage ($p>0.001$; correl. coefficient -0.48) (Fig. 27). There was no dependence of R_{10} on neither soil moisture nor the distance from the nearest tree.

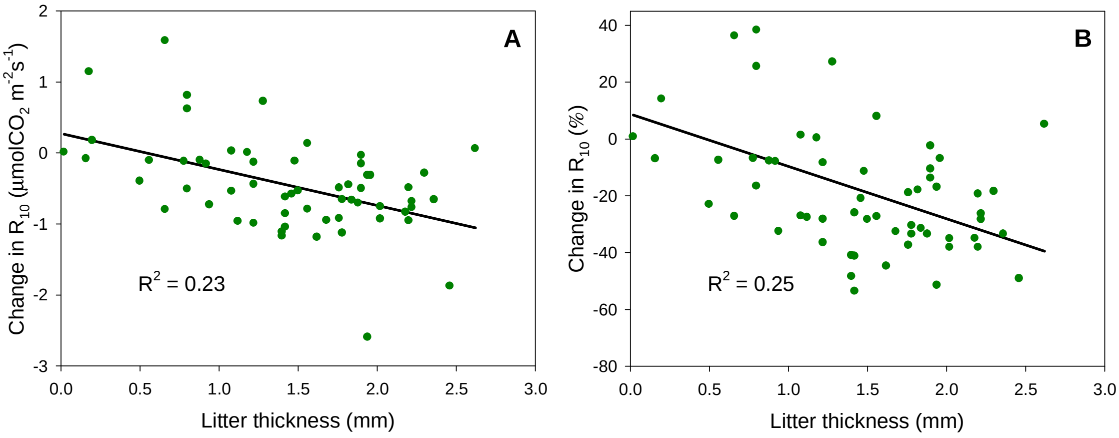

Fig. 27: Relationship of litter thickness and change in soil CO$_2$ efflux measured when litter was dry from that when litter was wet in the beech forest expressed in µmolCO$_2$ m^{-2} s^{-1} (A) and as a percentage (B).

In 2011, there were three measurement campaigns. The mean soil moisture during the first campaign (18 – 19 August) was 32.0 (±6.7) %. On 19 August after the measurements, there fell 11 mm of precipitation. Then there was no precipitation before the next campaign on 25 August, therefore, and soil moisture significantly decreased on 25.8 (±5.5) %. Before the third campaign (31 August), there was 14 mm of precipitation, however soil moisture did not increase and amounted 25.3 (±5.0) %.

We excluded two positions from other calculation as the soil CO_2 efflux measured on them was too high that they would bias the results. Then, mean R_{10} was 2.17 (±0.88), 1.59 (±0.44) and 2.67 (±1.13) µmolCO_2 m^{-2} s^{-1} during the first, second and third campaign, respectively. The R_{10} values differed significantly between each other. The lowest R_{10} was on 25 August after the period without rain. The variability of R_{10} was similar during the first and third campaign - 42 and 45 %, respectively. During the second campaign, after the non-rain period, it was the lowest - 27 % (Fig. 34).

As in 2009, no correlation between soil CO_2 efflux and litter thickness or distance from the nearest tree was observed in 2011. There was, however, found a significant negative correlation of soil CO_2 efflux and soil moisture during all three campaigns ($p<0.001$) (Fig. 28).

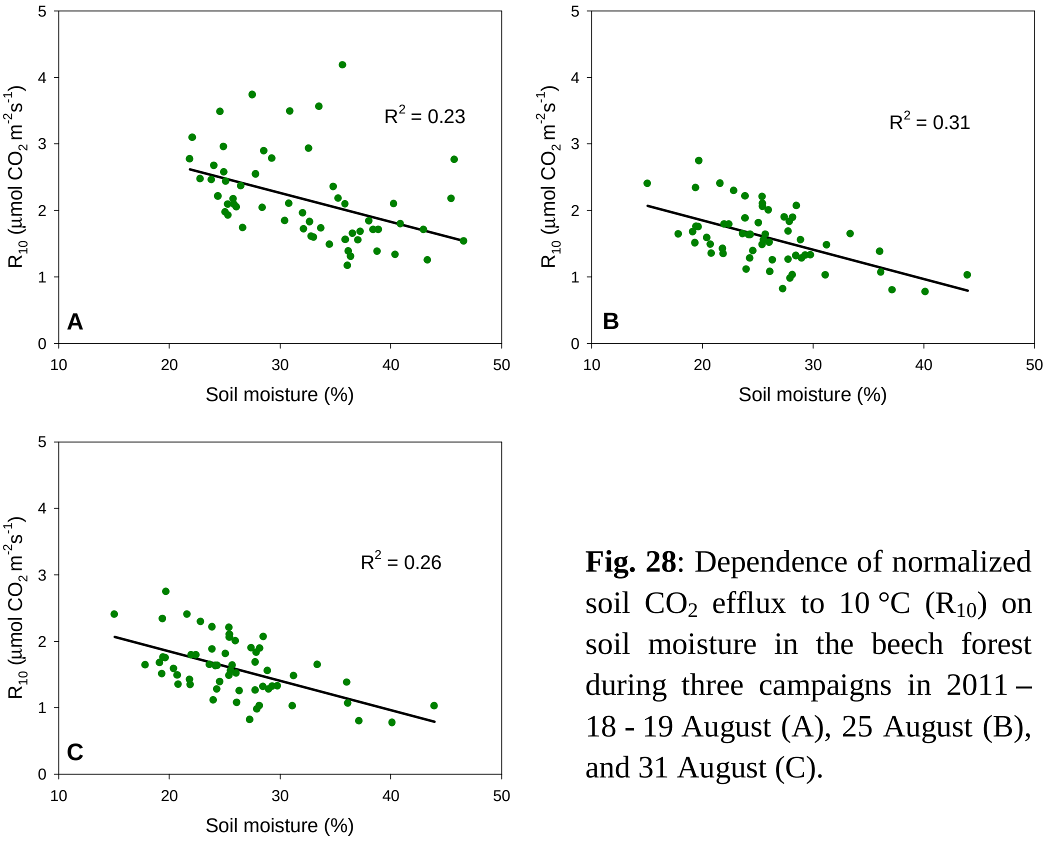

Fig. 28: Dependence of normalized soil CO_2 efflux to 10 °C (R_{10}) on soil moisture in the beech forest during three campaigns in 2011 – 18 - 19 August (A), 25 August (B), and 31 August (C).

Wetland

Measurements were carried out during the period when the water table was around soil surface. The collars were installed between hummocks of *Carex* tussocks, therefore above-ground plant organs were excluded from the CO_2 efflux measurement.

The mean value of R_{10} obtained from manual measurements on 30 positions was 1.37 (±0.78) µmolCO_2 $m^{-2}s^{-1}$, which was the lowest of all experimental sites. Coefficient of variation of R_{10} was, on the contrary, the highest – 57 % (Fig. 34). This variation was mostly caused by different soil water content as R_{10} significantly decreased with increasing soil water content. (Fig. 29).

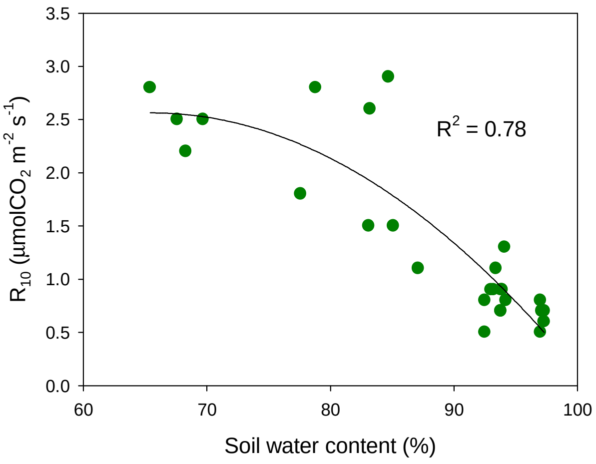

Fig. 29: Relationship between volumetric soil water content and R_{10} at the wetland site measured on fifteen positions.

Continuous measurements of soil CO_2 efflux using automated chamber ACSEM were done during 20 – 26 September 2010. During this period there was a controlled discharge of the lake therefore the water table slowly decreased till 25 September when it started raining. During this period the water table gradually decreased from +0.4 cm –8.0 cm. After the rain the water table increased up to +4.2 cm above the soil surface and on 26 September, measurement had to be stopped because of increasing water table and danger of damage of the measuring system. Soil CO_2 efflux fluctuated during days as it followed changes in temperature but simultaneously it had an increasing trend (Fig. 30). After the rain on 25 September when the water table raised above the soil surface, soil CO_2 efflux decreased fast to nearly zero.

In the investigated soil depth 0 to 10 cm, the amplitude of diurnal temperature fluctuation decreased from 9.3 °C at 0 cm to 1.1 °C at 10 cm in 21 – 24 September 2010 (before rain). Minima and maxima at depths of 1.5, 3, 5 and 10 cm lagged behind temperature of soil surface by 0.9, 1.3, 2.2 and 3.2 hours for minima, and 1.9, 2.9, 4.1 and 6.8 hours for maxima, respectively. After the rain, there was a low fluctuation of soil temperature and it was difficult to determine minima and maxima.

The dependence of soil CO_2 efflux on soil temperature was the tightest for temperature measured in the depth of 1.5 cm with R^2 value of 0.59. The Q_{10} value for CO_2 efflux normalization calculated from this temperature was 2.2.

Calculated R_{10} was plotted against the depth of water table (Fig. 31). The data were fitted with a modified exponential curve:

$$y = a \cdot e^{-0.5 \cdot \left| \frac{D_{WT} - (-b)}{c} \right|^{d}} \qquad [9],$$

where *a*, *b*, *c* and *d* are coefficients of the equation (*a*=1.54, *b*=10.34, *c*=10.27, *d*=3.96) and D_{WT} is depth of water table. This relationship was incorporated into the equation 6 for calculation of CO_2 efflux instead of parameter R_{10}. Then, the modeled soil CO_2 (R_m) was calculated as

$$R_m = \frac{R_{10}}{Q_{10}^{\frac{10-T_s}{10}}} = \frac{1.54 \cdot e^{-0.5 \cdot \left| \frac{D_{WT} + 10.34}{10.27} \right|^{3.96}}}{Q_{10}^{\frac{10-T_s}{10}}} \qquad [10]$$

When soil CO_2 efflux was modeled only on the base of measured temperature (equation 6) there was not good agreement with measured data (correlation coefficient 0.56, $p < 0.001$) (Fig. 32, 33). There was not observed the increasing trend of CO_2 efflux as the water table decreased. After the rain, this model estimated high CO_2 efflux (about 1.3 µmol $m^{-2}s^{-1}$) in comparison with measured data. When the depth of water table was included into the simple model (equation 10), modeled soil CO_2 efflux was in better agreement with measured data (correlation coefficient 0.97, Pearson correlation; $p<0.001$) (Fig. 33).

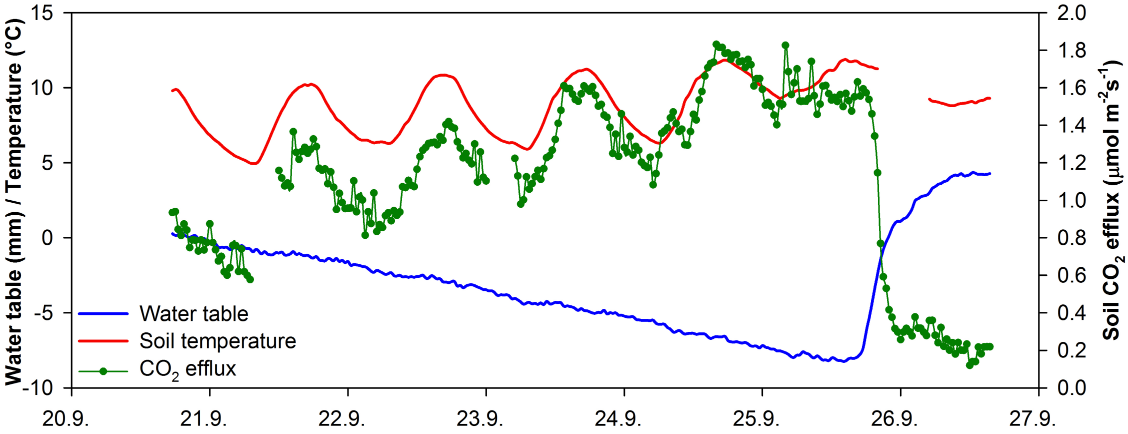

Fig. 30. Diurnal courses of studied parameters at the wetland site during 20 – 26 September 2011.

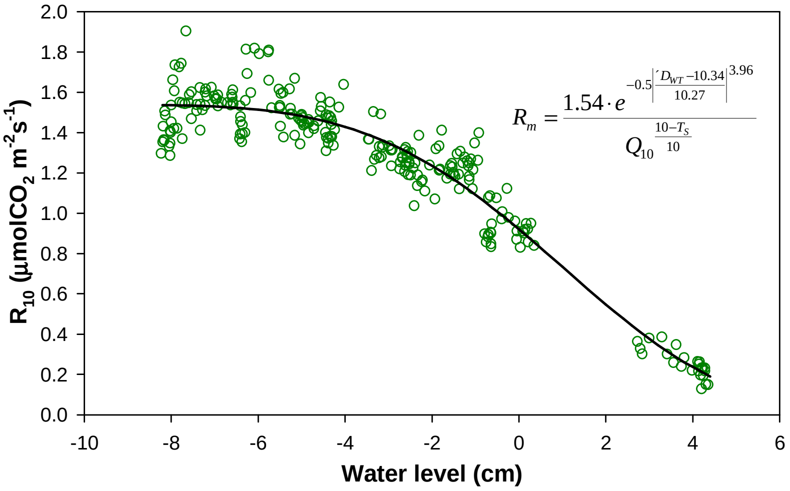

Fig. 31: Dependence of normalized CO$_2$ soil efflux on 10 °C (R$_{10}$) on fluctuating water table.

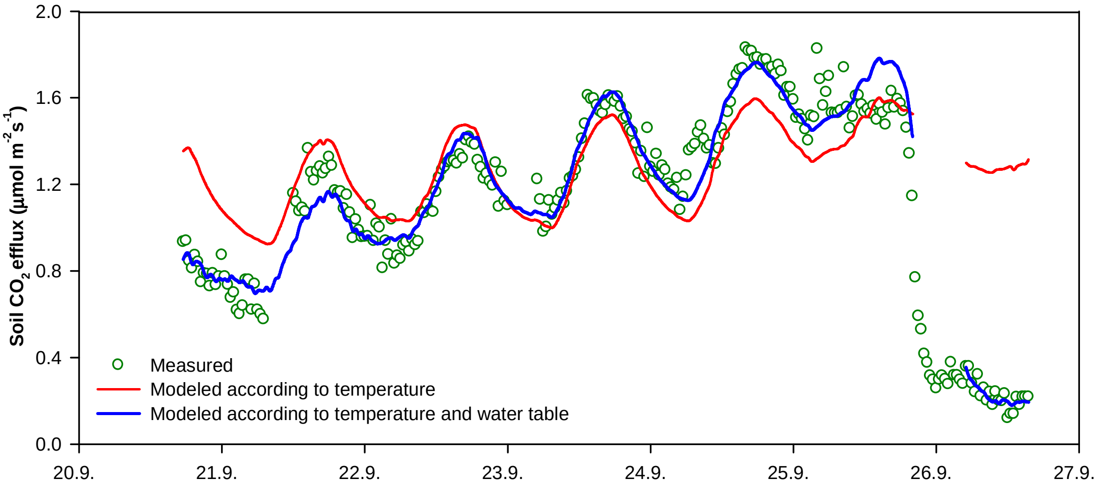

Fig. 32: Soil CO_2 efflux measured, modeled according to the soil temperature (equation 6) and modeled according to the soil temperature and the water level (see equation 10).

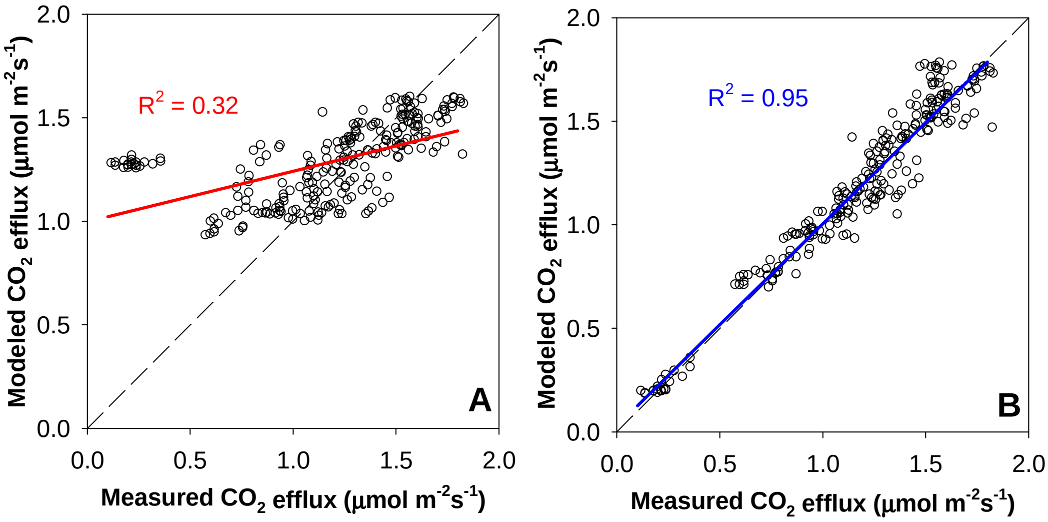

Fig. 33: Relationship between modeled soil CO_2 efflux and measured CO_2 efflux. A – model based only on soil temperature, B – model based on soil temperature and water level related to soil surface.

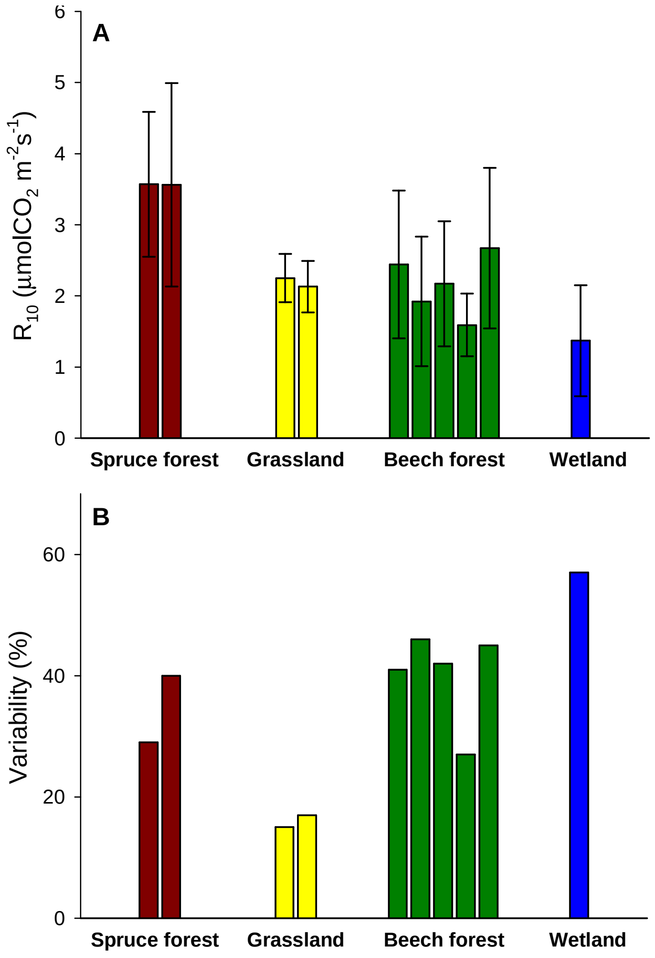

Fig. 34: Soil (or grassland ecosystem) CO_2 efflux normalized to 10 °C (R_{10}) (A) and its variability expressed as the coefficient of variation (B) during individual campaigns in four investigated ecosystems. Each bar represents one measurement campaign in the same order as stated in Tab. 12.

Determination of the number of measurement positions

Mean R_{10} from thousand selections for any individual *n* of positions did not significantly differ from mean R_{10} from the whole dataset (60 positions for spruce and beech forest, 64 for the grassland and 30 positions for the wetland). Standard deviation of R_{10} means from a thousand random selections decreased with an increasing number of sampled positions (a sample is drawn in Fig. 35-A). That shows that the less number of measurement positions, the higher dispersion of the R_{10} means of the individual thousand selections and the less probability of the correct mean R_{10}. To estimate soil CO_2 efflux with the maximum 5 % deviation of the whole dataset mean, it is necessary to measure at least on 35 positions in the spruce forest, on 10 positions in the grassland, on 35 positions in the beech forest and on 25 positions in the wetland.

Also standard deviations of SD calculated from thousand selections for any individual *n* of positions decreased with an increasing number of sampled positions (a sample is drawn in Fig. 35-B). Therefore, with an increasing number of positions, the accuracy of the estimation of the variability increased too. To estimate spatial SD (or variability) of soil CO_2 efflux with the maximum 5 % deviation of the whole dataset SD 60 positions in the spruce forest, on 50 positions in the grassland, on 55 positions in the beech forest and on 25 positions in the wetland.

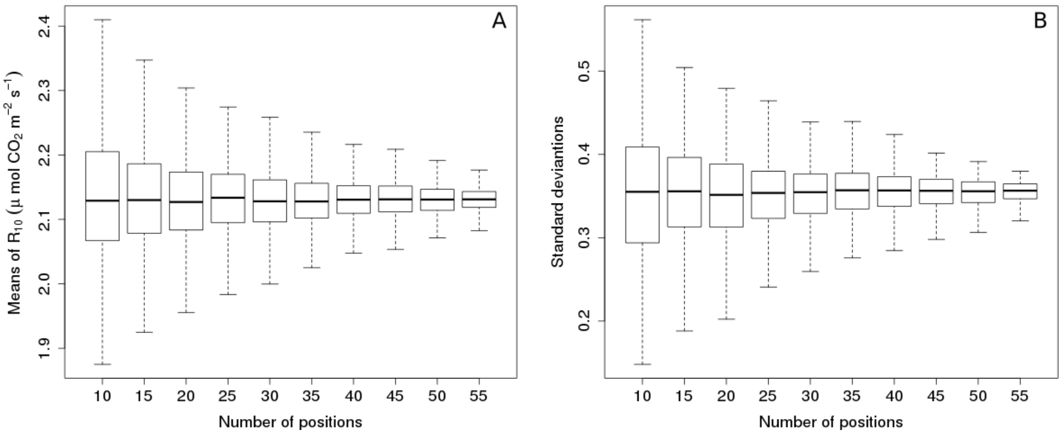

Fig. 35: Distribution of means (A) and SD (B) of soil R_{10} for different number of positions (*n*) sampled from the whole 64-position data set (a thousand ransom selections for each *n*) on 9 August 2009 at the grassland site. The bold line is the mean soil CO_2 efflux, the boxes refer to the 1st and 3rd quartiles and the whiskers refer to 10th and 90th percentile of soil CO_2 efflux.

5.2.3 Discussion

The variability in soil CO_2 efflux at the forest sites was found to range between 27 – 46 % (expressed as the coefficient of variation). That corresponds with the variability 20 – 60 % observed in other studies for forest soils (Kosugi et al. 2007, Law et al. 2001, Ohashi et al 2007, Yan et al. 2011, Yim et al. 2003). The variability in the spruce forest was lower than in the beech forest, except for the measurements in the beech forest on 25 August 2011 which followed after one week with no precipitation, and it was comparable with 39 % for this site observed in the study of Acosta et al (2013). In the beech forest, soil moisture measured manually in 0 – 6 cm was higher during the first campaign in 2011 than during the second which followed the period with no precipitations. The soil moisture did not responded to 1.4 mm precipitations which fell before the third campaign. That can be explained by the presence of a thick layer of litter covering the soil surface in the experimental beech forest. The litter layer can influence water and energy exchange between the soil and the air above. It may intercept a significant portion of throughfall (Putuhena and Cordery 1996), stop most of the incoming radiation and reduce consequently soil respiration (Ogee et al. 2001). Thus, the results in differences in CO_2 efflux between campaigns should be looked for in the shallow top soil layer and the litter, which are most affected by the moistening and the consequent drying. Therefore, thickness of the litter layer should affect soil CO_2 efflux as observed in previous studies (Fang et al. 1998, Rout and Gupta 1989). In 2011 no effect of litter thickness on the variability in soil CO_2 efflux was observed in the beech forest although the variability after the dry period was far lower than during the other two campaigns. However, in 2009 the correlation between litter thickness and difference between soil CO_2 effluxes during the day with the freshly wet litter after a gentle rain and the following day, when the litter got dry, was found (Fig. 27). These result showed that the litter layer is very important component of soil CO_2 efflux from the beech forest soil and in dependence on weather conditions it can influence changes in CO_2 efflux from the soil surface and that measurement of soil moisture in several centimeters deep in the soil can not record changes of water content in the litter layer.

Several studies determined dependence of soil CO_2 efflux on the distance from the nearest tree (Wiseman and Seiler 2004, Yan et al. 2011). The increasing distance of the measurement position can reflect in decrease in root biomass (Saiz et al. 2006), decrease in accumulation of organic matter (Butterbach-Bahl et al. 2002) or increase in solar irradiation and precipitation throughfall through lower leaf area index (Bequet et al. 2012). However this effect on the variability on soil CO_2 efflux was not observed at any of our forest sites. In the spruce forest, it can be explained by high tree density which results in more even root biomass distribution and a high amount of gravel in the soil, which variability can overshadow effect of other factors on spatial variation of soil CO_2 efflux. The beech forest represents deep-rooted tree species and as in the old stand, contribution of heterotrophic respiration to total soil respiration becomes high as supported by the study of Luan et al. (2011).

In 2011 in both spruce and beech forests, a negative correlation between soil CO_2 efflux and soil moisture was observed (Fig. 24 and 28). This is mostly observed under high soil moisture conditions when soil respiration is limited by the oxygen supply (Lopéz et al. 1998). However, lower mean R_{10} after the six-day period without rain at the beech site was observed. Therefore there should be another physical, biological and chemical properties co-varying with soil water which drive spatial variation of soil CO_2 efflux, as suggested by Kosugi et al. (2007).

At the grassland site, the spatial variability in soil CO_2 efflux was 15 and 17 %. These values are near the bottom of the range 17 to 29 % described in Hirota et al. (2010), Tang and Baldocchi (2005) and Wang et al. (2005). The ecosystem CO_2 efflux increased with the height of grass at measurement positions (Fig. 25). The above-ground biomass was determined to be an important factor of CO_2 efflux from grassland in several studies (Hirota et al. 2010, Wang et al. 2005). The influence of the amount of above-ground biomass can be attributed to the amount of biomass contributing to ecosystem respiration and to the amount of photosynthesis assimilate supply to roots which affect soil respiration (Kuzyakov and Cheng (2001). The biggest effect of the amount of the above-ground biomass on ecosystem CO_2 efflux and on heterogeneity of CO_2 efflux occurs in the summer when the activity of the above-ground biomass is high and contributes the most to total ecosystem respiration (Flanagan et al. 2002). Nevertheless, this was not confirmed by Nakano et al. (2008) as in their study the vegetation was very sparse and the ecosystem respiration was regulated not by plant respiration but by microbial decomposition of soil organic matter, which is not directly related to the amount of the above-ground biomass.

In the wetland, a period with water level around the soil surface was chosen for the measurement campaign as this is common conditions for this site. Mean R_{10} calculated from manual measurements was 1.41 $\mu CO_2\ m^{-2}s^{-1}$, which was the lowest from all four investigated sites, which was caused by the effect of high water content. When soil water content increases, water fills pores and the air-filled porosity and oxygen content decreases. Therefore, aerobic decomposition of organic matter is suppressed and starts to be alternate with slower anaerobic decomposition as described by Šantrůčková et al. (2004). That leads to evolution of methane (CH_4) and its release into the atmosphere (Altor and Mitsch 2008, Knorr et al. 2008).

In the wetland, the highest spatial variation (58 %) of soil CO_2 efflux from the investigated sites was observed. The measurement campaign took place in the period when water table moved around soil surface and there was a gradient of the water table level in the measurement plot caused by the increasing distance from the pond. Therefore, there was a high variability in soil water content between measurement positions, which resulted in high variation in soil CO_2 efflux (Fig. 29).

To normalize soil CO_2 efflux from both manual and continual measurements, Q_{10} equal 2.2 was determined from automated measurements which is in the range (1.4 – 3.4) of its values estimated for wetland or peatland soils in other studies (Bonnett et al., 2006; Vicca et al., 2009; Inglett et al., 2012). During continuous measurements R_{10} negatively correlated with the depth of water table. The most pronounced decrease of R_{10} with increasing water table was between levels –3 and +3 cm. Therefore, it can be stated that the most respiratory active layer is in 0 – 3 cm at this site and changing conditions, such as temperature or water content, at this layer will drive changes in soil CO_2 efflux. Other increase or decline of water table had a little effect on soil CO_2 efflux. Only few studies described a weak relationship between CO_2 efflux and water table position during season (Lafleur et al., 2005; Bubier et al., 1998). However, a strong negative relationship was found in most studies (e.g. Jaatinen et al., 2008; Lloyd, 2006; Vicca et al., 2009) similarly to our investigation.

CO_2 efflux model based on temperature is commonly used method how to easily estimate the amount of released CO_2 (Davidson et al. 2006a). That can be suitably used when soil temperature is the driving factor of temporal dynamics of CO_2 efflux. The influence of temperature can decrease when soil water content is very low (the temperature-CO_2 efflux can be even decoupled) (Xu et al., 2004) or, on contrary, too high which is common in wetlands or peatlands. Therefore, it is very important to include soil water conditions into models estimating CO_2 efflux. In this study, the depth of water table was used. The simple model (equation 6) described well the measured data and the model seems to be sufficient for this site which is characterized by the range of water table level between 0.2 m below and 1.0 m above the soil surface. Although the model was calculated for water table from

8 cm below to 4 cm above the soil surface, there would not be expected increase of soil CO_2 efflux with more decreasing water table. Similarly, soil CO_2 efflux close to or equal zero would be measured also under conditions of water table higher than measured during the experiment.

The study site is situated in the inundation area of the lake and there is a slight gradient of water table level, the further from the lake, the deeper is the water table from the soil surface. Therefore, when the water table is around the soil surface, the water table can significantly affect spatial variability of soil CO_2 efflux. Measurements of the depth of water table on several positions and consequent determination of its spatial gradient together with the model of soil CO_2 efflux should improve estimation of CO_2 efflux of the whole ecosystem.

5.3 Time of measurement

5.3.1 Experiment design and data analyses

The aims of this part is to determine the differences in the response of soil CO_2 efflux on temperature and to compare seasonal sums of released soil carbon calculated from continuous measurements and from models based on measurements taken at different times of day and night. For this study data from two growing seasons from 1 May to 11 October 2008 and 2009 were analysed. The continuous measurements of soil CO_2 efflux and soil temperature were carried out in the spruce forest using the automated system SAMTOC (see chapter 4.2.1).

The data sets from the continuous measurements were subsampled according to the time of day or night when individual measurements were made. Those measurement values were divided according to times closest (max 40 minutes = half of the measurement cycle) to the chosen hours, as follow: 12 midnight (00:00), 2 am (02:00), 4 am (04:00), 6 am (06:00), 8 am (08:00), 10 am (10:00), 12 noon (12:00), 2 pm (14:00), 4 pm (16:00), 6 pm (18:00), 8 pm (20:00) and 10 pm (22:00)

Values of Q_{10} were calculated for each position and the entire growing season for all data sets according to the equation 4. Then, CO_2 efflux was normalized for the temperature 10 °C (R_{10}) according to the equation 5. R_{10} was determined for each measurement and then the seasonal average was calculated for all data sets.

Parameters Q_{10} and R_{10} were used for estimating modelled soil CO_2 efflux (R_m) on the basis of continuously measured temperature (T_S) measured in 80-minute step using the following equation:

$$R_m = \frac{R_{10}}{Q_{10}^{\frac{10-T_S}{10}}} \;. \qquad [8]$$

Finally, the amounts of the released carbon ($C_{released}$) for the investigated seasons were calculated from measured values of CO_2 efflux and R_m calculated from the individual data sets. The values of CO_2 efflux were assumed as a mean value for the 80-minute interval (=one measurement cycle). Missing data of CO_2 efflux were filled using the equation [8] where Q_{10} reached a value calculated for the period in which the gap occurred and R_{10} was estimated on the base of mean R_{10} three days before and after the gap.

Statistical analysis was carried out using the software SigmaPlot 11.0 (Systat Software Inc.). To test differences of released carbon between the individual data sets the Bonfernoni procedure was applied and then Wilcoxon test was used. Statistical significance was tested at the level $\alpha = 0.05$. The test was applied for each of eight chambers. If the test was significant for four or more position in one year, then the difference between the measured carbon release and those for individual datasets was stated as significant.

5.3.2 Results

The mean daily soil temperatures at the depth of 1.5 cm in the stand were 11.2 °C and 11.7 °C for the experimental periods from 1 May to 11 October in 2008 and 2009, respectively. The temperature was about 5–8 °C in the beginning of May and reached a maximum of about 16 °C in summer for both years. The second half of September was much colder in 2008 than in 2009 and the daily mean soil temperature dropped on about 5 °C. There was however no statistically significant difference in mean soil temperature between years. Total precipitations were 637 mm (with 87 rainy days) and 468 mm (with 99 rainy days) for the experimental periods in 2008 and 2009, respectively. There was no so long period without precipitations which could cause severe drought.

Measured soil CO_2 efflux showed an increase with rising soil temperature for all data sets (Fig. 38). The average regression coefficients (R^2) for the relationship between soil CO_2 efflux and soil temperature from eight measured positions were 0.48 (±0.20) and 0.49

(±0.16) for 2008 and 2009, respectively. However, soil CO_2 efflux and soil temperature exhibited a closer relationship for the data sets between 00:00 and 08:00 and for 20:00 and 22:00 in both years. The looser relationship was found for the data sets between 10:00 and 16:00 (Tab. 25).

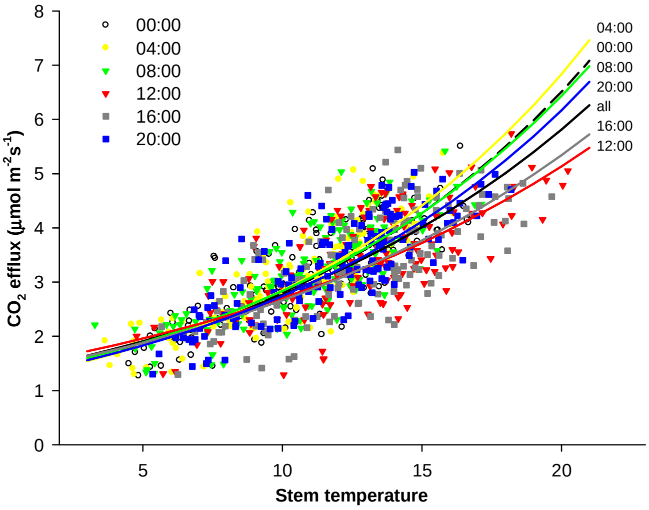

Fig. 38: Exponential dependence of soil CO_2 efflux on soil temperature obtained from continuous measurements (all) and from measurements at individual times of day and night at one position at the Bily Kriz site in 2009 (for better clarity only six datasets out of twelve were chosen).

The Q_{10} means from the eight measured positions obtained from all data of continuous measurement were 1.9 (±0.4) and 2.0 (±0.2) in 2008 and 2009, respectively. In both years, the Q_{10} values calculated for 00:00, 02:00, 04:00, 06:00, 08:00, 20:00 and 22:00 were higher, while the Q_{10} values calculated for 12:00, 14:00 and 16:00 were lower (Tab. 26). The average seasonal R_{10} values for the eight measured positions were 4.74 (±1.16) and 3.63 (±0.81) µmolCO_2 $m^{-2}s^{-1}$ in 2008 and 2009, respectively. Values of R_{10} were slightly above the average for 00:00, 02:00, 04:00 06:00, 08:00 and 22:00 and below the average 12:00, 14:00, 16:00, 18:00 and 20:00. The lowest difference was found for 10:00 (Tab. 14). The obtained parameters Q_{10} and R_{10} and the continuously measured soil temperatures for individual time data sets were used to estimate total carbon released from soil during the period from 1 May to 11 October 2008 and 2009 using equation [8]. The average cumulative amounts of carbon released from the eight measured positions calculated from continuous measurements were 9.0 t ha^{-1} (±2.3) and 7.5 t ha^{-1} (±1.6) in 2008 and 2009,

Tab. 14: Mean values (±SD) of temperature sensitivity of CO_2 efflux (Q_{10}) and CO_2 efflux normalized for the temperature of 10 °C (R_{10}, µmolCO_2 $m^{-2}s^{-1}$) calculated from the individual data sets, as well as regression coefficient (R^2) for the relationship between soil CO_2 efflux and soil temperature and the total amount of carbon released from soil during the experimental seasons in 2008 and 2009. The data sets were established according to the time of day and night when the measurements were taken ("all" denotes all continuously measured data). Asterisks indicate a statistically significant difference between $C_{released}$ calculated for individual data sets and $C_{released}$ calculated from continuously measured data.

2008

Time of day	Temp	Q_{10}	R_{10}	R^2	$C_{released}$
All	11.2 (±0.1)	1.9 (±0.4)	4.74 (±1.16)	0.48 (±0.20)	9.0 (±2.3)
0:00	10.4 (±0.1)	2.2 (±0.4)	4.84 (±1.21)	0.55 (±0.20)	9.4 (±2.5)*
2:00	10.2 (±0.1)	2.2 (±0.4)	4.89 (±1.23)	0.54 (±0.20)	9.5 (±2.5)*
4:00	9.9 (±0.1)	2.2 (±0.4)	4.91 (±1.24)	0.55 (±0.19)	9.6 (±2.5)*
6:00	10.0 (±0.1)	2.2 (±0.4)	4.90 (±1.23)	0.55 (±0.20)	9.6 (±2.5)*
8:00	10.6 (±0.1)	2.0 (±0.4)	4.80 (±1.22)	0.49 (±0.19)	9.2 (±2.5)*
10:00	11.7 (±0.3)	1.9 (±0.4)	4.74 (±1.17)	0.45 (±0.22)	8.9 (±2.3)*
12:00	12.5 (±0.3)	1.7 (±0.4)	4.66 (±1.14)	0.42 (±0.21)	8.7 (±2.2)*
14:00	12.9 (±0.2)	1.7 (±0.3)	4.67 (±1.12)	0.41 (±0.22)	8.6 (±2.1)*
16:00	12.5 (±0.1)	1.8 (±0.4)	4.63 (±1.08)	0.44 (±0.23)	8.6 (±2.1)*
18:00	12.0 (±0.1)	1.9 (±0.4)	4.62 (±1.07)	0.48 (±0.21)	8.7 (±2.1)*
20:00	11.2 (±0.1)	2.0 (±0.4)	4.69 (±1.12)	0.51 (±0.22)	9.0 (±2.2)
22:00	10.8 (±0.1)	2.1 (±0.4)	4.79 (±1.17)	0.54 (±0.20)	9.3 (±2.4)*

2009

Time of day	Temp	Q_{10}	R_{10}	R^2	$C_{released}$
All	11.5 (±0.1)	2.0 (±0.2)	3.63 (±0.81)	0.49 (±0.16)	7.2 (±1.6)
0:00	10.8 (±0.1)	2.3 (±0.2)	3.69 (±0.84)	0.57 (±0.14)	7.4 (±1.7)*
2:00	10.5 (±0.1)	2.3 (±0.2)	3.74 (±0.87)	0.57 (±0.13)	7.6 (±1.8)*
4:00	10.3 (±0.2)	2.3 (±0.2)	3.77 (±0.89)	0.57 (±0.13)	7.6 (±1.8)*
6:00	10.3 (±0.1)	2.3 (±0.2)	3.77 (±0.89)	0.57 (±0.13)	7.6 (±1.8)*
8:00	10.8 (±0.1)	2.2 (±0.2)	3.72 (±0.87)	0.53 (±0.15)	7.4 (±1.8)*
10:00	11.7 (±0.2)	2.1 (±0.3)	3.60 (±0.83)	0.47 (±0.16)	7.1 (±1.7)
12:00	12.6 (±0.4)	1.9 (±0.3)	3.55 (±0.78)	0.41 (±0.18)	6.8 (±1.6)*
14:00	13.1 (±0.4)	1.8 (±0.3)	3.52 (±0.74)	0.38 (±0.17)	6.7 (±1.5)*
16:00	12.9 (±0.2)	1.9 (±0.3)	3.51 (±0.71)	0.43 (±0.18)	6.8 (±1.4)*
18:00	12.3 (±0.2)	2.1 (±0.3)	3.49 (±0.72)	0.49 (±0.17)	6.8 (±1.4)*
20:00	11.7 (±0.1)	2.2 (±0.2)	3.56 (±0.75)	0.54 (±0.16)	7.1 (±1.5)
22:00	11.2 (±0.1)	2.2 (±0.2)	3.64 (±0.80)	0.55 (±0.15)	7.3 (±1.6)

respectively. Differences between the amounts of soil carbon actually measured as released and those calculated based on the parameters from the individual data sets and from continuously measured data ranged up to 7.5 %.

Generally, the models based on the measurements at 00:00, 02:00, 04:00, 06:00, 08:00 and 22:00 overestimated seasonal soil carbon flux, and models based on the measurements at 10:00, 12:00, 14:00, 16:00 and 18:00 underestimated seasonal soil carbon flux in both years. In 2008, statistically significant difference between $C_{released}$ calculated for individual data sets and $C_{released}$ calculated from continuously measured data was found for all data sets except for 20:00. In 2009, there was no significant difference for 10:00, 20:00 and 22:00. The lowest differences (0.1 % and 0.5 %) were found for the 20:00 subsample (Fig. 39).

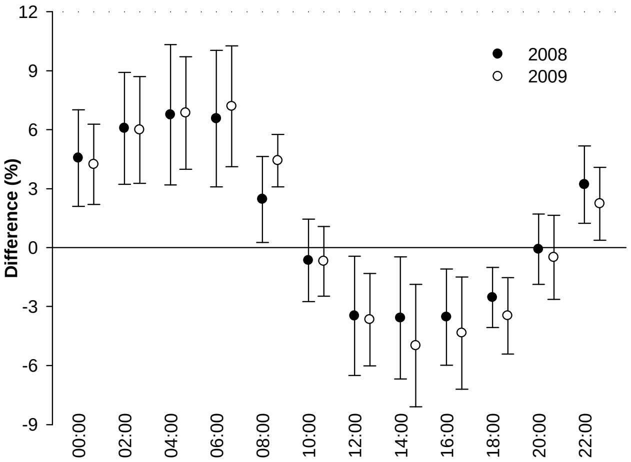

Fig. 39: Percentage differences between the seasonal amounts of released soil carbon calculated from continuously measured soil CO_2 efflux and from modelled soil CO_2 efflux using parameters Q_{10} (temperature sensitivity of CO_2 efflux) and R_{10} (CO_2 efflux normalized for the temperature of 10 °C) obtained from individual data sets. The data sets were established according to the time of day and night when the measurements were taken.

There was no statistically significant difference (< 1 %; $p > 0.05$) between the total amounts of released soil carbon as calculated from continuously measured data and from the model based on the entire data set at any measurement position. However, the seasonal course of soil CO_2 efflux modelled using single value of parameters R_{10} and Q_{10} calculated from the whole data set differed from measured soil CO_2 efflux. The model tended to overestimate (by up to about 60 %) soil CO_2 efflux during periods without rain, when the soil was dry, and to underestimate (by up to about 30 %) soil CO_2 efflux when rain events occurred and soil moisture increased (Fig. 40).

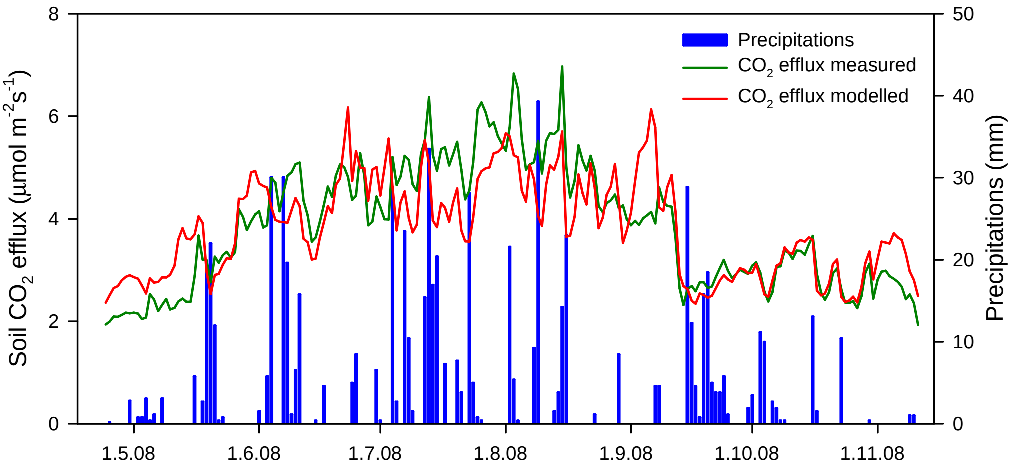

Fig. 40: Precipitation and measured and modeled soil CO_2 efflux at one position in the spruce forest in 2008. The soil CO_2 efflux was modeled using equation 8 (R_{10} and Q_{10} were calculated the whole data set).

5.3.3 Discussion

We used the relationship between soil CO_2 efflux and soil temperature to model soil CO_2 efflux. This relationship is often described by a simple exponential function (equation 3). The temperature sensitivity parameter (Q_{10}) can be determined from this relationship (Lloyd and Taylor 1994). The parameter Q_{10} is commonly used for normalizing measured CO_2 efflux to a reference temperature (equation 5) in order to investigate factors other than temperature (Jassal et al. 2008, Noormets et al. 2008), or it is used in carbon models to simulate soil or ecosystem CO_2 fluxes (equation 8) (Khomik et al. 2006, Wang et al. 2010). The mean values of Q_{10} estimated for the whole season from eight measured positions were 2.2 and 2.0 $\mu molCO_2\ m^{-2}s^{-1}$ in 2008 and 2009, respectively. The parameter Q_{10} was estimated for temperature measured at a depth of 1.5 cm. Similar Q_{10} values have been reported for spruce forest soil in other studies (Borken et al. 2002, Saiz et al. 2007).

Estimated cumulative seasonal (from 1 May to 11 October) carbon efflux from the forest soil based on continuous measurements was 9.0 and 7.5 t C ha^{-1} in 2008 and 2009, respectively, which is comparable to that determined in other studies on spruce forests (Borken et al. 2002; Bergeron et al. 2009; Gaumont-Guay et al. 2009). As there was no significant difference in mean soil temperature during the experimental period 2008 and 2009, the reasons for the difference between the years can be related to differences in the amounts of precipitation during these two seasons, as in 2008 the precipitation was by about 220 mm (35 %) higher than in 2009. During the experimental period in 2009 there was, however, by 12 more rainy days than in 2008. But there was no so long period without precipitations which could cause severe limitation of soil CO_2 efflux.

There was no significant difference (<1 %) between seasonal flux calculated from measured soil CO_2 efflux and soil CO_2 efflux modelled using parameters calculated from the whole data set (equation 8). The model tended to overestimate CO_2 efflux, however, when the soil was dry and CO_2 efflux was limited by water supply. On the other hand, the model tended to underestimate CO_2 efflux when soil moisture increased after rain events (Fig. 40). That is due to the effect of soil moisture on parameters Q_{10} and R_{10} (Qi et al. 2002, Davidson et al. 1998). It can be therefore considered that estimating just single values of Q_{10} and of R_{10} for the entire season can hide these effects.

The seasonal soil carbon flux obtained from data subsets differed by as much as 7 % from that obtained using the overall mean. The largest difference was for the 04:00 and 06:00 subsample and the lowest for those at 10:00 and 20:00 at which time of day mean annual temperature was also the most similar to that calculated from the whole data set. Generally, the measurements from 00:00 to 08:00 and at 22:00 overestimated seasonal soil carbon flux, while measurements from 12:00 to 18:00 underestimated seasonal soil carbon flux. Annual and/or seasonal cumulative soil carbon flux has been estimated in several studies on the basis of manual measurements over periods ranging in length from days to a month (e.g. Davidson et al. 1998, Epron et al. 2004, Khomik et al. 2006). The measured soil CO_2 flux was subsequently extrapolated to 24 hours and then interpolated between days when the measurements were performed (Savage et al. 2003, Parkin and Kaspar 2004, Savage et al. 2008). This method can inaccurately estimate soil carbon flux depending on the time of day at which the measurements are taken, as soil CO_2 efflux changes during the day (Flanagan and Johnson 2005). Parkin and Kaspar (2003), for example, found up to 40 % overestimation of daily soil CO_2 flux when measurements were performed in early afternoon. They found unbiased daily soil CO_2 efflux to occur around 08:30 and 19:00. Those authors also observed a decrease in the inaccuracy of daily soil CO_2 efflux estimation when they corrected measured soil CO_2 efflux for daily average temperature using the parameter Q_{10}.

Such a sampling strategy with several days between measurements can also miss important changes in soil moisture, such as a sharp increase due to rainfall (Liu et al. 2002, Harper et al. 2005). If the intervals between sampling days are too large, then the CO_2 flux response to rainfall may be inadequately characterized. Potential problems include underestimation of cumulative soil CO_2 flux if significant rainfall events are missed (Savage et al. 2008) or overestimation of cumulative soil CO_2 flux if flux measurements performed following rainfall events are weighted too heavily because of an unrepresentative number of dry periods being included into the data set (Parkin and Kaspar 2004). Savage et al. (2008) observed up to 23 % difference between estimates based on continuous, automated measurements and manual measurements carried out weekly between 09:00 and 15:00.

Khomik et al. (2006) estimated annual respiration of boreal forest soil on the basis of continuously measured temperature and CO_2 efflux manually measured once a month. This approach is not suitable for sites with highly variable soil moisture, where periods of limited water occur, and the model is not sensitive to tree physiology (e.g. variability in photosynthesis or root activity (Högberg et al. 2001, Misson et al. 2006).

The relationship between soil CO_2 efflux and soil temperature measured at the same time can be biased by time lag of soil CO_2 efflux behind soil temperature, assimilate supply to roots or transpiration stream. There is usually some delay of soil CO_2 efflux behind soil temperature measured at the same time and the length of the lag is highly dependent on the depth of the measured soil temperature (Parkin and Kaspar, 2003; Pavelka et al., 2007). When the soil temperature rises (in the morning), soil CO_2 efflux can be lower than expected from the actual temperature. On the contrary, when soil temperature decreases (in the afternoon or evening) soil CO_2 efflux can be higher than expected from the actual temperature

Assimilates transported by phloem from leaves to roots can increase root and rhizomicrobial respiration (Kuzyakov and Cheng 2001) and consequently to bias the relationship between soil CO_2 efflux and soil conditions. There is however time lag of measured CO_2 efflux from soil surface behind photosynthesis of leaves. The time lag depends on the transport distance between leaves and roots, uptake by micorhizal fungi, release of root exudates, respiration rate and CO_2 diffusion through soil (Kuzyakov and Gavrichkova 2010). According to Kuzyakov and Gavrichkova (2010) the time lag for our study stand can range from 1.5 to 4 days when considering stand age and height.

Soil CO_2 efflux can be also influenced by sap flow. CO_2 produced by root respiration can be dissolved in the xylem sap and moved upward into the stem via the transpiration stream and may contribute to trunk CO_2 efflux (Teskey and McGuire 2007). This transport of CO_2 from roots can lower the amount of CO_2 diffused from roots to soil and consequently to the atmosphere during daytime (Aubrey and Teskey 2009). Grossiord et al. (2012) suggested that, on average, 17 % of root respiration might be diverted from soil CO_2 efflux during the daytime, with a maximum of 24 % between 11:00 and 15:00 h

5.4 Drought experiment

5.4.1 Experiment design and data analyses

Six roofs (2 x 3 m) were installed at the grassland site in Bílý Kříž during the experimental seasons from May to October 2011 and 2012. The roofs consisted of a wooden construction and acrylate plates. There were two arrangements of the plates. On three roofs the plate arrangement resulted in capturing precipitations and induction of drought and on three roofs it resulted full release of precipitations through the roof (Fig. 41).

For CO_2 efflux measurements, the portable system was used (see chapter 4.2.4). Four collars under each roof were installed before the first measurement in 2011, then they remained at their positions through two years.

Soil moisture was measured continuously (in 10 min interval) using ThetaProbe Soil Moisture Sensor ML2x (Delta-T Devices, Cambridge, UK). A couple of the sensors were inserted at the depth of 10 cm under each roof.

The grass in the collars was clipped on 4 August 2011 and 10 July 2012 when the grassland was mowed. The grass from each collar was dried and weighted. On 9 August 2011 and 30 July 2012, wetting of the dry variant was performed. It simulated about 30 mm rainfall captured by roofs during the first half of the growing season.

The schedule of manual measurements and other actions is presented in Tab. 26.

T-test was performed to test potential differences of variables between individual variants using analytical software SigmaPlot 11.0 (Systat, USA). Statistical significance was tested at the level $\alpha = 0.05$.

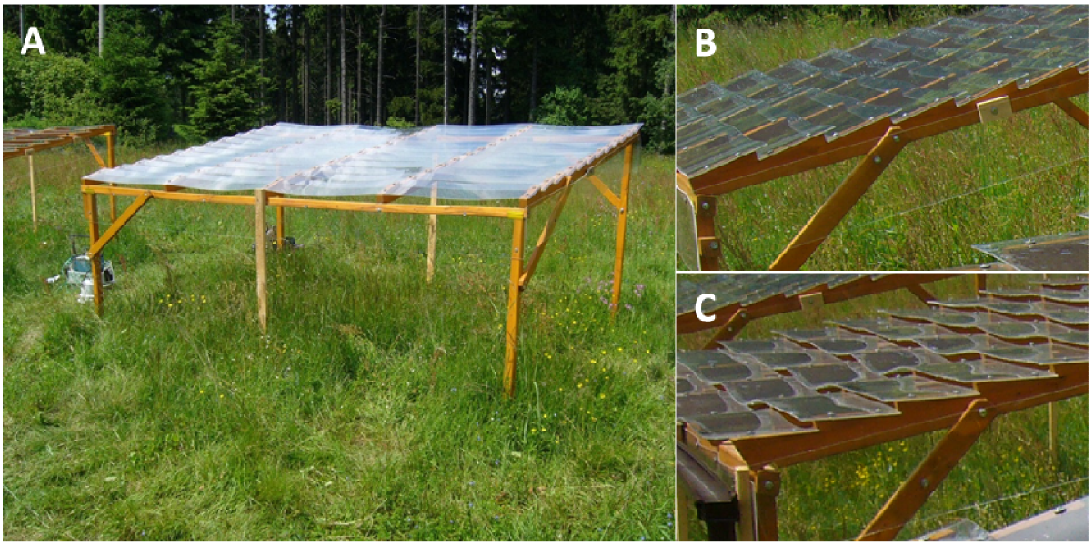

Fig. 41: A - one of six roofs installed in the grassland, B - arrangements of the plates resulting in capturing precipitations, C - arrangements of the plates resulting in drought induction.

5.4.2 Results

Measurements were carried during the growing season 2011 and 2012 and the schemes of the measurement dates and daily sums of precipitations are drawn in Fig. 42. The measurements of soil moisture in 2011 started after roof installation and it can be assumed that soil moisture was not different between the variants before the experiment. During the second measurement of CO_2 efflux (on 16 June 2011), soil moisture in the wet variants reached values about 50 %, while in the dry variants they were about 20 %. Soil moisture held this pattern till 9 August when the soil moisture measurements stopped due to failure of data logger (Fig. 43).

In 2012, soil moisture was slightly lower in the dry variant before roof installation. Then the difference in soil moisture between the dry and wet variants increased and the highest differences were on 7 June and 22 June as in this period intensive precipitations occurred.

After removal of the roofs soil moisture in the dry variant remained lower but the difference between variants was less remarkable (Fig. 44).

In several cases, soil temperature in the dry variant was significantly higher than in the wet variant. The most significant differences in 2011 occurred on 16 June and on 4 August, the day when the grass was clipped. Similarly in 2012, the highest difference in soil temperature between the variants was in the period around clipping of the grass (10 and 11 June) (Fig. 43, 44).

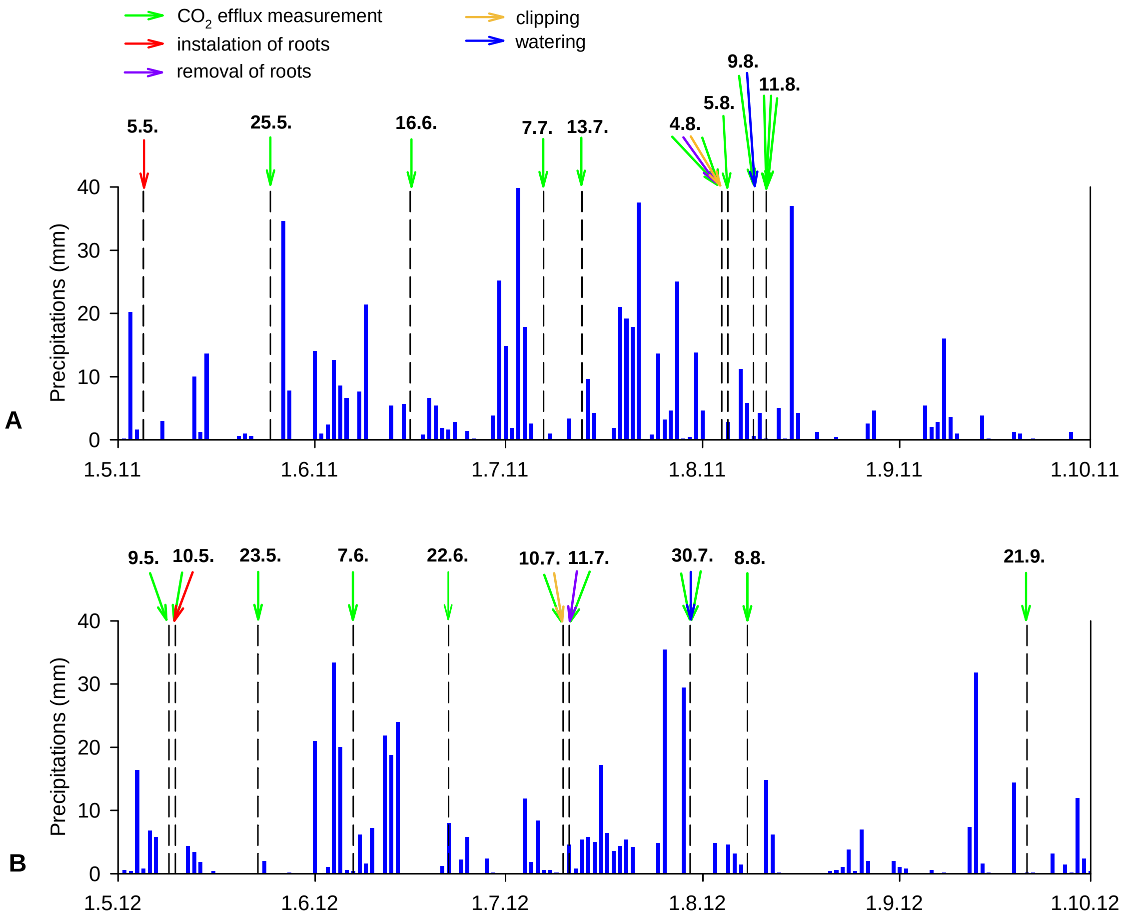

Fig. 42: Daily sums of precipitations during the growing season in 2011 (A) and 2012 (B) with marked days when measurements of CO_2 efflux, roof instalation/removal, clipping and watering were performed. The arrows represent individual actions. If there were more actions during one day, their sequence is shown by the order of the arrows.

Because of technical reasons in 2011, measurements of soil CO_2 efflux started after roof installation. There was no significant difference in CO_2 efflux between three roofs of the wet variant (One Way ANOVA, p=0.24) and low coefficient of variation of CO_2 efflux of the twelve positions of the wet variant (18.4 %) during the first two measurements of CO_2 efflux (25 May and 6 June). I do not, therefore, assume a significant difference of CO_2 efflux between wet and dry variants before the experiment. There was, however, a significant difference in CO_2 efflux between dry and wet variant already during the first measurement (25 May). The CO_2 efflux of the dry variant was by 19.2 % lower than CO_2 efflux of the wet variant. During following four measurements the difference was even about twofold (by 35.8 – 44.2 %). On 4 August 2011, clipping of the above-ground biomass in the collars was done. The difference in CO_2 efflux decreased on about 30 %. Then it slightly increased on 37 % up to the fifth day after the clipping (9 August 2011) (Fig. 43, 45). Clipping of the above-ground biomass had a significant effect on CO_2 efflux in both variants. The CO_2 efflux decreased by 28.7 and 11.8 % in the wet and dry variant, respectively. In the wet variant there was a significantly higher amount of aboveground biomass than in the dry variant (434.6 g m^{-2} (±71.3) and 181.4 g m^{-2} (±96.7) in the wet and dry variant, respectively) (Fig. 46). There was no correlation between CO_2 efflux and the amount of the clipped biomass (p=0.3) in the wet variant, in contrast to the dry variant, where the significantly positive correlation was observed (Fig. 46).

After the measurement on 9 August 2011, wetting of the dry variant was performed. The next measurements of CO_2 efflux were done on 11 August 2011 after 5 mm of total rainfall. During these measurements there was no significant difference in CO_2 efflux between variants (p>0.05).

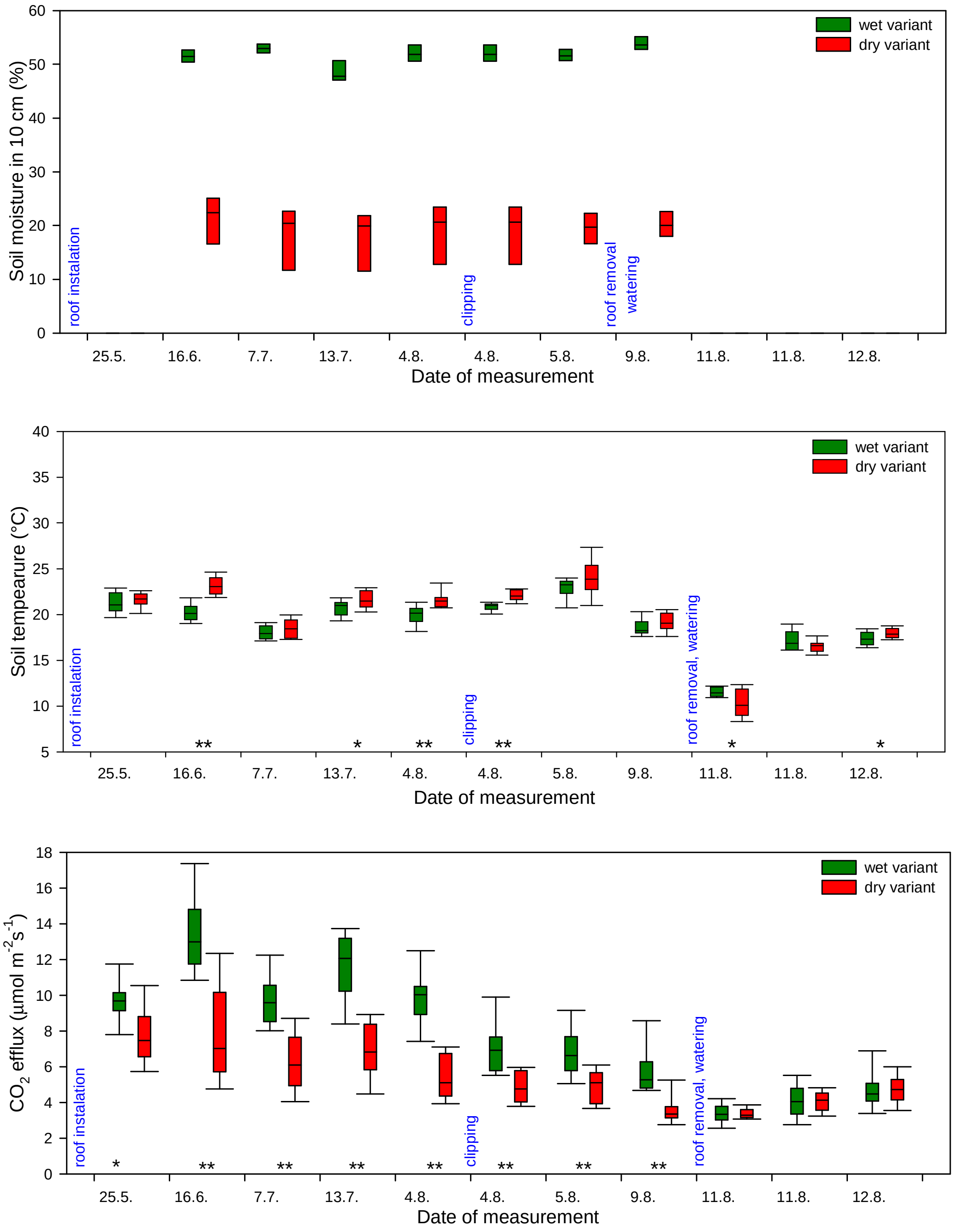

Fig. 43: Soil moisture, soil temperature and CO_2 efflux measured at the grassland ecosystem under roofs in 2011. Stars in graphs indicate statistically significant difference between wet and dry variants: * p>0.05, ** p>0.001.

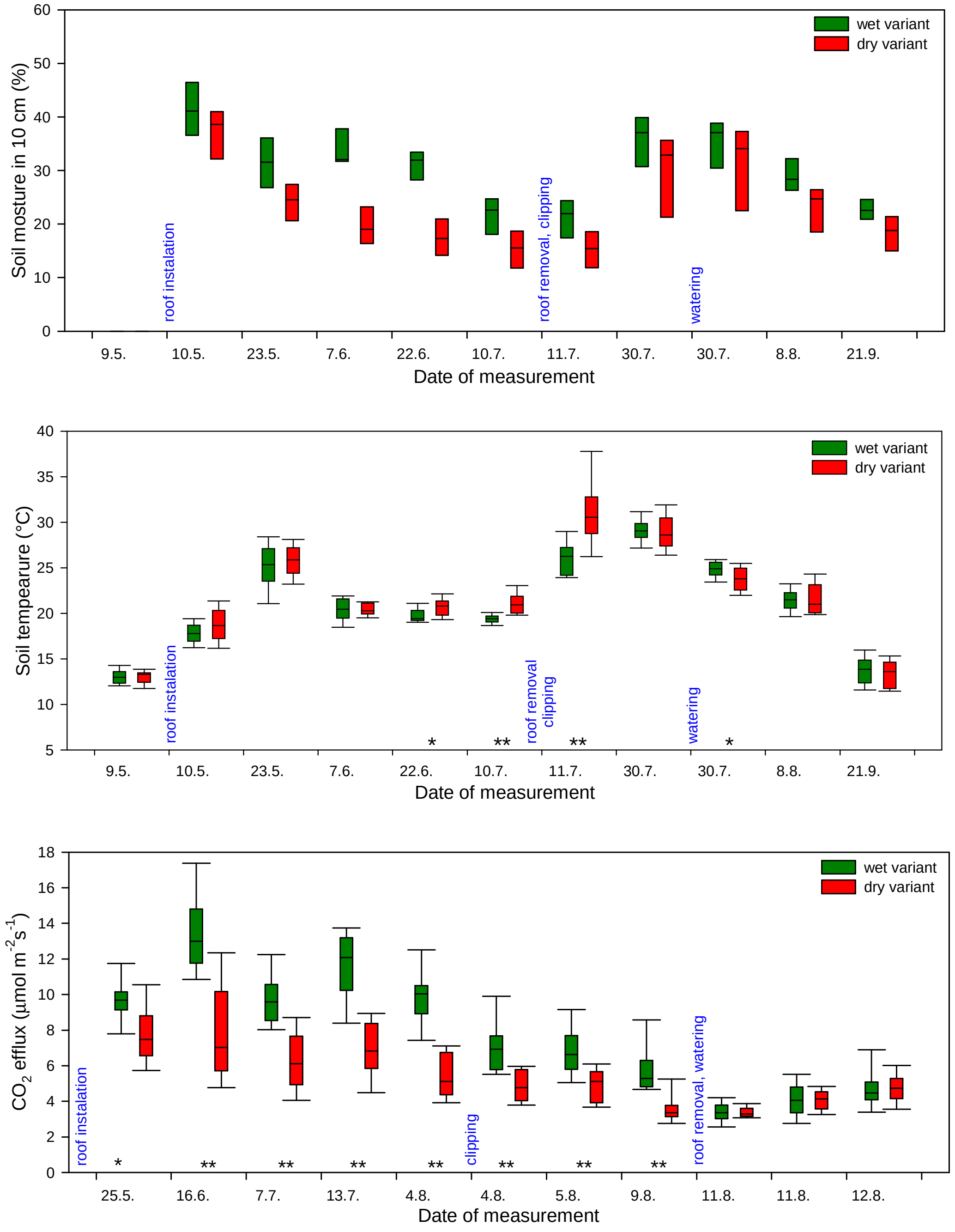

Fig. 44: Soil moisture, soil temperature and CO$_2$ efflux measured at the grassland ecosystem under roofs in 2012. Stars in graphs indicate statistically significant difference between wet and dry variants: * p>0.05, ** p>0.001.

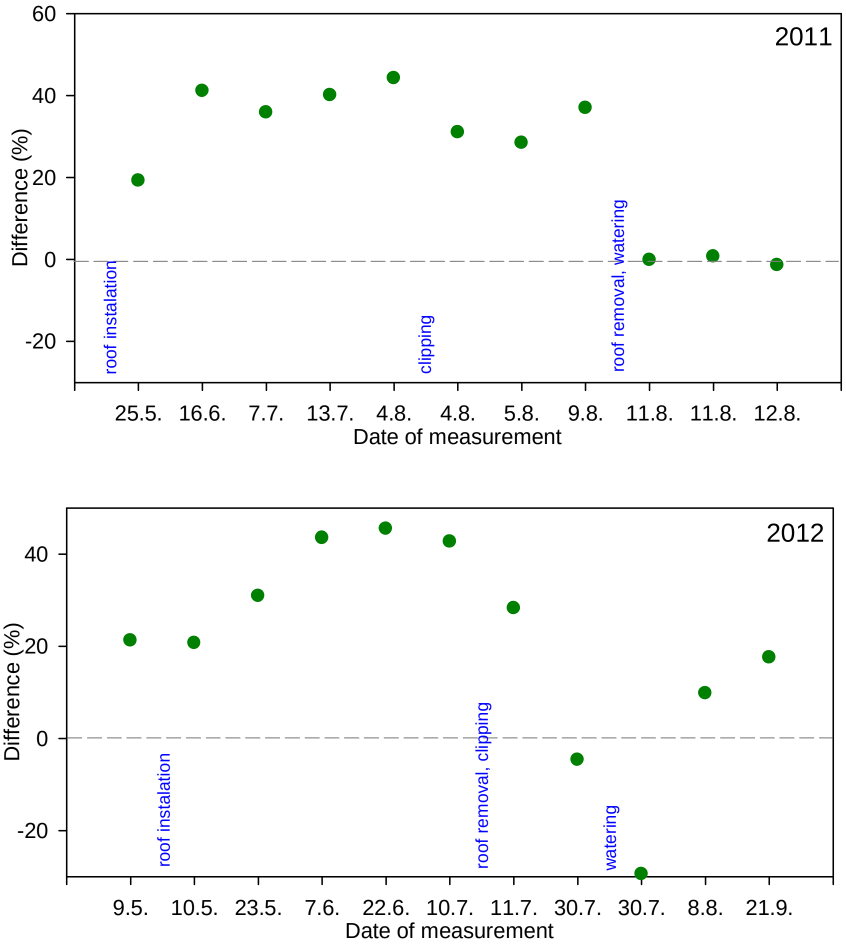

Fig. 45: Percentage difference in CO_2 efflux in the dry variant from the wet variant in 2011 and 2012.

In 2012, there was a significant difference in CO_2 efflux between the wet and dry variant already before the roof installation and the CO_2 efflux in the dry variant was by 23.1 % lower than in the wet variant (mean from two measurements on 9 and 10 May). The difference of CO_2 efflux in the dry variant from CO_2 efflux in the dry variant increased till June and then it remained on the same level (about 43 %). After clipping on 10 July 2012 the difference decreased on about 28.2 % (Fig. 44). Then the roofs were removed. The next measurement was performed on 30 July after 132 mm precipitations. There was no significant difference in CO_2 efflux between the variants. After the measurement, wetting of the dry variant was performed and significantly higher CO_2 efflux in the dry variant than in the wet variant was observed. Nine days after wetting (after 14 mm precipitation), there was no difference in CO_2 efflux between the variants again. The last measurements were done on 21 September 2012. CO_2 efflux in the dry variant was significantly lower than in the wet variant with the difference of 17.5 %.

After clipping on 10 July 2012, there was a significantly higher amount of clipped aboveground biomass in the wet variant (302.12 g m^{-2} (±107.2)) than in the dry variant (205.3 g m^{-2} (±85.1)) (Fig. 45). No correlation between CO_2 efflux and the amount of the clipped biomass was found in the wet variant. However, CO_2 efflux was significantly positively correlated with the amount of above-ground in the dry variant as in 2011 (Fig. 45).

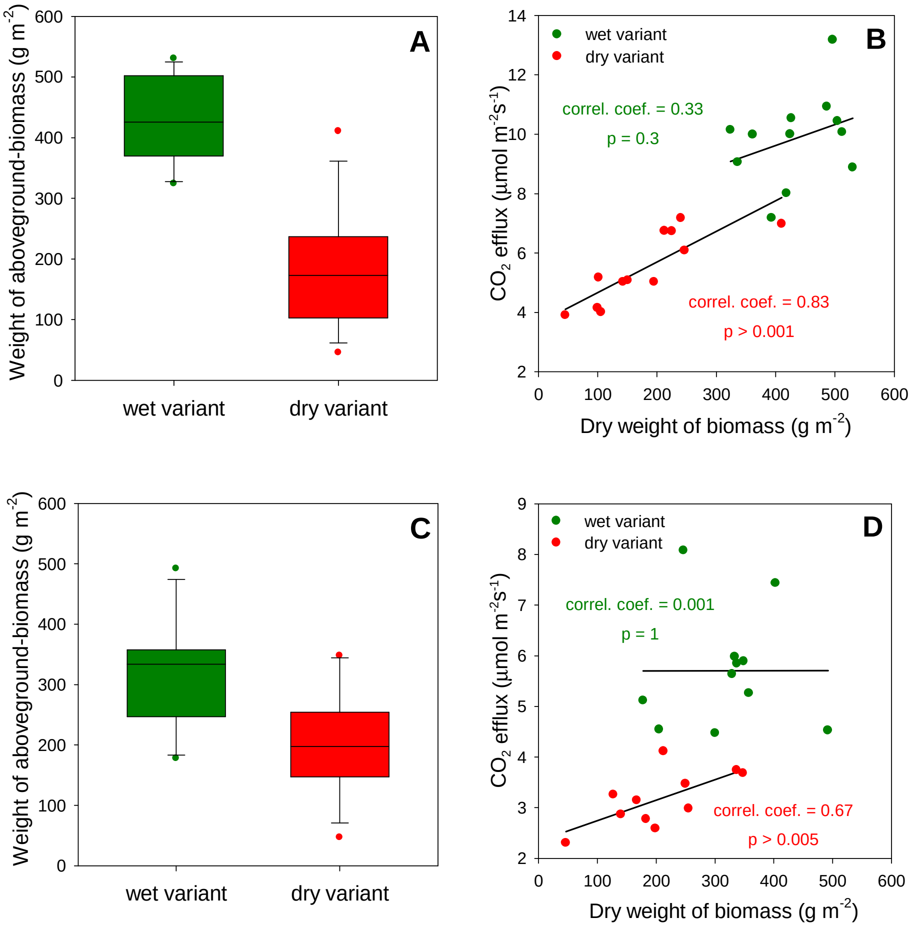

Fig. 46: Dry weight of above-ground biomass and its correlation with CO_2 efflux before clipping in 2011(A and B) and in 2012 (C and D).

5.4.3 Discussion

Expected global climate change includes an increase in global surface temperatures, change in intensity and frequency of precipitation as well as evapotranspiration in most regions of the earth (IPCC 2001). Many climate change predictions suggest that periodic droughts will become more common and extreme rainfall events more frequent (Mearns et al. 1995, Frederick and Major 1997, Easterling et al. 2000). The combination of increased dry periods interspersed with larger individual rainfall events will result in extended periods of soil moisture deficit and greater variability in soil water content (Giorgi et al. 1998, Jackson et al. 2001). This study investigated response of ecosystem CO_2 efflux of the grassland to induced drought in the first half of the growing season and rewetting with 30 mm simulated precipitation after this period.

During the experiment, higher soil temperature in the dry variant than in the wet variant was measured, especially during the period around clipping of the grass in measurement collars, performed at the time when the grassland was mowed (Fig. 43 and 44). That can be a result of the difference in the amount of above-ground biomass between the variants. That works as an isolation layer (prevents the sun radiation to warm the soil surface) and the lower amount of biomass resulted in faster warming of soil surface (Bremer et al 1998, Zhou et al. 2007). On the contrary, at night more intensive decrease of soil temperature at positions with low amount of grass could be expected because of higher heat flux from the soil surface.

The negative effect of the drought on the amount of the above-ground biomass was observed in both experimental years (Fig. 46). The drought in our experiment was induced in the first half of growing season, which is the most active period of plant growth, and therefore it has the highest potential to influence plant production. This assumption suggests that spring drought can be more critical to carbon dynamics than for example summer lack of precipitations as suggested by Kwon et al. (2008).

The decrease in the amount of above-ground biomass results also in decrease in the amount of photosynthesis assimilates going to the roots and then to the soil (Johnson et al. 2011). Therefore, the amount of the substrate for root/soil respiration is reduced and that results in lower soil CO_2 efflux. The drought effect on biomass growth may result in lower amount of plant remains and litter available for decomposition and long-term effect on soil CO_2

efflux. This can explain the lower CO_2 efflux from the dry variant than from the wet variant at the beginning of the second season of our experiment.

Ecosystem CO_2 efflux significantly decreased in the dry variant within two weeks after roof installation. This decrease was likely caused mainly by decrease in soil CO_2 efflux as soil respiration responds faster to the lack of precipitation than plant respiration as the most active is the top of soil which is sensitive to drying (Davidson et al. 2006b). Plants can postpone the response to drought as they can reach water from deeper horizons through their root system (Dong et al. 2011). Other decrease in CO_2 efflux was caused by above mentioned lower amount of plant biomass and photosynthesis assimilates.

Removal of the roofs and watering of the dry variant resulted in significant increase in the grassland CO_2 efflux. That even exceeded CO_2 efflux from the wet variant in 2012 (Fig. 45). Sudden rewetting of the dry soil can increase its respiration activity due to enhanced availability of labile organic substrates through microbial death and cell lysis (Halverson et al. 2000) or by destabilizing soil aggregates, making soil organic matter accessible to microbes (Denef et al. 2001).

The manipulation of precipitation pattern had an immediate effect observed during the first experimental year. But the manipulation reflected also in the beginning of the next growing season before roof installation as significantly lower CO_2 efflux in the dry variant than in the wet one was observed. That can be explained as a certain time-lagged response of the productivity of plants to restoring ambient precipitations (roof removal in our case) resulting in the lower amount of biomass (Yahdjian 2006). The CO_2 efflux course in 2012 had a similar trend as in the previous season. CO_2 efflux in the dry variant, however, temporarily exceeded efflux in the wet variant after watering. This measurement of CO_2 efflux was done shortly after watering in contrast to 2011 when the measurement was done after a rain event occurred. Therefore a stronger response of CO_2 efflux in 2012 than in 2011 was observed.

The drought has an immediate effect on grassland carbon balance but it can significantly affect the carbon balance during following periods. For example Zhang et al. (2012) found that spring drought negatively affected also primary productivity of the grassland in summer. In this study, it was confirmed that changing precipitation distribution with drought in the first half of the growing season has long term effect on CO_2 efflux from the grassland ecosystem.

6 Conclusions

In the frame of ecosystem stations equipped with eddy-covariance tower to measure carbon balance at four ecosystems (spruce forest, grassland, beech forest and wetland), the supporting measurements of soil CO_2 efflux were carried out. The spatial heterogeneity of soil CO_2 efflux was assessed at each ecosystem and, moreover, temporal dynamics of soil CO_2 efflux in the spruce forest and ecosystem CO_2 efflux in the grassland was investigated. The possible effect of the time of the manual measurements of soil CO_2 efflux and soil temperature on the seasonal cumulative estimation of released carbon from the forest floor was also analyzed. And, finally, the impact of induced drought and change in precipitation distribution on the grassland respiration was studied.

The main factor driving temporal dynamics of soil CO_2 efflux in the case of the spruce forest and ecosystem CO_2 efflux in the case of the grassland was soil temperature. The next important factor affecting soil CO_2 efflux of the spruce forest was soil moisture as there was often a strong positive response of soil CO_2 efflux on rain events. In summer months, an increase in soil respiration activity was observed even after the exclusion of the effect of soil temperature. That can be assumed to be an effect of the growth of fine root biomass and enhanced gross production. On the contrary, rain events did not have such a strong effect on CO_2 efflux from the grassland ecosystem. Instead, the amount of the growing above-ground biomass was an important factor of the ecosystem CO_2 efflux. The study confirmed that soil moisture and phenological phases influence determination of the parameters of CO_2 efflux dependence on temperature.

The spatial heterogeneity in CO_2 efflux, respiration activity and the influence of factors differed among investigated ecosystems. In the grassland, the variability amounted 15 – 17 % and was the lowest from the investigated ecosystems. Differences in CO_2 efflux among positions were caused mainly by the increase of CO_2 efflux with soil moisture and with the height of the above-ground biomass. In the forest stands, the variability of soil CO_2 efflux was higher than in the grassland and amounted 27 – 46 %. We were quite unsuccessful to sufficiently explain the cause of the variability. Several times a negative effect of soil moisture on soil CO_2 efflux rate on the positions was found. The other causes should be probably looked for in the soil properties, such as the amount of organic matter, litter, fine roots or gravel. The variability is at these sites very high, therefore manual measurements on a similar number of positions as in this study is highly recommended to be provided several times per year to accompany continuous measurements in order to correctly estimate carbon losses through soil respiration.

The lowest respiration activity and, on the contrary, the highest spatial variability of CO_2 efflux was found in the wetland. That was because of the high level of water table, which results in reduction of organic matter decomposition, and of the gradient of the water table at the experimental site. Because of the high variability, it would be difficult to precisely estimate soil CO_2 efflux from the ecosystem. Therefore, more measurements of water table and recording of its gradient together with the model described in this study should contribute to correct estimation of soil CO_2 efflux at this site.

The results of this study confirmed, that time of the day when the manual measurements of soil CO_2 efflux are performed can have the effect on determination of parameters R_{10} and Q_{10} and then on calculation of the total amount of carbon released during the season using these parameters and continuously measured temperature. Measurements from 00:00 to 08:00 and at 22:00 overestimated, and the measurements from 12:00 to 18:00 underestimated estimation of the seasonal soil carbon flux. The lowest differences were found for the measurements at 10:00 and 20:00. The time when the bias of estimation of the seasonal soil carbon flux is the smallest, is individual for different ecosystems. Although the intervals between measurements can have a greater effect on the estimation, the effect of the measurement time of the day should not be neglected. There should be some ways how to minimize the effect of the measurement time. First, the time when the effect is the smallest can be found and measurements done about this part of day. Or, measurements can be done at different parts of day.

In the study the induced drought has and immediate effect on the grassland ecosystem. It reflected in lower soil moisture, respiration and the amount of biomass, and in an increase in soil temperature. Changing precipitation distribution with drought in the first half of the growing season had the effect on CO_2 efflux from the grassland ecosystem also in the beginning of the following year.

This study brings important knowledge about soil CO_2 efflux, as a main component of ecosystem respiration, at the investigated sites, which is crucial for understanding of carbon balance at the investigated sites, and the results will contribute to knowledge of CO_2

exchange measured by eddy-covariance method. The study will also contribute to design sufficient protocols of CO_2 efflux measurements at these sites. And finally, the study will help to better understanding of response of CO_2 efflux at the individual ecosystems to external factors.

7 Souhrn

V současné době je velká pozornost věnována koloběhu uhlíku v ekosystémech, jelikož během posledních desetiletích došlo v atmosféře k výraznému nárůstu koncentrace oxidu uhličitého (CO_2), který je významným skleníkovým plynem. Tato práce se proto soustředila na tok CO_2 uvolněného z půdy, případně celého ekosystému, jakožto významného zdroje CO_2 v atmosféře.

V rámci práce byla ve čtyřech ekosystémech (smrkový les, bukový les, louka a mokřad) prováděna měření toku CO_2 z půdy/ekosystému pomocí automatických i manuálních systémů. Ve všech čtyřech ekosystémech byla sledována prostorová heterogenita toku CO_2 z půdy/ekosystému a ve smrkovém porostu a na louce byla navíc sledována časová dynamika toku CO_2 z půdy (les) a z ekosystému (louka). Dále byl analyzován vliv denní doby manuálního měření na odhad množství uhlíku uvolněného z půdy smrkového porostu během růstové sezóny. A nakonec byl sledován vliv sucha a změny distribuce srážek na tok CO_2 z lučního ekosystému.

Hlavním faktorem řídícím časovou dynamiku toku CO_2 z půdy ve smrkovém porostu a z lučního ekosystému byla teplota půdy. Dalším důležitým faktorem ovlivňujícím tok CO_2 z půdy ve smrkovém porostu byla půdní vlhkost a byla sledována silná pozitivní reakce toku CO_2 z půdy na srážky. V letních měsících byl sledován nárůst respirační aktivity půdy, který mohl být způsobený nárůstem jemných kořenů a zvýšenou primární produkcí lesního ekosystému. Na rozdíl od lesní půdy, srážky neměly tak velký efekt na tok CO_2 z lučního ekosystému. Zde byl spíše hlavním faktorem množství rostoucí nadzemní biomasy. Studie potvrdila, že vlhkost půdy a fenonologické fáze mají vliv na stanovení parametrů závislosti toku CO_2 na teplotě.

Prostorová heterogenita toku CO_2 a respirační aktivita půdy/ekosystému i vliv faktorů se lišily mezi sledovanými ekosystémy. Luční ekosystém vykazoval variabilitu toku CO_2 z ekosystému 15 – 17 % a tato heterogenita byla nejnižší ze sledovaných ekosystémů. Rozdíly mezi měřenými pozicemi v toku CO_2 byly ovlivněny především množstvím nadzemní biomasy a vlhkostí půdy. V lesních porostech byla variabilita toku CO_2 z půdy vyšší než u louky a činila 27 – 46 %. Nepodařilo se mi zcela vysvětlit příčinu této variability. V několika případech byl nalezen negativní vliv půdní vlhkosti na tok CO_2. Dalšími příčinami by mohly být vlastnosti půdy, jako je např. množství organického materiálu, opadu, jemných kořenů nebo kamenů. Heterogenita toku CO_2 byla v těchto ekosystémech vysoká, proto by bylo pro správné stanovení uhlíkových ztrát z půdy vhodné rozšířit automatická měření toku CO_2 z půdy manuálními měřeními na více pozicích, a to několikrát v průběhu roku.

Nejnižší respirační aktivita, ale naopak největší prostorová heterogenita toku CO_2 byla nalezena na mokřadním ekosystému. Toto bylo způsobeno vysokou hladinou podzemní vody, která měla za následek zpomalení rozkladu organického materiálu, a jejím gradientem na experimentálním stanovišti. Kvůli vysoké variabilitě by bylo složité správně odhadnout tok CO_2 z půdy celého ekosystému. Proto by více měření hloubky vodní hladiny a zaznamenání jejího gradientu společně s modelem popsaným v této práci mohly přispět k přesnějšímu stanovení toku CO_2 z půdy na tomto experimentálním stanovišti.

Výsledky této práce potvrdily, že čas, který jsou prováděna měření toku CO_2 z půdy a půdní teploty, může mít vliv na stanovení parametrů R_{10} a Q_{10} a následně na výpočet celkového množství uhlíku uvolněného z půdy během růstové sezony za pomocí těchto parametrů a kontinuálně měřené teploty půdy. Měření od 0:00 do 8:00 a ve 22:00 nadhodnocovaly a měření od 12:00 do 20:00 podhodnocovaly stanovení celkového množství uvolněného uhlíku. Nejmenší rozdíly vykazovala měření v 10:00 a 20:00. Čas měření, kdy je odhad toku uhlíku z půdy nejpřesnější je různý pro různé ekosystémy. Ačkoli délka intervalu mezi manuálními měřeními může mít na výsledky větší vliv, ani vliv doby měření by neměl být zanedbán. Toho lze dosáhnout tím, že pro daný ekosystém najdeme dobu, kdy je zkreslení výsledků nejmenší, nebo že provádíme měření v různou hodinu.

Tato práce potvrdila, že periody sucha mají okamžitý efekt na luční ekosystém. To se odrazilo v poklesu půdní vlhkosti, toku CO_2 z ekosystému a množství biomasy, a naopak zvýšení teploty půdy. Změna rozložení srážek s obdobím sucha v první polovině růstové sezony mělo negativní vliv na tok CO_2 s ekosystému i na začátku následující růstové sezony. To potvrzuje, že dlouhé periody sucha by mohly mít i dlouhodobý vliv na celkovou uhlíkovou bilanci lučních ekosystémů.

Tato práce přináší důležité poznatky o tocích CO_2 z půdy, která je, jakožto důležité složky ekosystémové respirace, důležitá pro porozumění uhlíkové bilance na experimentálních stanovištích. A výsledky dále přispějí k poznatkům ekosystémové výměny CO_2 měřené eddy-kovarianční metodou. Práce také přispěje k tvorbě vhodných protokolů měření toku CO_2 z půdy/ekosystému na těchto stanovištích. A tato práce také pomůže lépe porozumět odpovědí toku CO_2 v jednotlivých ekosystémech na měnící se vnější podmínky.

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