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Soil CO_2 efflux from mountainous windthrow areas: dynamics over 12 years post-disturbance

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Abstract

Windthrow driven changes in carbon (C) allocation and soil microclimate can affect soil carbon dioxide (CO_2) efflux (F_{soil}) of forest ecosystems. Although F_{soil} is the dominant C flux following stand-replacing disturbance, the effects of catastrophic windthrow on F_{soil} are still poorly understood. We measured F_{soil} at a montane mixed forest site and at a subalpine spruce forest site from 2009 until 2012. Both sites consisted of undisturbed forest stands and two adjacent windthrow areas which differed in time since disturbance. The combination of chronosequence and direct time-series approaches enabled us to investigate F_{soil} dynamics over 12 years post-disturbance. In the initial phase after disturbance (1–6 years), F_{soil} rates did not differ significantly from those of the undisturbed stands, but in the later phase (9–12 years after disturbance) F_{soil} rates were significantly higher than corresponding undisturbed stand values. The higher F_{soil} rates in the later phase post-disturbance are likely explained by a dense vegetation cover and correspondingly higher autotrophic respiration rates. Soil temperature increased significantly following windthrow (by 2.9–4.8 °C) especially in the initial phase post-disturbance when vegetation cover was sparse. A significant part (20–36 %) of F_{soil} from the windthrow areas was thus attributed to disturbance induced changes in soil temperature. According to our estimates, ~ 500 to 700 $g\,C\,m^{-2}\,yr^{-1}$ are released via F_{soil} from south-facing forest sites in the Austrian Calcareous Alps in the initial 6 years after windthrow. With high game pressure suppressing primary production in these areas, post-disturbance loss of ecosystem C to the atmosphere is likely to be substantial unless management is proactive in regenerating such sites. An increase in the frequency of forest disturbance by windthrow could therefore decrease soil C stocks and positively feedback on rising atmospheric CO_2 concentrations.

BGD

11, 6383–6417, 2014

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M. Mayer et al.

1 Introduction

The global carbon dioxide (CO_2) efflux from soil (F_{soil}) was recently estimated at 98 ± 12 Pg carbon (C) yr^{-1} (Bond-Lamberty and Thomson, 2010), representing the major pathway by which terrestrial ecosystems release CO_2 into the atmosphere (Schlesinger and Andrews, 2000). In forests, F_{soil} typically accounts for roughly 40 to 80 % of the total ecosystem respiration (Curiel Yuste et al., 2005; Davidson et al., 2006; Janssens et al., 2001) and offsets a large part of the CO_2 sequestered via gross primary production (Janssens et al., 2001). The relative contribution of F_{soil} to forest C budgets can however be even greater following forest disturbance (Janssens et al., 2001) thereby reducing the ecosystem C sink strengths (Lindroth et al., 2009). As natural forest disturbance regimes are likely to be altered by climate change (Dale et al., 2001), a detailed understanding of disturbance impacts on F_{soil} is essential if the forests role in the global C cycle, and thus the climate system, is to be evaluated correctly.

Natural and anthropogenic disturbance events, such as stand replacing fires, insect infestations, windthrow or forest harvests, can influence many biotic and abiotic factors (Amiro, 2001; Amiro et al., 2010; Kurz et al., 2008; Lindner et al., 2010; Katzensteiner, 2003; Christophel et al., 2013) and thereby affect F_{soil}. Catastrophic storms are responsible for more than half of the damage in European forests (Gardiner et al., 2010), and the risk of wind damage is expected to increase in the future (Schelhaas et al., 2010). According to the conceptual trajectory of Odum (1969) the pre-disturbance ecosystem is sequestering C, until disturbance causes an initial, rather discrete loss of C, which is followed by a period of recovery. In the case of windthrow, the initial C loss is due to the increase in heterotrophic respiration following the sharp decline in photosynthetic C fixation. Considering the windthrow is stand replacing (all trees killed), F_{soil} is likely the main C flux before and during the primary phase of forest recovery (Knohl et al., 2002). The role of F_{soil} in post-disturbance ecosystem C cycling is thus very important. Considering C decomposition and potentially F_{soil} significantly increases after disturbance, a large amount of ecosystem C can be lost to the atmosphere (Kurz et al., 2008; Cov-

BGD
11, 6383–6417, 2014

ington, 1981), however in cases where F_{soil} decreases post-disturbance, net loss of C to the atmosphere will be correspondingly small (Moore et al., 2013). A quantification of this flux is therefore highly important to better understand the overall effects of disturbances on forest ecosystem C dynamics and potential C loss to the atmosphere. Following windthrow, soil initially receives a pulse of organic C inputs in the form of litter and woody debris from killed trees. Roots of dead trees decompose and represent a further source of organic C. However, after this initial C inputs, tree litter production and active transport of labile C from the trees to the rhizosphere cease (Högberg et al., 2001; Levy-Varon et al., 2012; Singh et al., 2008; Olajuyigbe et al., 2012; Tang et al., 2005) with renewed C inputs depending on subsequent vegetation establishment. Litter from populating pioneer herbs and grasses can for instance differ in quality and quantity to that provided pre-disturbance (Spielvogel et al., 2006). All these dynamic changes in soil C supply will influence the quantity and quality of soil organic matter (SOM) as well as the microbial community (Holden and Treseder, 2013) and thereby affect F_{soil}. Windthrow can also affect microclimatic variables such as soil temperature and moisture, which are key drivers of SOM decomposition (Davidson et al., 1998; Davidson and Janssens, 2006; Lloyd and Taylor, 1994). Complete or partial removal of the tree layer, and the associated changes in insolation at the ground and transpiration demand on the soil can lead to altered soil temperature and soil moisture regimes (Payeur-Poirier et al., 2012; Kulmala et al., 2014; Peng and Thomas, 2006; Pumpanen et al., 2004; Singh et al., 2008). Due to the complex interplay of rate limiting and favourable factors regarding organic matter decomposition, the overall response of F_{soil} to windthrow depends on many site and ecosystem specific factors. Post-disturbance F_{soil} is thus difficult to estimate with generalized paradigms of ecosystem behaviour. Furthermore, the temporal evolution of F_{soil} post-windthrow is a particularly "grey" area as many studies have conducted only short (1–2 years) measurement campaigns (Vargas, 2012; Vargas and Allen, 2008; Wright and Coleman, 2002; Köster et al., 2011; Thuille et al., 2000).

BGD
11, 6383–6417, 2014

In the European Alps complex topographic preconditions and a tendency towards increasingly aged stands (Seidl et al., 2011) promote susceptibility to larger scale windthrow damage. Across Europe soil C stocks increase significantly with altitude (Sjögersten et al., 2011), and the largest organic carbon contents were found in the upper soil horizons of forests in alpine regions (Baritz et al., 2010). High soil C contents and the potential increase in windthrow event frequency mean that these ecosystems could be future hotspots of ecosystem C loss. Despite this threat, the effects of windthrow on F_{soil} in mountainous regions of the European Alps have been rarely quantified.

We studied two mountainous forest stands which had periodically been hit by larger-scale windthrow events. Together the study sites offered two undisturbed forests and four windthrow areas in varying stages after disturbance. Combining time series and chronosequence approaches the areas were investigated to track development of F_{soil} over 12 years post-disturbance. Our main objectives were to investigate the effects of windthrow disturbance on soil microclimate and F_{soil}, and to address the post disturbance dynamics in relation to ground vegetation re-establishment. We hypothesized that F_{soil} would decrease in the first years post-disturbance (due to a decrease in autotrophic respiration), and reach pre-disturbance levels with subsequent ground vegetation establishment.

2 Materials and methods

2.1 Study sites

The study took place at the Rax mountain area (henceforth "Rax"; 47°43′37′′ N, 15°41′20′′ E) and in the Höllengebirge mountain range (henceforth "Höllengebirge"; 47°47′19′′ N, 13°38′21′′ E), located in the eastern and the central part of the Austrian Calcareous Alps, respectively (Fig. 1). Rax is a subalpine, coniferous dominated forest site at an altitude of 1470 m a.s.l., and Höllengebirge is a montane, broadleaved–

coniferous mixed forest site at an altitude of around 1000 m a.s.l. Both sites are south to south-west exposed. Climatic conditions at the sites are cool and humid, characterized by distinctive precipitation maxima during summer and precipitation minima during spring and fall (Kilian et al., 1994). Average (2002–2012) air temperature and precipitation were 3.8 °C and 1424 mm at the Rax site (closest climate station ~ 7 km apart at similar altitude) and 6.6 °C and 1964 mm at the Höllengebirge site (interpolated values from the closest climate stations both ~ 10 km apart) respectively (ZAMG, 2013). Growing season at both sites is between May and September.

The forest stand at the Rax site was dominated by Norway spruce (*Picea abies*) with a stand age of 185 years in 2012. The ground vegetation cover consisted of a very sparse herbal and grass layer (*Lycopodium sp.*, *Luzula luzuloides*). The forest stand at Höllengebirge was dominated by European beech (*Fagus sylvatica*), co dominated by Norway spruce (*Picea abies*) and Silver fir (*Abies alba*) and intermixed by Sycamore (*Acer pseudoplatanus*) and European ash (*Fraxinus excelsior*). The average stand age was 219 years in 2012. Ground vegetation was also very sparse composed of herbs (*Mycelis muralis*, *Prenanthes purpurea*), grasses (*Calamagrostis varia*) and a few, infrequently occurring understory trees (*Picea abies*).

In winter 1999/2000 the Rax site was affected by a storm event where several hectares of the forest stand were either blown over or suffered wind-snap. A subsequent windthrow in winter/spring 2007 then worked its way from the exposed forest edge eastwards (Fig. 1a). Respective areas are denoted as "Rax windthrow 2000" (RW00) and "Rax windthrow 2007" (RW07) treatments in the following. The unaffected intact stand adjacent to the windthrow areas served as a control (RC). At the Höllengebirge site a windthrow in winter/spring 2007 and subsequent bark beetle events cleared roughly 25 ha of forest. This was then followed by subsequent windthrow disturbance in winter/spring 2009, which opened up a further 4 ha (Fig. 1b). The denotation of these specific areas is "Höllengebirge windthrow 2007" (HW07) and "Höllengebirge windthrow 2009" (HW09) treatments accordingly. The unaffected stand beside the windthrow areas again served as a control (HC).

At both sites most of the coarse woody debris, predominately the stem fraction was harvested by cable yarding operations immediately after the disturbance events. Ground vegetation reestablishment at the disturbed areas at both sites comprised initially herbaceous plants (*Senecio jacobaea*, *Adenostyles glabra*, *Eupatorium cannabinum, Cirsium arvense*, *Urtica dioica*) followed by grass vegetation (*Luzula luzuloides*, *Calamagrostis varia, Calamagrostis villosa*). Except for sparse groups of spruce (*Picea abies*) remaining from a pre-disturbance understory tree layer at HW07, natural tree regeneration was largely inhibited at both sites.

The Rax and the Höllengebirge sites were similar to one another regarding bedrock and soil conditions. The parent bedrock was mainly limestone in paragenesis with dolomite. Chromic Cambisols, Rendzic Leptosols and Folic Histosols (WRB, 2006) were the dominant soil types and Moder and Tangel (Zanella et al., 2011) the main humus forms. A slope line transect showed that Folic Histosols and Rendzic Leptosols tended to occur at steeper terrain and Chromic Cambisols at flatter areas. The heterogeneous conditions typical of *Karst* meant the above soil- and humus types were often found within meters of one another. Soil depth as well as organic layer thickness varied substantially with 0 to 68 cm at Rax, and 0 to 100 cm at Höllengebirge. Carbon content of the organic layer ranged between 18.2 to 50.9 % at Rax and 25.2 to 58.7 % at Höllengebirge. On average 13 % and 27 % of the total area was constituted by rock outcrops at Rax and Höllengebirge respectively.

2.2 Experimental design

The assessment of F_{soil} at undisturbed areas and windthrown areas which differed in time since disturbance, together with direct time series measurements of F_{soil} at all windthrow and stand areas allowed us to combine time series and chronosequence approaches. Time series of F_{soil} were measured at both sites, but spatial and temporal resolution of measurements was higher at the Höllengebirge site which was a core site of the INTERREG project "SicAlp". At the Rax site six to eight plots were established at the individual treatments. Plots were arranged along slope line transects

(Fig. 1a). Measurements of F_{soil} and soil temperature at Rax started in July 2009 and were supplemented by soil moisture measurements from July 2010 onwards. Measurements were accomplished at irregular intervals (monthly to three month) during the snow-free periods and ended in November 2012. At Höllengebirge, 89 plots were arranged in a nested (multi – stage) sampling scheme (Fig. 1b), composed of different distance stages (Webster and Oliver, 2007). The distance stages were 100 m, 50 m, 25 m, 12.5 m and < 12.5 m. In sum 21, 35 and 33 plots were established at HC, HW09 and HW07 respectively. Such a design was chosen to conduct additional geostatistical analysis of F_{soil} and to cover the footprint area of an eddy covariance tower at the windthrow area. Thus, more plots were established at the disturbed areas compared to the control (HC). Results from geostatistics and eddy-covariance analysis will be discussed in separate publications. Measurements of F_{soil}, soil temperature and soil moisture were taken biweekly to monthly from August to November 2010 and monthly from April to November 2011 and May to November 2012 (during snow free conditions). Additional measurements were carried out in January 2011 due to snow free conditions. Due to limited manpower, plots of the 100 m and 50 m distance stages (Fig. 1b small crosses) had to be left out in 2012. Thus, measurements were taken only at plots of the 25 m distance stage and smaller, which reduced the number of the plots to 13, 29 and 23 at HC, HW09 and HW07 respectively. The reduced replication of plots however had no significant effect on variance and mean values of F_{soil}, soil temperature and soil moisture. Therefore these 65 plots were used for further analyses at the Höllengebirge site.

2.3 Measurements of soil CO_2 efflux, soil microclimate, and ground vegetation

Two weeks prior to the first F_{soil} measurements, a single PVC collar (4 cm height, 10 cm inner diameter) was installed at each plot. The collars were inserted 3 cm into the soil surface (including litter layer) and were kept in place throughout the whole study. Establishing vegetation inside the collars was clipped regularly at both sites. Measurements of F_{soil} were conducted by means of the closed chamber technique, using a portable infrared gas analyser (model EGM-4, PP Systems International, Inc. Amesbury, MA, USA) and an attached mobile respiration chamber (model SRC-1, PP Systems International, Inc. Amesbury, MA, USA). For each plot the chamber was placed over the respective collar and measured the concentration increase in the chamber headspace. Adjacent to the collars, soil temperature and soil moisture were measured simultaneous to the F_{soil} measurements. Soil temperature was measured at a soil depth of 5 cm (including litter layer) using a handheld thermometer. Soil moisture, measured as volumetric water content, was determined for 0 to 7 cm soil depth (including litter layer) by means of time domain reflectometry (TDR) using a calibrated soil moisture meter (model Field Scout, Spectrum Technologies, Inc. Plainfield, IL, USA). The measurement cycles took ~ 2 h at Rax and between ~ 8 h (65 plots) and ~ 14 h (89 plots) at Höllengebirge. Plots at both sites were measured in the same order throughout the study. Soil temperature in 5 cm depth (including litter layer) was continuously measured with thermocouple elements at RC and at HW09 as well. The data were recorded by Minicube data loggers (EMS, Brno, Czech Republic) at 15 min and 30 min storage intervals at RC and HW09, respectively (Fig. 1). Ground vegetation surface cover in percentage was assessed at Rax during the growing seasons of 2009 and 2011 and at Höllengebirge during the growing seasons of 2010 and 2012. Percentages of herbs, grass and young trees were estimated within a 1 × 1 m quadrat at each plot.

2.4 Data analysis

Effects of windthrow on F_{soil}, soil temperature, and soil moisture were tested by means of ANOVA and subsequent Tukey's HSD tests with a mixed effects model structure (Pinheiro and Bates, 2000) at each site. To account for the repeated measurement structure within the data, the plots were assumed as random effects and the treatments were assumed as fixed effects in each ANOVA and subsequent Tukey's HSD tests. Mixed effects ANOVA and Tukey's HSD tests were calculated by means of the R package "NLME" (Pinheiro et al., 2014).

BGD
11, 6383–6417, 2014

Soil CO_2 efflux was strongly correlated with soil temperature (Fig. 2). We fitted a simple Q_{10} function to the F_{soil} and soil temperature data (Janssens et al., 2003):

$$F_{soil} = F_{10} Q_{10}^{\left(\frac{T-10}{10}\right)}, \quad (1)$$

where F_{soil} and T are the soil CO_2 efflux rates [μmol CO_2 m^{-2} s^{-1}] and soil temperature [°C] at 5 cm soil depth respectively, F_{10} represents soil CO_2 efflux at a soil temperature of 10 °C, and Q_{10} represents the temperature sensitivity of the soil CO_2 efflux (the factor by which the F_{soil} increases during a temperature rise of 10 °C). To account for limiting moisture conditions on F_{soil} as well, we added a soil moisture term to Eq. (1):

$$F_{soil} = F_{10} Q_{10}^{\left(\frac{T-10}{10}\right)} e^{(a\ M)}, \quad (2)$$

where M is soil moisture measured as volumetric water content [vol%], and a is a further model parameter. Non-linear fitting was done by means of the R package "minpack.lm" (Elzhov et al., 2013). Equations (1) and (2) were fitted to the data of each plot as well as to the daily averages of each treatment.

To disentangle the effects of windthrow driven changes in soil temperature, soil moisture and C dynamics on F_{soil}, we normalized F_{soil} for soil temperature and moisture effects. In a first step we used the individual Q_{10} parameters (Eq. 1) of each plot to normalize F_{soil} at a soil temperature of 10 °C (F_T),

$$F_T = F_{soil} / Q_{10}^{\left(\frac{T-10}{10}\right)}. \quad (3)$$

Temperature normalization was only accomplished for measuring dates when soil moisture was considered non-limiting (> 34 vol%). Beneath this 34 vol% critical threshold, F_{soil} decreased sharply, so confounding effects of limited moisture conditions on the temperature response of F_{soil} were therefore avoided. Temperature normalized F_{soil} was statistically analysed as described above (mixed effects models) in order to identify potential windthrow effects separate from a windthrow driven soil temperature effect.

BGD
11, 6383–6417, 2014

In a second step we used the individual (plot specific) model parameters Q_{10} and a of Eq. (2) to calculate plot specific F_{soil} normalized for 10 °C soil temperature and 40 vol% soil moisture (F_{TM}):

$$F_{TM} = F_{soil}/Q_{10}^{\left(\frac{T-10}{10}\right)} e^{(a(M-40))}. \tag{4}$$

Normalization was applied for all measurement dates. Statistical analyses (mixed effects models) of F_{TM} data allowed for testing of windthrow effects independent of windthrow associated changes in soil microclimate.

We used the plot specific model parameters of Eqs. (1) and (2) to quantify the effects of altered soil microclimate on the soil CO_2 efflux at the different windthrow areas. Soil CO_2 efflux was modelled for three microclimatic scenarios; firstly under the actual average soil temperature and soil moisture conditions; secondly under actual average soil moisture conditions but under the same average soil temperature conditions as in the corresponding undisturbed stands; and thirdly under the same average soil microclimatic conditions (soil temperature and moisture) as in the undisturbed stands.

We used the continuous soil temperature data to obtain approximations of annual sums of F_{soil} for all treatments. As soil temperature was only measured continuously at RC and HW09, we first had to generate soil temperature estimates for all plots. We used simple linear relationships between the plot specific manually gathered soil temperature measurements and the continuous measurements during the corresponding time (R^2 ranged from 0.71 to 0.93), in order to interpolate hourly soil temperatures for the study period. Plot specific model parameters derived from Eq. (1) together with the interpolated hourly soil temperature were subsequently used to calculate hourly F_{soil} for each plot. Model simulations were summed up per plot and mean values and respective standard errors were calculated for each treatment. Annual sums were calculated just for 2012, as distinct summer droughts such as in 2011 were absent at both sites.

Correlation analysis was performed to investigate the influence of plant functional types on F_{soil}. Plot specific annual mean values of F_{soil} were correlated with the plot specific ground vegetation surface coverage in 2010 and 2012. This analysis was performed for the Höllengebirge site only due to the higher number of plots.

All statistical analysis and plotting were done in R, an environment for statistical computing and graphics (R Core Team, 2013).The level of significance for the statistical analysis was a p value < 0.05.

3 Results

3.1 Soil microclimate

Soil temperature in 5 cm depth showed typical seasonal patterns at both sites and at each treatment (Fig. 3a and d). Average soil temperatures over the whole study period were 8.1, 12.9, and 11.3 °C at RC, RW07 and RW00, and 13.1, 17.2 and 16.0 °C at HC, HW09 and HW07 respectively. Soils in the disturbed treatments were significantly warmer compared to the soils in the undisturbed stands (Table 1). Soil temperature was significantly higher at HW09 than at HW07 (p value > 0.05), whereas soil temperatures at the windthrow areas at Rax did not differ significantly. No clear seasonal patterns in soil moisture were detected for either Rax or Höllengebirge throughout the measurement campaign (Fig. 3b and e). Apart from discrete drought periods at Höllengebirge in August 2011 and at Rax in October 2011, soil moisture was rather stable around 40 to 50 vol% at both sites. At Rax no significant differences in soil moisture could be shown for the treatments (Table 1). At Höllengebirge soil moisture was 6 vol% and 5 vol% lower at HC than the respective disturbed treatments (Table 1). No significant difference in soil moisture could be determined between the disturbed treatments. Average soil moisture over the whole study period was 38 vol%, 44 vol%, and 43 vol% at HC, HW09 and HW07 respectively.

BGD
11, 6383–6417, 2014

3.2 Soil CO_2 efflux

Soil CO_2 efflux (F_{soil}) showed clear seasonal variations at all treatments, strongly following the patterns in soil temperature (Fig. 3). Soil CO_2 efflux was significantly higher at RW00 when compared to RC and RW07, but no significant difference in F_{soil} was determined for RC and RW07 (Table 1). At Höllengebirge, F_{soil} was slightly lower at the windthrow areas, but the difference between intact stand and windthrow areas was statistically not significant (Table 1). According to our windthrow chronosequence, soil CO_2 efflux at the windthrow areas tented to be rather similar until the sixth year after disturbance, followed by a rebound and increase during years 6 to 12 post-disturbance (Fig. 4).

A clear exponential relation between F_{soil} and soil temperature in 5 cm depth was observed for each treatment (Fig. 2). Soil temperature alone explained 79 % to 86 % and 66 % to 87 % of the temporal variation in F_{soil} at Rax and Höllengebirge respectively. Below a threshold of 34 vol% soil moisture became a limiting factor for F_{soil} and interfered with the response to soil temperature at each treatment. Excluding respective dates with water limiting conditions from the data, strongly improved the relation between F_{soil} and soil temperature, with soil temperature explaining 94, 83, 85 % of the variation in F_{soil} at RC, RW07 and RW00 respectively, and 87, 88, 90 % of the variation in F_{soil} at HC, HW09 and HW07 respectively. The temporal variation in F_{soil} at the Höllengebirge site was best explained by the model accounting for both, soil temperature and soil moisture, explaining 76 %, 83 % and 91 % of the temporal variation in F_{soil} at HC, HW09 and HW07, respectively. At Höllengebirge, soil moisture and F_{soil} were positively related in each treatment. At Rax, soil moisture had no significant explanatory value. The Q_{10} values during non-water limited conditions were 4.23, 2.44 and 2.82 at RC, RW07 and RW00 and 2.95, 2.38 and 2.49 at HC, HW09 and HW07, respectively (Fig. 2).

Corresponding soil CO_2 efflux rates from windthrow areas decreased substantially after normalizing F_{soil} for respective temperature-, and temperature plus moisture effects (Table 1, Fig. 5). Normalized soil CO_2 efflux (F_T, F_{TM}) from the undisturbed stands was significantly higher when compared to the corresponding disturbed treatments at RW07, HW09 and HW07 (Table 1). Only at RW00 F_T was still slightly enhanced but statistically not significantly different from that in the undisturbed stand (RC) (Table 1). Between 20 to 36 % of the CO_2 efflux at the disturbed treatments was attributed to warmer soil conditions (Fig. 5). Increased soil moisture accounted for 2 % of F_{soil} from windthrow areas at Höllengebirge.

Average annual sums of soil CO_2 efflux for the sampling year 2012 of 717 ± 42 (± SE, $n = 8$), 800 ± 64 ($n = 6$) and 1273 ± 141 ($n = 6$) $\mathrm{g\,C\,m^{-2}\,yr^{-1}}$ were calculated for the Rax treatments RC, RW07, and RW00 respectively. For the Höllengebirge site, corresponding values of 780 ± 104 ($n = 13$), 638 ± 40 ($n = 29$) and 674 ± 51 ($n = 23$) $\mathrm{g\,C\,m^{-2}\,yr^{-1}}$ were calculated for HC, HW09 and HW07 respectively. Taking into account that on average 13 % and 27 % of the total area was constituted by rock outcrops at Rax and Höllengebirge respectively, up scaled annual sums were reduced accordingly.

3.3 Ground vegetation cover

Ground vegetation surface cover was clearly higher at older than younger windthrow areas (Fig. 6). Ground vegetation was dominated by herbaceous plants in the first years after disturbance, followed by a transition to a dominating grass community within roughly the first decade after disturbance. Except of HW07 practically no tree regeneration was present at the disturbed areas. Total ground vegetation cover and F_{soil} as well as grass vegetation cover and F_{soil} were strongly correlated at HW07, although these relationships were only significant for data from 2012 (Table 2). At HW09 no correlation between vegetation variables and F_{soil} could be detected.

4 Discussion

The hypothesized initial decrease in post-disturbance F_{soil} was not confirmed at both sites. Soil CO_2 efflux showed no significant decline throughout the first six years post disturbance, and remained close to pre-disturbance levels (Fig. 4). We hypothesized that the reduced F_{soil} would be driven by a large decrease in autotrophic respiration which would outweigh the additional CO_2 release from the decomposition of litter from killed trees (needles and dead fine roots). Due to complete tree mortality and sparse vegetation cover (Fig. 6), it is almost certain that autotrophic soil respiration rates were lower for the younger windthrow areas than the corresponding undisturbed stands. However, as F_{soil} rates between the young windthrow areas and control stands were not statistically different (Table 1), it appears that the decrease in autotrophic soil respiration was in fact offset by accelerated heterotrophic soil respiration i.e. SOM decomposition. Rates of SOM decomposition are driven by changes in the soil microbial community (Holden and Treseder, 2013), substrate availability and/or changes in soil microclimate (Davidson and Janssens, 2006; Davidson et al., 1998). Although all such changes are likely to have occurred at our windthrow areas, the normalized soil CO_2 fluxes indicate F_{soil} of the younger windthrow areas was principally held at pre-disturbance levels by microclimatic factors. When normalized for differences in soil temperature and soil moisture, soil CO_2 efflux (F_T and F_{TM}) significantly declined throughout the first years after windthrow (Table 1). The higher than hypothesized F_{soil} in the initial years post disturbance thus appears to be partially driven by rate-accelerating soil microclimatic conditions.

During the CO_2 measurement campaigns, soil in the windthrow areas was on average $4.2 \pm 0.7\,^{\circ}C$ (HW09) and $2.9 \pm 0.4\,^{\circ}C$ (HW07) warmer than in the undisturbed treatment (HC) at Höllengebirge, and $4.8 \pm 0.7\,^{\circ}C$ (RW07) and $3.2 \pm 0.7\,^{\circ}C$ (RW00) warmer than in the undisturbed treatment (RC) at Rax (Table 1). Such an increase in soil temperature after stand disturbance is a commonly observed response in forest ecosystems (Payeur-Poirier et al., 2012; Kulmala et al., 2014; Classen et al., 2005;

Pumpanen et al., 2004; Singh et al., 2008), driven by the loss of shading by the tree canopy and subsequently higher insolation at the forest floor. The decreasing temperature difference between windthrow area and undisturbed stands with increasing time post disturbance is likely connected to increased shading by the developing ground vegetation. In addition to soil temperature effects, removal or died back of the tree layer can lead to changes in the soil moisture regime, often producing wetter soil conditions post-disturbance (Payeur-Poirier et al., 2012; Classen et al., 2005; Peng and Thomas, 2006; Pumpanen et al., 2004). This effect, which is mainly due to the ceased water uptake by trees, was observed at Höllengebirge but not at Rax. This may have been due to the smaller transpiration demand on soil of the Norway spruce dominated stand at Rax compared to that of the Beech dominated stand at Höllengebirge (Hietz et al., 2000) and the already higher ground vegetation coverage at the Rax site. As mentioned already, the above changes in soil microclimate were substantial factors in maintaining higher F_{soil} after disturbance. Simulations with different microclimatic scenarios revealed that 22 to 36 % of the windthrow soil CO_2 fluxes were driven by disturbance-induced changes in soil microclimate (Fig. 5).

Soil CO_2 efflux showed a strong relationship to soil temperature in all treatments but apparent Q_{10} values were higher for the intact stands; a pattern which had been observed after clear-cutting as well (Zu et al., 2009; Payeur-Poirier et al., 2012). This however does not necessarily mean that the real temperature sensitivity of SOM decomposition differed at windthrow and stand areas. More likely, the higher Q_{10} in the intact stand to an extent reflect the seasonal trend of autotrophic soil respiration, which often correlates with the seasonal development of soil temperatures, and hence increases apparent Q_{10} (Schindlbacher et al., 2009). The slightly higher Q_{10} at RW00 which was already densely populated by grasses also points toward this direction.

Together with soil microclimate, C availability is likely to have influenced the temporal development of the soil CO_2 efflux post-windthrow. Initial C input due to dead tree foliage and fine roots is typically high after windthrow. Our results however do not point towards a flush in heterotrophic decomposition during the first years after windthrow.

BGD
11, 6383–6417, 2014

When normalized for soil microclimate, the soil CO_2 efflux rates from the 1 to 6 year old windthrow areas were at ~ 60–70 % of those of the undisturbed stands (Fig. 5). This is in the range of the reported heterotrophic contributions to F_{soil} of temperate forest ecosystems (Hanson et al., 2000; Ruehr and Buchmann, 2010; Schindlbacher et al., 2009). Hence, it seems that rather than an initial discrete increase in decomposition and subsequent decline, the disturbance C input is slowly, but continually utilised in the initial 6 years after disturbance, thus maintaining decomposition rates.

Soil CO_2 efflux from the oldest windthrow area (RW00) was significantly higher when compared to both, F_{soil} from the more recent windthrow (RW07) and F_{soil} from the undisturbed stand (RC) at the same site. Soil CO_2 efflux remained still roughly a 1/3 higher when normalized for soil temperature effects (Fig. 5). The oldest windthrow site was characterized by dense grass vegetation which fully covered the soil surface. The development of this dense grass community and the correspondingly increasing autotrophic respiration and litter input is most likely responsible for the higher CO_2 efflux observed after 9–12 years post-disturbance, as reported by Pumpanen et al. (2004). Soil CO_2 efflux was found to be, on average, 20 % higher in grasslands compared to forest stands (Raich and Tufekciogul, 2000), which concurs with our findings. A significant positive relation between F_{soil} and grass cover at HW07 also supports this explanation (Table 2).

Average annual F_{soil} (during 2012) was estimated at ~ 6.2 and 5.7 t C ha^{-1} yr^{-1} (up scaled estimates account for a rock outcrop of 13 % and 27 % of the total area at Rax and Höllengebirge respectively) for RC and HC respectively, which is comparable with values reported for other temperate forest sites (Etzold et al., 2011; Knohl et al., 2008; Ruehr et al., 2010; Schindlbacher et al., 2012). Annual estimates for F_{soil} from the more recent windthrow areas were within this range (4.7–7.0 t C ha^{-1} yr^{-1}, up scaled estimates are deducted by 13 % and 27 % at Rax and Höllengebirge respectively). In the intact forest stands, the loss of C through the soil CO_2 efflux was likely offset by the C gain by photosynthesis and growth (Luyssaert et al., 2008). At the windthrow areas, the soil CO_2 efflux estimates indicate a substantial loss of C from the ecosystem, espe-

BGD
11, 6383–6417, 2014

cially during the initial stage when ground vegetation cover was sparse. Our C loss estimates from the windthrow areas is somewhat lower than that from Knohl et al. (2002) who observed an annual C release of 8 t ha^{-1} from a windthrow area in a boreal forest. At their site, roughly 1/3 of the released CO_2 was from dead-wood decomposition, whereas at our sites, most dead wood was removed. The comparably high soil CO_2 efflux rates at our windthrow areas were related to the warm soil conditions created by loss of canopy shading. All windthrow areas in our study were on steep, south exposed slopes, thus receiving large amounts of solar radiation. The effects of windthrow on soil temperatures may be less pronounced for other aspects. For north exposed slopes for example, disturbance may have little or no effect on soil temperature. Finally, while the above annual estimates are subject to a number of uncertainties (e.g. uncertainties in model parameters (Eq. 1), uncertainties in simulated temperatures), they nonetheless point toward substantial C losses from such sites after windthrow disturbance.

The respiratory C loss of $\sim$ 11.1 t C ha^{-1} yr^{-1} (up scaled estimates are deducted by 13 %) at RW00 is high for forest ecosystems, but is within the range of annual F_{soil} rates estimated for European grasslands (Bahn et al., 2008). Considering almost 100 % grass vegetation cover at this site, the above estimates are thus plausible. Whether this 12 year old windthrow area acts as a C sink or source cannot be assessed with our data. Rhizosphere respiration will contribute a large share of the overall F_{soil} (Chen et al., 2006; Subke et al., 2006) and the dense grass cover produces comparatively high amounts of above and below ground litter (Freschet et al., 2013). Therefore, it is likely that the old windthrow area is losing comparatively less C than the more recently disturbed areas.

It has been shown that it takes 10–25 years until forest ecosystems turn from C sources to C sinks after stand replacing disturbances (Amiro et al., 2010; Pfeifer et al., 2011). The recovery time until the ecosystem turns into a C sink depends on the disturbance effects on (soil) respiratory processes and on the recovery of vegetation productivity. If disturbance largely reduces ecosystem respiration, than the disturbance effects will be small and a balance in net C flux can be restored quickly (Moore et al., 2013). If the respiration does not decrease post-disturbance as observed in our study and elsewhere (Knohl et al., 2002; Köster et al., 2011; Morehouse et al., 2008; Toland and Zak, 1994) then the recovery of the C sink capacity strongly depends on forest re-growth. At none of the sites of our windthrow chronosequence, a significant tree seedling establishment or tree re-growth was observed. The study regions, just like much of Austria's mountain forests, are characterized by high population densities of roe deer, red deer, and chamois and correspondingly high browsing pressure (Ammer, 1996; Reimoser and Gossow, 1996; Reimoser and Reimoser, 2010). Therefore, a fast re-establishment of forest stands on windthrow areas is hardly possible without post-disturbance management such as artificial regeneration and subsequent fencing against browsing. Here we could show that if such measures are not undertaken, a large amount of soil C can be lost to the atmosphere during the first decade after windthrow. Consequently, more frequent forest disturbance by windthrow in mountainous regions (Seidl et al., 2011) could reduce these soil C stocks and positively feedback on rising atmospheric CO_2 concentrations.

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BGD
11, 6383–6417, 2014

Soil CO_2 efflux from mountainous windthrow areas

M. Mayer et al.

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BGD
11, 6383–6417, 2014

Soil CO_2 efflux from mountainous windthrow areas

M. Mayer et al.

Table 1. Site specific effects of disturbance by windthrow on soil temperature (T) [°C], soil moisture (M) [vol%], measured soil CO_2 efflux (F_{soil}), temperature normalized soil CO_2 efflux (F_T) and soil CO_2 efflux normalized for temperature and soil moisture (F_{TM}) [$\mu mol\, CO_2\, m^{-2}\, s^{-1}$], as assessed by Tukey's HSD tests with mixed effects model structure.

Variable	Rax Differences RC – RW07	 RC – RW00	 RW07 – RW00	Höllengebirge Differences HC – HW09	 HC – HW07	 HW09 – HW07
T	−4.80 (0.69)[c]	−3.22 (0.70)[c]	1.59 (0.75) n.s	−4.16 (0.38)[c]	−2.89(0.39)[c]	1.27(0.32)[c]
M	0.75 (2.49) n.s.	−2.84 (2.49) n.s.	−3.59 (2.67) n.s.	−6.31 (1.60)[c]	−5.36(1.66)[b]	0.95(1.34) n.s.
F_{soil}	−0.36 (0.42) n.s.	−2.21 (0.42)[c]	−1.85 (0.45)[c]	0.42 (0.35) n.s.	0.57(0.36) n.s.	0.15(0.29) n.s.
F_T	0.99 (0.36)[a]	−0.57 (0.36) n.s.	−1.57 (0.39)[c]	0.79 (0.25)[b]	0.78 (0.26)[a]	−0.01 (0.21) n.s.
F_{TM}	–	–	–	1.07 (0.29)[c]	1.10 (0.30)[c]	0.03 (0.24) n.s.

Values in parentheses represent standard error. Significance levels:
n.s., not significant;
[a] p value < 0.05;
[b] p value < 0.01;
[c] p value < 0.001.

BGD
11, 6383–6417, 2014

Soil CO_2 efflux from mountainous windthrow areas

M. Mayer et al.

Table 2. Pearsons correlation coefficients between F_{soil} and the ground vegetation cover of different plant functional types for the two disturbed areas at Höllengebirge. Surveys were performed during the growing seasons of 2010 and 2012.

Variable	HW09		HW07	
	2010	2012	2010	2012
Herbaceous plants (%)	−0.169 n.s.	0.141 n.s.	−0.222 n.s.	0.016 n.s.
Grasses (%)	0.333 n.s.	−0.263 n.s.	−0.337 n.s.	0.426*
Tree regeneration (%)	–	–	0.373 n.s.	0.188 n.s.
Total ground vegetation (%)	−0.003 n.s.	−0.081 n.s.	−0.166 n.s.	0.475 *

Significance levels: n.s., not significant; *, p value < 0.05.

BGD
11, 6383–6417, 2014

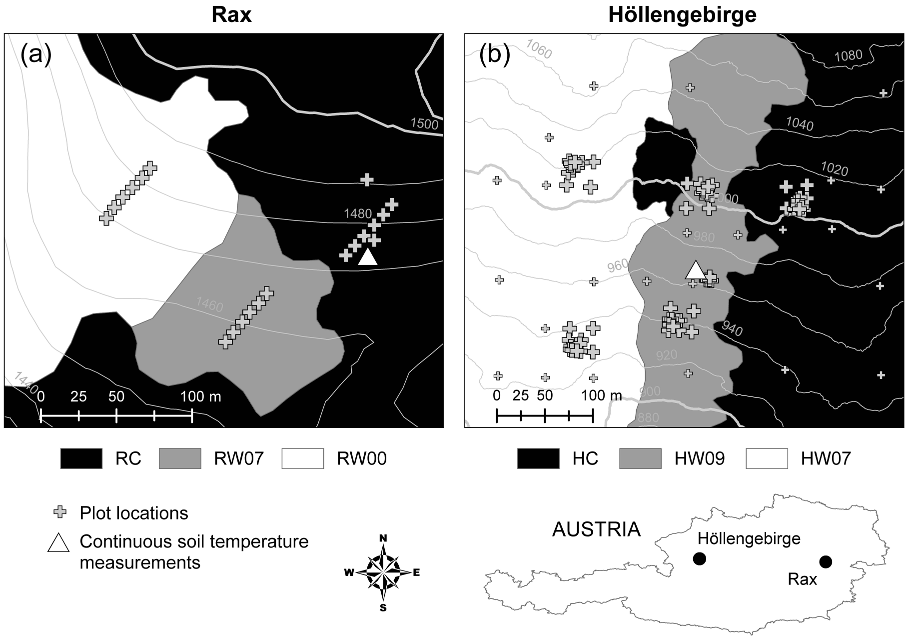

Fig. 1. Windthrow areas (white, grey) and unaffected forest stands (black) at the two study sites **(a)** Rax (RC, control; RW07, windthrow 2007; RW00, windthrow 2000) and **(b)** Höllengebirge (HC, control; HW09, windthrow 2009, HW07, windthrow 2007). Crosses represent the plot locations for soil CO_2 efflux, soil temperature and soil moisture measurements.

BGD
11, 6383–6417, 2014

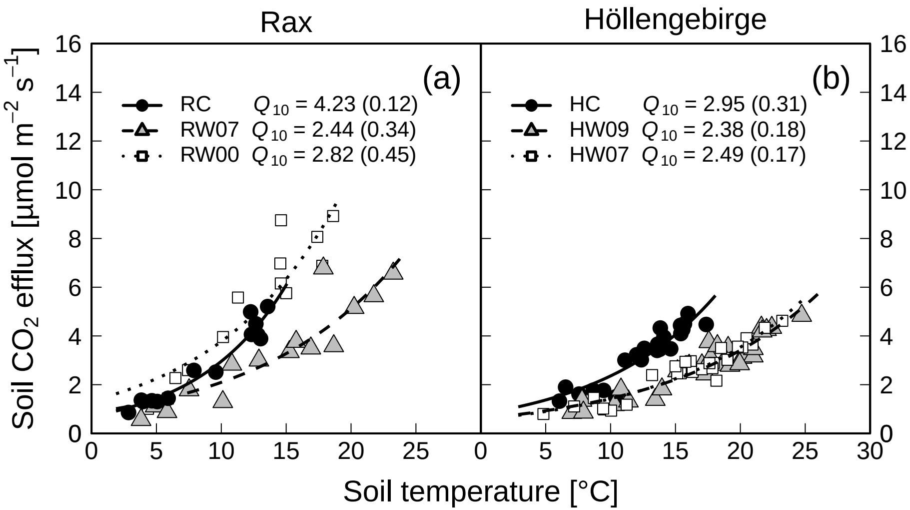

Fig. 2. Relationship between mean soil temperature and mean soil CO_2 efflux during all measurement dates with non-limiting soil moisture conditions (> 34 vol%) at **(a)** Rax (control, RC; windthrow 2007, RW07; windthrow 2000, RW00) and **(b)** Höllengebirge (control, HC; windthrow 2009, HG09; windthrow 2007, HG07). Curves show the fit of a Q_{10} function (Eq. 1). Shown are Q_{10} values and respective standard errors of the parameter estimation (in brackets).

BGD
11, 6383–6417, 2014

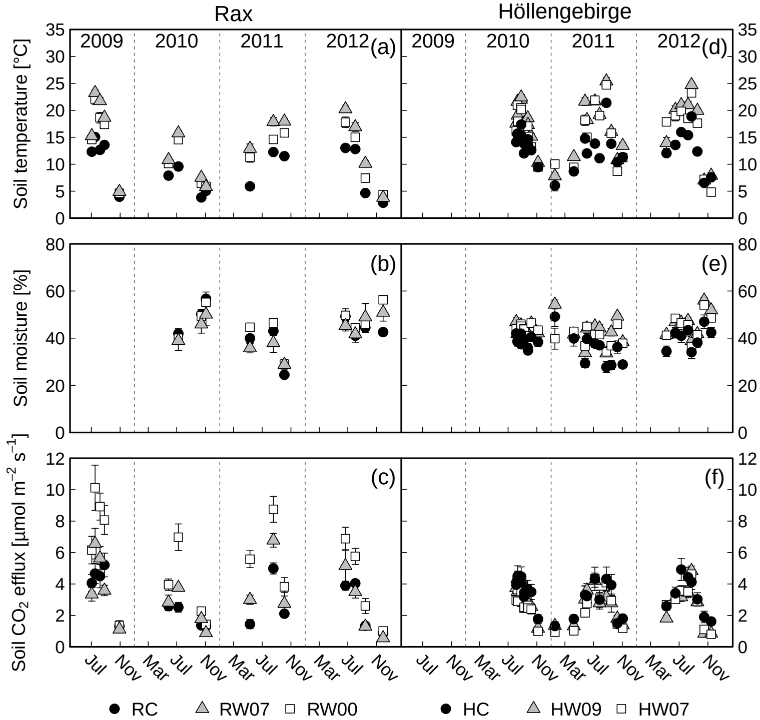

Fig. 3. Soil temperature, soil moisture and soil CO_2 efflux (F_{soil}) at Rax **(a–c)** and Höllengebirge **(d–f)** for the years 2009 to 2012. Plotted are mean values for each measurement date for Rax (control, RC; windthrow 2007, RW07; windthrow 2000, RW00) and Höllengebirge (control, HC; windthrow 2009, HG09; windthrow 2007, HG07). Error bars represent standard error of the mean (RC: $n = 8$, RW07: $n = 6$, RW00: $n = 6$, HC: $n = 13$, HW09: $n = 29$, HW07: $n = 23$).

BGD
11, 6383–6417, 2014

Soil CO_2 efflux from mountainous windthrow areas

M. Mayer et al.

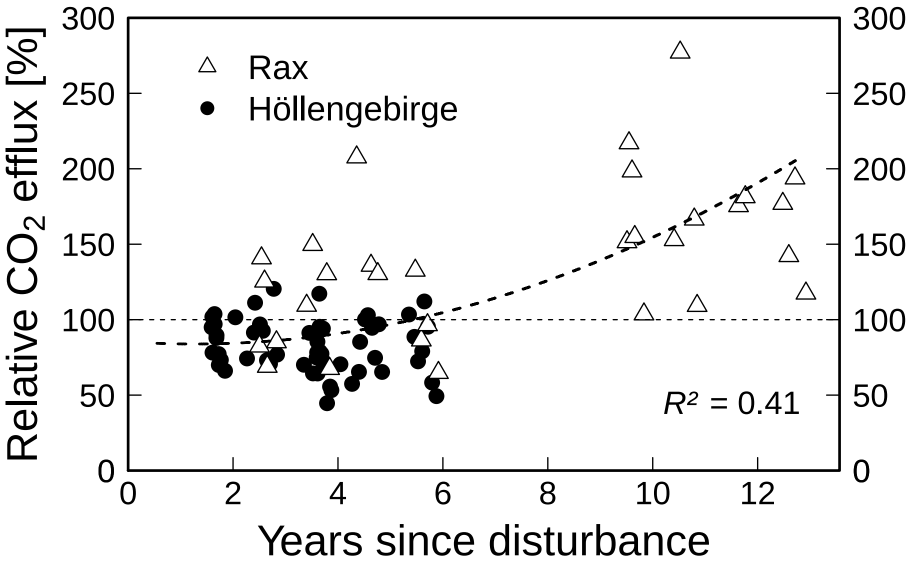

Fig. 4. Post-disturbance development of soil CO_2 efflux relative to the respective undisturbed control treatments at Rax and Höllengebirge chronosequences. The curve shows the fit of a parabolic function to the pooled data of both sites (*Relative CO_2 efflux* [%] = $8.54 \times 10^1 - 6.39 \times 10^{-3}$ *DSD* + 6.95×10^{-6} *DSD*^{2}). Note: "Days since disturbance" are represented as "Years since disturbance" on the x-axis of the figure.

BGD
11, 6383–6417, 2014

Soil CO_2 efflux from mountainous windthrow areas

M. Mayer et al.

Title Page
Abstract | Introduction
Conclusions | References
Tables | Figures
Back | Close
Full Screen / Esc
Printer-friendly Version
Interactive Discussion

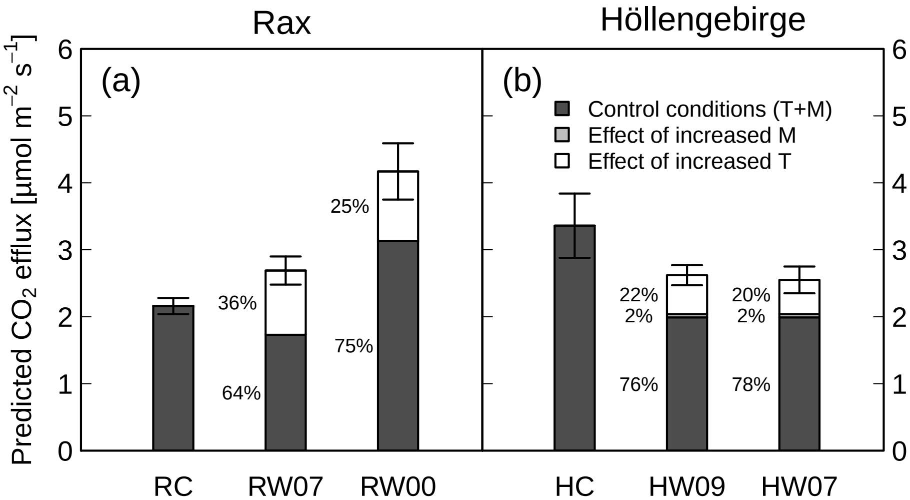

Fig. 5. Soil CO_2 efflux under three different microclimatic scenarios for **(a)** Rax (control, RC; windthrow 2007, RW07; windthrow 2000, RW00) and **(b)** Höllengebirge (control, HC; windthrow 2009, HG09; windthrow 2007, HG07). Grey bars represent modelled CO_2 efflux at average soil microclimate of the intact stands. White and light grey bars indicate the effect of altered soil microclimate at the windthrow areas. The effect of increased soil moisture is only addressed at Höllengebirge.

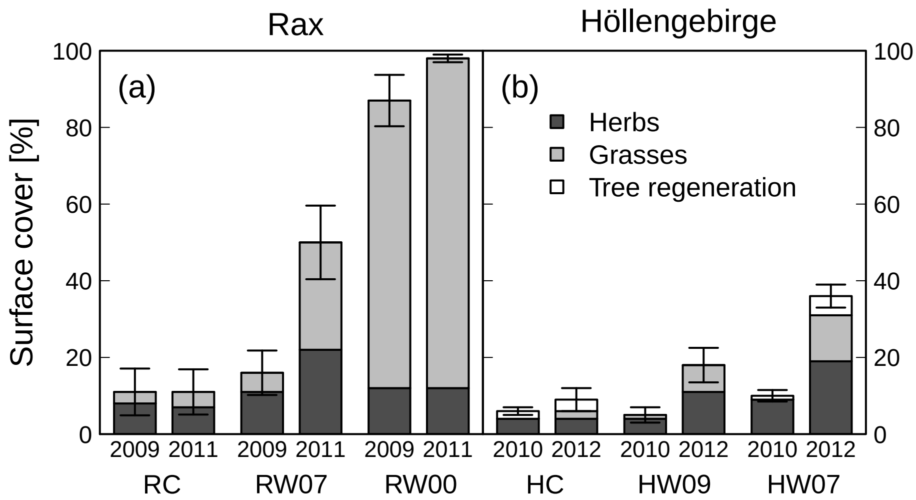

Fig. 6. Ground vegetation surface cover of the different treatments at **(a)** Rax (control, RC; windthrow 2007, RW07; windthrow 2000, RW00) and **(b)** Höllengebirge (control, HC; windthrow 2009, HG09; windthrow 2007, HG07) determined in 2009 and 2011 at Rax, and in 2010 and 2012 at Höllengebirge respectively. Bars represent mean values of the plant type's surface cover. Error bars represent standard error of the mean total cover of the plots (RC: $n = 8$, RW07: $n = 6$, RW00: $n = 6$, HC: $n = 13$, HW09: $n = 29$, HW07: $n = 23$).

BGD
11, 6383–6417, 2014