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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}) from 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. Each site consisted of an undisturbed forest stand and two adjacent partially cleared (stem-fraction-harvested) windthrow areas, which differed with regard to the time since disturbance. The combination of chronosequence and direct time-series approaches enabled us to investigate F_{soil} dynamics over 12 years post-disturbance. At both sites F_{soil} rates did not differ significantly from those of the undisturbed stands in the initial phase after disturbance (1–6 years). In the later phase after disturbance (9–12 years), F_{soil} rates were significantly higher than in the corresponding undisturbed stand. 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 (15–31 %) of F_{soil} from the windthrow areas was attributed to the increase in soil temperature. According to our estimates, ~500–700 g C m^{-2} year^{-1} are released via F_{soil} from south-facing forest sites in the Austrian Calcareous Alps in the initial 6 years after windthrow. With a high browsing pressure suppressing tree regeneration, post-disturbance net loss of ecosystem C to the atmosphere is likely to be substantial unless forest management is proactive in regenerating such sites. An increase in the frequency of forest disturbance by windthrow could therefore decrease soil C stocks and feed back positively on rising atmospheric CO_2 concentrations.

1 Introduction

The global carbon dioxide (CO_2) efflux from soil (F_{soil}) was recently estimated at 98 ± 12 Pg carbon (C) year^{-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 40–80 % of the total ecosystem respiration (Curiel Yuste et al., 2005b; 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 forest's 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) which 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; Seidl et al., 2014). According to the conceptual trajectory of Odum (1969), the pre-disturbance ecosystem sequesters C until disturbance causes an initial, fairly 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) and thus determines the magnitude of initial net ecosystem emission/uptake of CO_2. In cases of increased F_{soil} after disturbance, large amounts of ecosystem C can be lost to the atmosphere (Kurz et al., 2008; Covington, 1981). However, where F_{soil} decreases post-disturbance, net ecosystem–atmosphere CO_2 fluxes may show very little difference between pre- and post-disturbance levels (Moore et al., 2013). Quantifying post-disturbance changes in F_{soil} is, therefore, crucial in improving our understanding of disturbance impacts on ecosystem C dynamics and the potential risk of ecosystem C loss.

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 input, 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. However, litter from populating pioneer herbs and grasses can 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 on 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., 2004b; Singh et al., 2008). Due to the complex interplay of various rate-limiting 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).

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 (Seidl et al., 2014). 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 rarely been quantified.

We studied two mountainous forest stands which had been hit by successive larger-scale windthrow events. Together the study sites offered two undisturbed forests and four managed windthrow areas in varying temporal stages after disturbance. Combining time series and chronosequence approaches, the areas were investigated to track the 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 in 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, 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 (data from a climate station located ∼ 7 km away at a similar altitude) and 6.6 °C and 1964 mm at the Höllengebirge site (interpolated values from the closest climate stations, both ∼ 10 km apart) (data provided by Zentralanstalt für Meteorologie und Geodynamik – ZAMG). Growing season at both sites is between May and September.

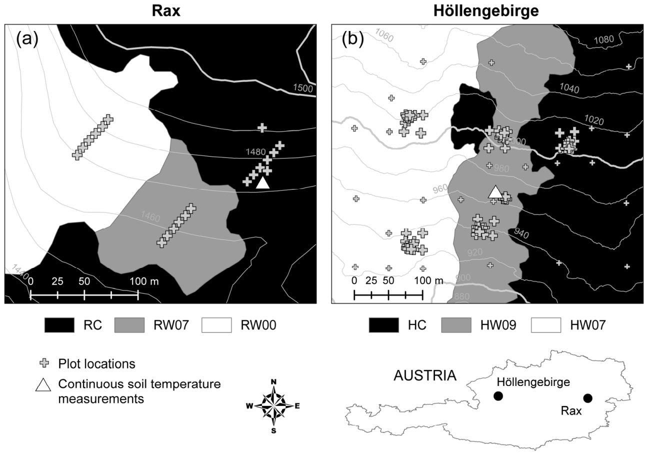

Figure 1. Windthrow areas (white, grey) and unaffected forest stands (black) at the two study sites: **(a)** Rax (RC – control; RW07 – windthrow 2007; RW00 – windthrow 2000) and **(b)** Höllengebirge (HC – control; HW09 – windthrow 2009; HW07 – windthrow 2007). Crosses represent the plot locations for soil CO_2 efflux, soil temperature and soil moisture measurements. Only plots represented by a large cross were used for analysis at the Höllengebirge site. Small crosses represent plots which were only measured in 2010 and 2011 as part of a different investigation.

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 (*Mercurialis perennis*, *Calamagrostis sylvatica*). The forest stand at Höllengebirge was dominated by Norway spruce (*Picea abies*), European beech (*Fagus sylvatica*) 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 understorey trees (*Picea abies*).

In the winter of 1999/2000, the Rax site was affected by a storm event during which several hectares of the forest stand were either blown over or destroyed by wind snap. A subsequent windthrow in the winter/spring of 2007 then worked its way from the exposed forest edge eastwards (Fig. 1a). The respective areas are henceforth denoted as "Rax windthrow 2000" (RW00) and "Rax windthrow 2007" (RW07) treatments. The unaffected, intact stand adjacent to the windthrow areas served as a control (RC). At the Höllengebirge site a windthrow in the winter/spring of 2007 and subsequent bark beetle events totally destroyed roughly 25 ha of forest. This was then followed by a subsequent windthrow disturbance in the winter/spring of 2009, which opened up a further 4 ha (Fig. 1b). Accordingly, the designation of these specific areas is "Höllengebirge windthrow 2007" (HW07) and "Höllengebirge windthrow 2009" (HW09) treatments. The unaffected stand beside the windthrow areas again served as a control (HC). The area comprised of pits and mounds contributed only slightly (< 5 %) to the total area of each windthrow site.

Table 1. Mean soil characteristics of the undisturbed control stands at Rax and Höllengebirge.

	Rax	Höllengebirge
Soil C stock (kg m^{-2}) O horizon	8.3 (1.5)	7.5 (0.7)
C content (%) O horizon	45 (2)	42 (2)
C : N ratio O horizon	24.9	19.1
pH (H_2O)	5.3	4.7
Layer thickness (cm) O horizon	12 (2)	15 (2)
Total soil depth (cm)	17 (4)	38 (3)

Values in parentheses represent standard error.

The windthrow areas at both sites were actively managed. Sites were partially cleared of stemwood immediately after the disturbance events in order to prevent bark beetle infestations. About 15 % of the stem fraction was left in place. Branches and stumps were kept on site. Wind-snapped trees were cut, and the logs were harvested as well. Only a marginal number of mature trees survived the disturbance events at both sites, and these were not harvested after the windthrow. Ground vegetation re-establishment in the disturbed areas at both sites initially comprised herbaceous plants (*Senecio ovatus*, *Adenostyles glabra*, *Eupatorium cannabinum*, *Cirsium arvense*, *Urtica dioica*), followed by grass vegetation (*Carex alba*, *Calamagrostis varia*). 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 in steeper terrain and Chromic Cambisols in flatter areas. Nonetheless, the heterogeneous conditions typical of *Karst* meant the above soil and humus types were often found within metres of one another. According to forest inventory data from both sites, pre-disturbance stand conditions (tree species composition, stand age, stand structure) of the windthrown areas were similar to those of the respective adjacent control stands. Furthermore, at both sites, exposition, slope, soil types and humus forms were similar between the respective disturbed and undisturbed areas. Detailed information about the soil characteristics is given in Table 1.

2.2 Experimental design

The assessment of F_{soil} in undisturbed and in windthrown areas which differed with regard to the time since disturbance, together with 3–4 years of repeated measurements of F_{soil} in 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" (Sustainable Management of Forest Soils in the Calcareous Alps). At the Rax site six to eight plots were established at the individual treatments. Plots were defined by a rectangular area of 1×1 m and 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 carried out at irregular intervals (monthly to 3 months) during the snow-free periods and ended in November 2012. At Höllengebirge, 65 1×1 m plots were arranged in a nested (multi-stage) sampling scheme (Fig. 1b, large crosses), composed of different distance stages (Webster and Oliver, 2007). The distance stages were 25, 12.5 and < 12.5 m. In sum 13, 29 and 23 plots were established at HC, HW09 and HW07, respectively. The higher number of plots and large spatial extent of the sampling area at the Höllengebirge site was partially due to concurrent eddy covariance measurements at this site (data not presented here) and the subsequent need to cover the flux footprint. Measurements of F_{soil}, soil temperature and soil moisture were taken at biweekly to monthly intervals from August to November 2010 and monthly intervals 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.

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 in the centre of each plot at each site. The collars were inserted 3 cm into the soil surface (including litter layer) and were kept in place throughout the whole study. Vegetation establishing itself 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. The temporal CO_2 increase inside the chamber headspace was measured over a maximum period of 120 s, though the period was cut short once the temporal increase of CO_2 exceeded 50 ppm. The recording interval of CO_2 efflux (ppm) was 4.8 to 5 s. These were the standard settings from the company (EGM4, PP-Systems International, Inc. Amesbury, MA, USA), which were shown to produce reliable soil CO_2 efflux rates (Pumpanen et al., 2004a). Within each plot, 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 0–7 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 ~ 8 h at Höllengebirge. Plots at both sites were measured in the same order throughout the study. The long duration of measurements at the Höllengebirge site posed the risk of bias due to changing soil conditions (temperature, moisture) throughout the day. To account for that and to ensure comparability between undisturbed and disturbed sites, measurements were undertaken moving uphill in a crisscross fashion. After every seventh plot, the treatment (HC, HW09, HW07) was changed, thus essentially moving across the slope and between all three of the treatments before moving to the plots further upslope. Soil temperature at 5 cm depth (including litter layer) was continuously measured with thermocouple elements at RC and at HW09. The data were recorded by Minicube data loggers (EMS, Brno, Czech Republic) at 15 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 the 1×1 m area of each plot.

2.4 Data analysis

Effects of windthrow on F_{soil}, soil temperature and soil moisture were tested by means of ANOVA (analysis of variance) and subsequent Tukey's HSD (honestly significant difference) 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" (Linear and Nonlinear Mixed Effects Models) (Pinheiro et al., 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):

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

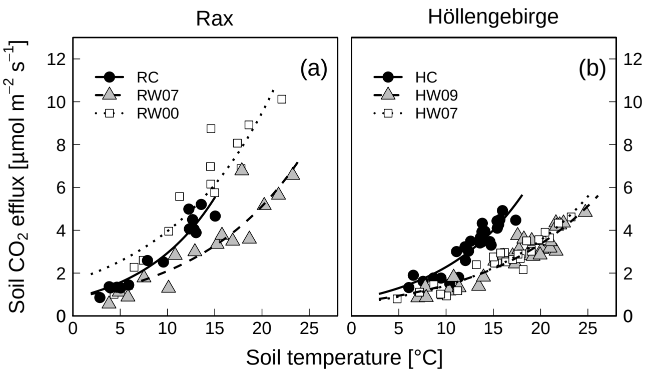

Figure 2. Relationship between mean soil temperature and mean soil CO_2 efflux under nonlimiting soil moisture conditions at **(a)** Rax (control – RC; windthrow 2007 – RW07; windthrow 2000 – RW00) and **(b)** Höllengebirge (control – HC; windthrow 2009 – HG09; windthrow 2007 – HG07). Curves show the fit of a Q_{10} function (Eq. 1).

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 the basal 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 soil moisture (Fig. 3b, e), we added an exponential soil moisture term (Knohl et al., 2008; Soe and Buchmann, 2005) to Eq. (1). This, however, only marginally improved the model. Therefore, only parameters from Eq. (1) were used for further analysis in this study. Nonlinear fitting was done by means of the R package “minpack.lm” (Elzhov et al., 2013). Equation (1) was fitted to the data of each plot as well as to the daily averages of each treatment. In order to dig deeper into processes related to basal CO_2 efflux and temperature sensitivity of F_{soil}, the data were also separated into seasonal windows. Equation (1) was, accordingly, fitted to the daily averages of each treatment for a mid-season (01.06–31.08) and for an early/late season (01.09–31.05). Student’s t tests were used to test for treatment differences in the parameters of Eq. (1).

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 continuous 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 simulate hourly soil temperatures for the study period. Plot-specific model parameters derived from Eq. (1) were subsequently used together with the simulated hourly soil temperature to calculate hourly F_{soil} for each plot. Model simulations were summed per plot, and mean values and respective standard errors were calculated for each treatment. Annual sums were calculated for 2012, as dry conditions during summer weakened the model performance in 2011.

In order to disentangle the effects of altered soil temperature on F_{soil} in the different windthrow areas, annual courses in F_{soil} rates in the windthrow areas were also modelled under theoretical pre-disturbance soil temperature conditions. For this purpose we used the plot-specific (windthrow plots only) model parameters of Eq. (1) together with the interpolated hourly average soil temperature from the respective undisturbed control stands.

Relative F_{soil} rates were calculated for the windthrow areas in order to compare both sites within one longer-term disturbance chronosequence. Daily average F_{soil} rates of the windthrow areas were divided by the daily average F_{soil} rates of their respective control stand. This procedure should minimize possible site differences (stand differences, differences in air temperature) but nonetheless indicate longer-term dynamics in F_{soil} following the disturbance of such ecosystems.

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 2009 and 2011 at Rax and in 2010 and 2012 at Höllengebirge.

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 at 5 cm depth showed typical seasonal patterns at both sites and in each treatment (Fig. 3a, 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 2). Soil temperature was significantly higher at HW09 than at HW07, whereas soil temperatures in 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, e). Apart from discrete drought periods at Höllengebirge in August 2011 and at Rax in October 2011, soil moisture was fairly stable, around 40–50 vol % at both sites. At Rax no significant differences in soil moisture could be shown for the treatments (Table 2). Average soil moisture over the whole study period was 43, 43 and 46 vol % at RC, RW07 and RW00, respectively. At Höllengebirge soil moisture was roughly 6 and 5 vol % lower at HC than HW09 and HW07 (Table 2). No significant difference in soil moisture could be determined between the disturbed treatments. Average soil moisture over the whole

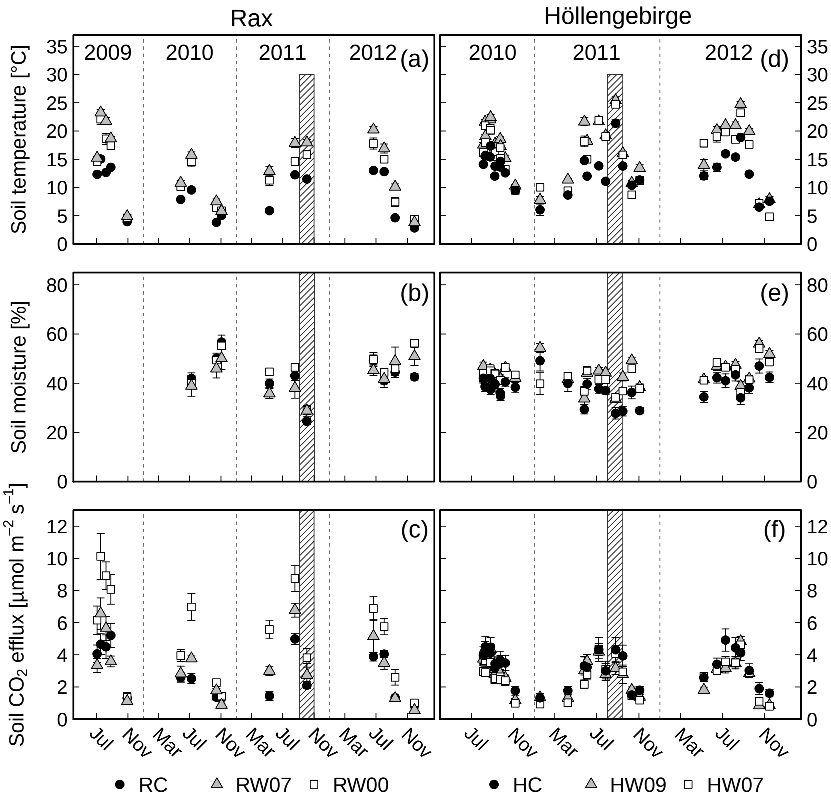

Figure 3. Soil temperature, soil moisture and soil CO_2 efflux (F_{soil}) at Rax **(a, b, c)** and Höllengebirge **(d, e, f)** for the years 2009 to 2012. Mean values for each measurement date for Rax (control – RC; windthrow 2007 – RW07; windthrow 2000 – RW00) and Höllengebirge (control – HC; windthrow 2009 – HG09; windthrow 2007 – HG07) are plotted. Error bars represent the standard error of the mean (RC: $n = 8$; RW07: $n = 6$; RW00: $n = 6$; HC: $n = 13$; HW09: $n = 29$; HW07: $n = 23$). The hatched areas highlight measurement periods during water-limiting conditions.

Table 2. Site-specific effects of windthrow on soil temperature (T) (°C), soil moisture (M) (vol %) and soil CO_2 efflux (F_{soil}) (µmol CO_2 m^{-2} s^{-1}), as assessed by Tukey's HSD tests with mixed-effects model structure.

Variable	Rax differences			Höllengebirge differences		
	RC – RW07	RC – RW00	RW07 – RW00	HC – HW09	HC – HW07	HW09 – HW07
T	−4.80 (0.69)**	−3.22 (0.70)**	1.59 (0.75) n.s.	−4.16 (0.38)**	−2.89(0.39)**	1.27(0.32)**
M	0.75 (2.49) n.s.	−2.84 (2.49) n.s.	−3.59 (2.67) n.s.	−6.31 (1.60)**	−5.36(1.66)*	0.95(1.34) n.s.
F_{soil}	−0.36 (0.42) n.s.	−2.21 (0.42)**	−1.85 (0.45)**	0.42 (0.35) n.s.	0.57(0.36) n.s.	0.15(0.29) n.s.

Values in parentheses represent standard error. Significance levels: n.s. – not significant; * = p value < 0.01; ** = p value < 0.001.

study period was 38, 44 and 43 vol % at HC, HW09 and HW07, respectively.

3.2 Soil CO_2 efflux

F_{soil} showed clear seasonal variations in all treatments, strongly following the patterns in soil temperature (Fig. 3). F_{soil} 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 2). At Höllengebirge, F_{soil} was slightly lower in the windthrow areas, but the difference between intact stand and windthrow areas was statistically not significant (Table 2).

A clear exponential relation between F_{soil} and soil temperature at 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. However, under dry soil conditions in October 2011 and August 2011 at Rax and Höllengebirge, respectively, (soil moisture declined to a minimum of 23 and 27 vol % at Rax and Höllengebirge, respectively),

Table 3. Seasonality of basal soil CO_2 efflux at 10 °C soil temperature and temperature sensitivity for the different treatments of the Rax and Höllengebirge site. Model results of Eq. (1) (F_{10}, Q_{10}, R^2) for the whole campaign (All), for a mid-season (01.06.–31.08.) and for an early/late season (01.09.–31.05.). Letters indicate statistical differences (p value < 0.05) between the model parameters within one site and season.

Site	Treatment	F_{10}	Q_{10}	R^2	Season
Rax	RC	2.94 (0.15) a	3.53 (0.50) a	0.91	All
	RW07	2.10 (0.28) b	2.44 (0.38) b	0.83	All
	RW00	3.96 (0.39) c	2.40 (0.29) b	0.85	All
	RC	3.31 (0.42) a	2.46 (0.96) a	0.52	Mid
	RW07	2.55 (0.76) b	2.02 (0.60) a	0.49	Mid
	RW00	5.38 (0.79) c	1.67 (0.30) a	0.54	Mid
	RC	3.74 (0.44) a	6.91 (1.85) a	0.90	Early/late
	RW07	1.99 (0.21) b	4.45 (1.74) b	0.79	Early/late
	RW00	4.13 (0.15) a	8.62 (1.46) a	0.98	Early/late
Höllengebirge	HC	2.28 (0.12) a	3.08 (0.35) a	0.83	All
	HW09	1.44 (0.12) b	2.33 (0.19) b	0.86	All
	HW07	1.42 (0.09) b	2.49 (0.17) c	0.90	All
	HC	2.93 (0.22) a	2.02 (0.29) a	0.75	Mid
	HW09	2.00 (0.40) b	1.80 (0.32) a	0.51	Mid
	HW07	1.79 (0.17) b	2.02 (0.18) a	0.86	Mid
	HC	2.14 (0.14) a	3.37 (0.65) a	0.79	Early/late
	HW09	1.42 (0.12) b	2.17 (0.24) b	0.82	Early/late
	HW07	1.36 (0.13) b	2.53 (0.39) c	0.80	Early/late

Values in parentheses represent standard errors. All model parameters shown in the table were significant (p value < 0.05).

soil moisture became a limiting factor for F_{soil} and interfered with the response to soil temperature in each treatment (Fig. 3, hatched area). As suggested by, e.g., Curiel Yuste et al. (2005a) and Ruehr and Buchmann (2010), respective dates with water-limiting conditions were excluded from the data, which strongly improved the relation between F_{soil} and soil temperature, with soil temperature subsequently explaining 91, 83 and 85 % of the variation in F_{soil} at RC, RW07 and RW00, respectively, and 83, 86 and 90 % of the variation in F_{soil} at HC, HW09 and HW07, respectively (Table 3). However, the addition of an exponential soil moisture term to Eq. (1) only marginally improved the explanatory value of the F_{soil} models at the Höllengebirge site, while at Rax no significant model improvement was observed (data not shown).

The basal CO_2 efflux, as represented by the F_{10} parameter of Eq. (1), was significantly higher in the undisturbed control stands when compared to the corresponding disturbed treatments at RW07, HW09 and HW07 (Table 3). Only at the oldest windthrow site (RW00) was F_{10} significantly higher when compared to the undisturbed stand (RC) (Table 3). Except for RW00, the same pattern in F_{10} could also be demonstrated when analysing the mid-season (01.06–31.08) and early/late season (01.09–31.05) separately (Table 3).

The Q_{10} values during non-water-limited conditions were 3.53, 2.44 and 2.40 at RC, RW07 and RW00 and 3.08, 2.33 and 2.49 at HC, HW09 and HW07, respectively (Table 3). The seasonal separation of the data also revealed that Q_{10} values across all treatments were lower during the growing season than during the dormant season (Table 3).

Average annual sums of F_{soil} for the sampling year 2012 of 626 ± 37 (±SE, $n = 8$), 696 ± 56 ($n = 6$) and 1130 ± 115 ($n = 6$) g C m^{-2} year^{-1} were calculated for the Rax treatments RC, RW07 and RW00, respectively. For the Höllengebirge site, corresponding values of 551 ± 72 ($n = 13$), 463 ± 29 ($n = 29$) and 492 ± 37 ($n = 23$) g C m^{-2} year^{-1} were calculated for HC, HW09 and HW07, respectively. The annual sums were corrected for surface rock outcrops, which, on average, accounted for 13 and 27 % of the total area at Rax and Höllengebirge, respectively.

By means of the modelling approach with two temperature scenarios (actual soil temperature and stand soil temperature), 31, 20, 15 and 20 % of the annual CO_2 efflux was attributed to warmer soil conditions at RW07, RW00, HW09 and HW07, respectively (Fig. 4).

According to the longer-term chronosequence of relative F_{soil} rates, the efflux tended to be rather similar until the sixth year after disturbance followed by a rebound and an increase during years 6–12 post-disturbance (Fig. 5).

Table 4. Pearson's correlation coefficients between F_{soil} and the ground vegetation surface cover of different plant functional types (herbaceous vegetation, grass vegetation, tree regeneration) for the disturbed areas at Rax and Höllengebirge. Surveys were performed during the growing seasons of 2009 and 2011 at Rax and during the growing seasons of 2010 and 2012 at Höllengebirge.

Variable	Rax				Höllengebirge			
	RW07		RW00		HW09		HW07	
	2009	2011	2009	2011	2010	2012	2010	2012
Herbs (%)	−0.310 n.s.	0.620 n.s.	0.259 n.s.	−0.378 n.s.	−0.169 n.s.	0.141 n.s.	−0.222 n.s.	0.016 n.s.
Grasses (%)	−0.275 n.s.	−0.241 n.s.	0.544 n.s.	0.606 n.s.	0.333 n.s.	−0.263 n.s.	−0.337 n.s.	0.426*
Trees (%)	–	–	–	–	–	–	0.373 n.s.	0.188 n.s.
Total (%)	−0.335 n.s.	0.244 n.s.	0.427 n.s.	0.620 n.s.	−0.003 n.s.	−0.081 n.s.	−0.166 n.s.	0.475*

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

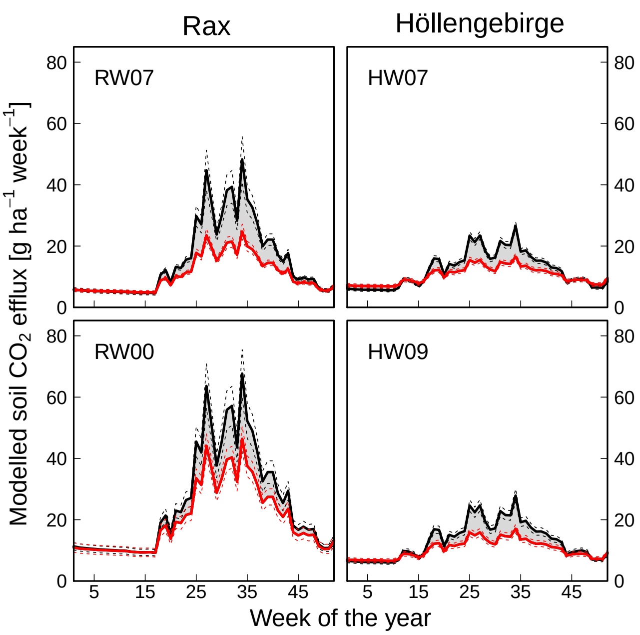

Figure 4. Modelled annual courses of soil CO_2 efflux for the Rax (windthrow 2007 – RW07; windthrow 2000 – RW00) and the Höllengebirge (HG09; HG07) windthrow areas for the year 2012 using actual soil temperature (black) and soil temperature of the adjacent undisturbed stand (red). The grey area represents the effect of increased soil temperature on the soil CO_2 efflux of the respective windthrow areas. Dashed lines represent the standard error of the mean.

3.3 Ground vegetation cover

Ground vegetation surface cover was clearly higher in older than in 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 for 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 4). At HW09, RW07 and RW00, 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. F_{soil} showed no significant decline throughout the first 6 years post-disturbance, and remained close to pre-disturbance levels (Table 2, Fig. 5). 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). The basal CO_2 efflux at 10 °C (F_{10}) was 30–40 % lower when compared to the control stands (Table 3). This percentage corresponds roughly to the autotrophic contribution to F_{soil} in intact forest ecosystems similar to ours (Hanson et al., 2000; Ruehr and Buchmann, 2010; Schindlbacher et al., 2009). However, as measured F_{soil} rates between the young windthrow areas and control stands were not statistically different (Table 2), 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 in our windthrow areas, it could be shown that the increase in soil temperature was key in maintaining F_{soil} rates at pre-disturbance levels (Figs. 4, 5). The higher-than-hypothesized F_{soil} in the initial years post-disturbance thus appears to be primarily driven by rate-accelerating soil microclimatic conditions.

During the CO_2 measurement campaigns, soil in the windthrow areas was on average 4.8 ± 0.7 °C (RW07) and 3.2 ± 0.7 °C (RW00) warmer than in the undisturbed treatment (RC) at Rax and 4.2 ± 0.4 °C (HW09) and 2.9 ± 0.4 °C (HW07) warmer than in the undisturbed treatment (HC) at Höllengebirge (Table 2). Such an increase in soil temperature

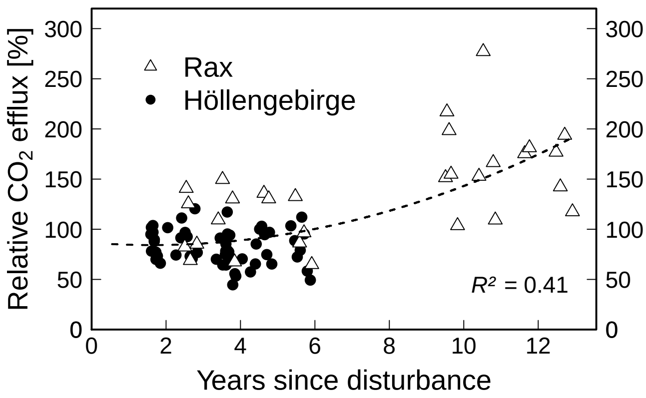

Figure 5. Post-disturbance development of soil CO_2 efflux relative to the respective undisturbed control treatments at the Rax and Höllengebirge chronosequence.

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., 2004b; Singh et al., 2008; Vanderhoof et al., 2013), driven by the loss of shading by the tree canopy and the subsequently higher insolation at the forest floor. The decreasing temperature difference between windthrow areas 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 dieback 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., 2004b). 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). A higher ground vegetation coverage and a consequently higher water demand in the Rax windthrow areas (Fig. 6a) are also likely to decrease soil moisture, since evapotranspiration increases rapidly with vegetation re-establishment following forest disturbance (Williams et al., 2014). As mentioned already, the above changes in soil microclimate were substantial factors in maintaining higher F_{soil} after disturbance. Simulations with two soil temperature scenarios (with soil temperature from the windthrow areas and from the control stands) revealed that disturbance-induced changes in soil microclimate were responsible for 15–31 % of the CO_2 flux magnitude of the windthrow areas (Fig. 4). Especially during warmer periods in summer, the temperature-related effect on F_{soil} was pronounced. Although soil moisture was also higher in the Höllengebirge windthrow areas, the effect on F_{soil} rates was marginal ($\sim$ 2 %, data not shown).

F_{soil} showed a strong relationship to soil temperature in all treatments, but apparent Q_{10} values were higher for the intact stands (Table 3); a pattern which has also been observed after clear-cut (Zu et al., 2009; Payeur-Poirier et al., 2012). This, however, does not necessarily mean that the real temperature sensitivity of SOM decomposition differed in windthrow and stand areas. More likely, the higher Q_{10} values 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). Similar mid-season Q_{10} values within each site (Table 3) therefore suggest a rather small disturbance effect on the real temperature sensitivity.

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. As ground vegetation cover was quite sparse in the initial period post-disturbance (Fig. 6), heterotrophic respiration was assumed to be the dominant contributor to F_{soil}. Hence the additional C input during disturbance seems to be slowly, but continually utilized, thus maintaining high decomposition rates.

F_{soil} and F_{10} from the oldest windthrow area (RW00) were significantly higher when compared to both F_{soil} and F_{10} from the more recent windthrow (RW07) and F_{soil} and F_{10} from the undisturbed stand (RC). The oldest windthrow site was characterized by dense grass vegetation which fully covered the soil surface (Fig. 6). The development of this dense grass community and the correspondingly increasing autotrophic respiration and litter input, as well as an input of easily decomposable exudates to the heterotrophic community, is likely responsible for the higher CO_2 efflux observed after 9–12 years post-disturbance, as reported by Pumpanen et al. (2004b). A significant positive relation between F_{soil} and grass cover at HW07 also supports this explanation (Table 4). Williams et al. (2014) reported an autotrophic contribution of $\sim$ 30 % after 4 years post-clear-cut. However, already after 4 years, nearly 100 % of the site was covered by ground vegetation, while it took much longer at the sites in our study region. In addition to the effects of ground vegetation cover, a delayed decomposition of woody debris might have contributed to higher F_{soil} rates in a later phase post-disturbance as well.

Average annual F_{soil} (during 2012) was estimated at $\sim$ 6.3 and 5.5 t C ha^{-1} year^{-1} 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 (4.6–7.0 t C ha^{-1} year^{-1}). In the intact forest stands, the loss of C through soil CO_2 efflux was likely offset by the C gain by photosynthesis and growth (Luyssaert et al., 2008). In the windthrow areas, the F_{soil} estimates indicate a substantial loss of C from the ecosystem, especially during

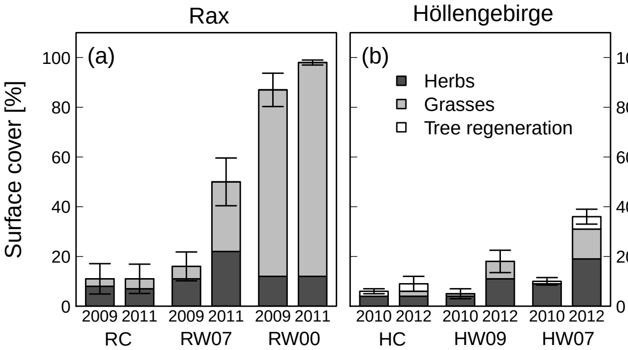

Figure 6. Ground vegetation surface cover of the different treatments at **(a)** Rax (control – RC; windthrow 2007 – RW07; windthrow 2000 – RW00) and **(b)** Höllengebirge (control – HC; windthrow 2009 – HG09; windthrow 2007 – HG07) determined in 2009 and 2011 at Rax and in 2010 and 2012 at Höllengebirge. Bars represent mean values of the plant type's surface cover. Error bars represent the 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: $n = 23$).

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 $8\,\mathrm{t\,ha^{-1}}$ 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 F_{soil} rates in our windthrow areas were primarily related to the warm soil conditions created by the loss of canopy shading (Fig. 4). 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. On 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 $\sim 11.3\,\mathrm{t\,C\,ha^{-1}\,year^{-1}}$ 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 that there is 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 begin to act as C sinks again after stand-replacing disturbances (Amiro et al., 2010; Pfeifer et al., 2011). This recovery time depends on disturbance effects on (soil) respiratory processes and on the recovery of vegetation productivity. If the disturbance largely reduces ecosystem respiration, then 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 (soil respiration only) 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 regrowth. At none of the sites of our windthrow chronosequence could significant tree seedling establishment or tree regrowth be observed (Fig. 6). 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 are thus subject to high browsing pressures (Ammer, 1996; Reimoser and Gossow, 1996; Reimoser and Reimoser, 2010). Therefore, a fast re-establishment of forest stands in windthrow areas is extremely difficult without post-disturbance management, such as artificial regeneration and subsequent fencing against browsing. If such measures are not undertaken, forest regrowth is hardly feasible. As carbon uptake in the successional phase of pioneer vegetation is lower compared to the phase of tree recovery (Williams et al., 2014), the C uptake at such windthrow sites is likely to be low. Consequently, more frequent forest disturbance by windthrow in mountainous regions (Seidl et al., 2011, 2014) poses a significant risk to soil C stocks in the European Alps and may feed back positively on rising atmospheric CO_2 concentrations.

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