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Abstract: During the last 15 years the frequency of small-scale wind disturbance and/or local bark beetle infestations has increased in Austrian mountain forests. We studied the C dynamics at the long term ecological research (LTER) site Zöbelboden where a mature stand dominated by Norway spruce (Picea abies) was hit by the storms "Kyrill" and "Emma" in 2007 and 2008 and subsequently infested by bark beetles. In the disturbed area, roughly 28% of the spruce trees were killed and salvaged. Aboveground C stock declined by approximately 35% resulting in a 30% reduction of biomass increment and litterfall during the study year 2011. Soil CO2 efflux was significantly lower in the disturbed area (7.0 ± 0.5 t C ha-1) than in the undisturbed area (8.7 ± 0.6 t C ha-1) in 2011. The contribution of autotrophic soil respiration was lower in the disturbed (annual mean 24%) than in the undisturbed stand (29%). Heterotrophic soil respiration was lower in the disturbed area as well (2011 undisturbed 6.17 t ha-1¬; disturbed 5.37 t ha-1). The 2011 annual net ecosystem productivity (NEP) was 0.14 t C ha-1 at the undisturbed and - 0.10 t C ha-1 at the disturbed forest, both being nearly C neutral. Our data showed that the NEP of the Norway spruce forest was hardly affected in year four after the initial disturbance and the associated management measures.

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Dear Editorial Board,

Please find enclosed the manuscript “Carbon dynamics of a managed Norway spruce forest after small-scale disturbance by windthrow and bark beetle” by Johannes Kobler, Robert Jandl, Thomas Dirnböck, Michael Mirtl and Andreas Schindlbacher, which we wish to be considered for publication in "Forest Ecology and Management".

Sincerely Your's

Andreas Schindlbacher and co-authors

Carbon dynamics of a managed Norway spruce forest after small-scale disturbance by windthrow and bark beetle

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Abstract

During the last 15 years the frequency of small-scale wind disturbance and/or local bark beetle infestations has increased in Austrian mountain forests. We studied the C dynamics at the long term ecological research (LTER) site Zöbelboden where a mature stand dominated by Norway spruce (*Picea abies*) was hit by the storms "Kyrill" and "Emma" in 2007 and 2008 and subsequently infested by bark beetles. In the disturbed area, roughly 28% of the spruce trees were killed and salvaged. Aboveground C stock declined by approximately 35% resulting in a 30% reduction of biomass increment and litterfall during the study year 2011. Soil CO_2 efflux was significantly lower in the disturbed area (7.0 ± 0.5 t C ha^{-1}) than in the undisturbed area (8.7 ± 0.6 t C ha^{-1}) in 2011. The contribution of autotrophic soil respiration was lower in the disturbed (annual mean 24%) than in the undisturbed stand (29%). Heterotrophic soil respiration was lower in the disturbed area as well (2011 undisturbed 6.17 t ha^{-1}; disturbed 5.37 t ha^{-1}). The 2011 annual net ecosystem productivity (NEP) was 0.14 t C ha^{-1} at the undisturbed and - 0.10 t C ha^{-1} at the disturbed forest, both being nearly C neutral. Our data showed that the NEP of the Norway spruce forest was hardly affected in year four after the initial disturbance and the associated management measures.

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Introduction

Climate change and increasingly aged stands leave Europe's forests exposed to natural disturbance (Schelhaas *et al.*, 2003; Seidl *et al.*, 2011). Disturbance can affect forest carbon (C) cycling with potential feedback effects on climate change (Knohl *et al.*, 2002; Kurz *et al.*, 2008; Lindroth *et al.*, 2009; Amiro *et al.*, 2010). Large-scale studies have shown that forest ecosystems, in general, are C sinks (Janssens *et al.*, 2003; Luyssaert *et al.*, 2010; Pan *et al.*, 2011). National governments have the option to include forest management as terrestrial carbon sinks in order to meet their emission reduction targets under the Kyoto protocol (UNFCCC, 1997). However, the sink strength of forest ecosystems is highly variable across spatial and temporal scales (e.g. Anderl *et al.*, 2012). Prominent disturbance agents lowering or even reversing positive NEP are extreme climatic events (i.e. fire, drought, storms) (Knohl *et al.*, 2002; Ciais *et al.*, 2005; Lindroth *et al.*, 2009), biotic disturbances (i.e. insects, pathogens) (Kurz *et al.*, 2008; Morehouse *et al.*, 2008) and human activities (i.e. deforestation, harvest) (Houghton, 2002; Amiro *et al.*, 2010; Pan *et al.*, 2011). Wind is one of the prominent agents of natural disturbance regime of forests causing gaps of varying sizes in forested landscapes (Ulanova, 2000). Schelhaas *et al.* (2003) quantified the share of wind to the average annual damage (35 mio. m^3) in Europe within the period 1950-2000 with 53 percent. Forest devastation by wind is an on-going issue in Europe, as several outstanding storms hit Europe's forests in the last decades (Gardiner *et al.*, 2010). Storm "Lothar" in 1999 caused a damage of approximately 16 million tons C in 1999, which equals to roughly 30% of the net biome production in Europe (Lindroth *et al.*, 2009). Beside devastated forests, residual debris and poor tree conditions caused by storms favor the subsequent outbreaks of insects such as bark beetles (Hicke *et al.*, 2012) which became increasingly evident in Austria during the last decades (Tomiczek and Schweiger, 2012). Many studies have focused on the effect of large scale disturbances on the function of forests as a C sink (Schelhaas *et al.*, 2003; Kurz *et al.*, 2007; Hicke *et al.*, 2012). However, in Austrian managed forests prevention measures against bark beetle are required by the Forest Act (except for core zones of national parks) and include the immediate removal of beetle infested trees and of trees in close vicinity. The consequences are gaps in the canopy and a patchy structure of the forest.

The intention of our study was quantifying the effects of such smaller-scale disturbances on the forest C dynamics. We studied the effects at the well documented long-term monitoring (LTER) forest site "Zöbelboden". We hypothesized that a combination of decreased stand productivity and higher soil CO_2 efflux due to higher soil temperatures in the gaps caused a substantial decrease in the NEP of the disturbed stand.

Materials and Methods

Site description and study set-up

The studied forest stand was located within the Austrian LTER site “Zöbelboden” in the northern part of the Austrian national park "Northern Limestone Alps" (N 47°50'30", E 14°26'30"). The long-term average annual air temperature was 7.8°C (1996-2011). Mean annual rainfall between 1996 and 2011 was 1645 mm. Snowfall occurred between October and May with an average duration of snow cover of about four months. The study site was located on an almost flat plateau at ~ 950 m.a.s.l. Soil types varied on a small scale between Lithic to Rendzic Leptosols and Chromic Cambisols, which partly showed stagnic properties. The underlying bedrock was dolomite. Norway spruce interspersed with beech (*Fagus sylvatica*) was planted after a clear cut around the year 1910. In 2007 and 2008, the storms “Kyrill” and “Paula” caused windthrow of single trees at the site. Subsequently, bark beetle infested individual trees around the windthrow gaps. Beetle infested trees were felled and removed soon after the infestation was observed. Windthrow and removal of infested trees caused a gap-wise structure in roughly half of the stand while the other half was unaffected. Characteristics of the disturbed and the undisturbed stand area are shown in Table 1. The CO_2 efflux from soil was not permanently monitored within the LTER scheme, but measurement campaigns were conducted during individual years. We analyzed the data of the year 2011 during which most parameters (biometric, soil respiration, climate) were available for a quantitative assessment of the disturbance effect.

Long term monitoring

Climate parameters (i.e. air temperature, precipitation, vapor pressure, solar radiation, wind speed and wind direction) were recorded at a meadow in close vicinity to the experimental stand since 1993 in half-hourly resolution. Soil temperature was measured in two soil profiles (disturbed area: 3, 10 and 20 cm; undisturbed area: 5, 15, 35 cm soil depth; Fenwall-Thermistor Th2-f, UMS, Germany). In November 2010, temperature data loggers (iButton® devices, Maxim Integrated, San Jose, CA, U.S.) were buried at 5 cm depth at each of the eighteen CO_2 measurement plots and each trenching plot and control plot. The iButton® loggers stored soil temperature data at three-hourly intervals.

Biomass C and woody increment

Stand inventories were conducted in 2007, 2009 and 2012 at the undisturbed area and in 2003 (pre-disturbance) and 2012, at the disturbed area. The position, the height, the diameter at breast height (dbh; 1.37m), the condition and the species of all trees were assessed. Biomass of stem wood, branches, needles/foliage, coarse and fine roots were separately calculated for each tree at the undisturbed and the disturbed area. Stem wood biomass was estimated based on tree species-specific volume equations (Zianis *et al.*, 2005). As these equations estimate the volume of single trees at fresh mass, the resulting volume was lowered by a species-specific fraction (i.e., shrinking factor) (Norway spruce: 0.119, European beech: 0.179). Subsequent, the resulting volumes were converted to stem wood biomass by species-specific conversion factors (Picea abies: 0.43, Fagus sylvatica: 0.68). The biomasses of branches, needles/foliage and coarse roots were estimated by selected biomass equations for coniferous tree (branches: Eckmüllner (2006), needles: Eckmüllner (2006), coarse roots: Bolte *et al.* (2004)) and deciduous trees (branches: Ledermann and Neumann (2006), foliage: Bartelink (1997), coarse roots: Bolte *et al.* (2004)). Fine root biomass was estimated by a constant factor (0.05) of coarse roots (Perruchoud *et al.*, 1999). The standing biomass prior to the disturbance was calculated by adding the biomass of removed trees (estimated from the dbh and tree height) to the standing stock. The annual increments of the biomass components were calculated by multiplying the biomasses of the components by the means of the relative annual increments of the respective biomass components. The C content of the biomass was estimated as 50% of the dry weight.

Litterfall

Above ground litterfall was collected with 15 regularly spaced litterfall samplers (0.49 m^2) during the growing season in monthly intervals (April-November) at the undisturbed area from 2008 to 2013 and at the disturbed area from 2010 to 2013. During winter, litter fall was sampled using 8 collectors (0.31 m^2). Below ground litter fall was estimated from the fine root stock. The biomass equation computes a fine root stock of 5% of the coarse roots (Perruchoud *et al.*, 1999). Assuming a ~ 0.5 to 1 year turnover time of the fine roots (Ostonen *et al.*, 2005), the potential annual below ground litter production ranges between one and two times of the estimated fine root stock. The C content of litter was 50% of the dry weight.

Soil organic carbon (SOC) stock

Soil depth was measured in a 10 x 10 m grid at the undisturbed and the disturbed area in 2008 and 2011, respectively by driving a steel pole (l = 1.2 m, d = 0.01 m) into the soil. To account for the small-scale variation of soil depth at the plateau, soil depth was measured 5-fold in a cross-like design with 1-m distance between the single locations at each grid point. The soil depths measurements were subsequent regionalized by inverse distance weighting (IDW) to produce maps of soil depths of both areas (Fig. 1). The estimated soil depths were classified in three soil depth classes (<50cm, 50-75cm, >75 cm). Three sampling plots were defined within the area of each soil depth class. The forest floor was sampled with a 0.09 m^2 frame. The mineral soil was sampled with a stainless soil column cylinder auger (d = 7 cm) at the undisturbed (2008) and the disturbed area (2012). Within each of the 18 soil sampling plots, 3 soil cores were taken, placed in polystyrene cases and divided into the geometric horizons 0-5, 5-10, 10-20, 20-30 and 30-50 cm, respectively. Samples were dried at approximately 30°C until constant weight, sieved through a 2.0 mm sieve and weighted. Roots and stones (>2 mm) were separated and stones were weighted. A subsample of each sample (litter: 2 g, mineral soil: 10 g) was dried at 105°C for calculation of the oven-dry mass. Total C content (TC) of the samples was analyzed by dry combustion. The total content of $CaCO_3$ (TIC) in soil was measured via addition of HCl and volumetrical determination of the released CO_2 ("Scheibler"). The total content of soil organic C (TOC) was calculated by subtracting the total content of $CaCO_3$ from the total C content. Soil organic C stocks ($t\ ha^{-1}$) were calculated for each horizon by multiplying SOC concentration (%) (oven-dry mass), bulk density ($g\ cm^{-3}$) and thickness of the horizon (cm).

Soil respiration measurements

Soil respiration was measured along two transects consisting of nine individual plots (spacing ~ 5m) within the disturbed and the undisturbed stand area (Fig. 1). At each of the nine plots, three plastic rings (10 cm diameter, 4 cm height) were inserted 2 cm into the mineral soil in autumn 2009. The inserted plastic rings served as base for the soil respiration measurements. Soil respiration was measured with an EGM-4 infrared gas analyzer connected to a SRC-1 soil respiration chamber (PP-Systems, Amesbury, USA). CO_2 efflux was calculated automatically by fitting a quadratic function to the increasing CO_2 headspace concentration. A mean CO_2 efflux rate was calculated from the three sub-plot values for each of the nine individual plots. Soil respiration was measured at monthly intervals starting in November

2009 until December 2011. During winter 2009-2010, soil respiration was measured on the same spots by using a snow probe according to Schindlbacher et al. (2007). A soil respiration measurement campaign lasted for almost five hours. Chambers along the transects were measured in a completely random order to avoid any error by the effect of temporal variations in soil respiration. During each soil respiration measurement, soil temperature was measured with a hand held probe at 5 cm soil depth.

To estimate the contribution of autotrophic and heterotrophic soil respiration to the total soil CO_2 efflux, we installed six trenching plots. Three trenching plots were installed randomly in the undisturbed area, whereas three trenching plots were installed in the center of larger gaps. Trenches around 1.5 x 1.5 m plots were dug down to the bedrock and all roots entering the trenches were cut. The trenches were sealed with a plastic foil in order to restrict root in-growth into the trenched plots. Adjacent to each trenching plot, a corresponding control plot was established. Each of the trenched and control plots was equipped with three plastic rings as described above for CO_2 chamber measurements. CO_2 efflux was measured monthly, parallel to the measurements conducted at the two transects.

Because soil CO_2 efflux was closely related to soil temperature at 5 cm soil depth, we used a simple linear regression model with log-transformed measured soil CO_2 efflux data as response and soil temperature data as predictor to estimate hourly soil CO_2 efflux. The model was parameterized for each single plot along the two transects and the trenching plots by using the measured soil respiration and soil temperature at 5 cm soil depth.

$$\log(CO_2\ \text{efflux}) = a+b*T \quad (1)$$

Where log (CO_2 efflux) is the log-transformed measured soil CO_2 efflux, *a* is the intercept of the linear regression model, *b* is the slope of the linear regression model and *T* is the measured soil temperature at 5 cm soil depth. Modeled values were summed up and an annual soil CO_2 efflux for 2011 was calculated for each single plot. We used the trenching plots which were located in the undisturbed stand to estimate the heterotrophic component in the undisturbed area as well as for the single plots under tree cover in the disturbed area. For the plots which were located in gaps (4 out of 9 plots in the disturbed area), we used data from the trenching plots in gap areas. To estimate the heterotrophic component of the annual soil CO_2 efflux, we estimated the mean monthly heterotrophic contribution for each single plot and summed up to annual values. Mean cumulative annual CO_2 efflux values for the disturbed and undisturbed area were than calculated from the nine plots at each corresponding transect. The effect of disturbance on the soil CO_2 efflux was tested by repeated measures ANOVA. Years 2010 and 2011 were tested interpedently. All statistics were carried out with SAS 9.2 (SAS Institute, www.sas.com) at a significance level of 95 %.

Results

Both stand areas showed similar stand characteristics prior to the disturbance (Tab. 1). The standing volume of beech was originally 55 m^3 ha^{-1} higher in the afterwards disturbed area whereas the standing stock of Norway spruce, was similar (866 m^3 ha^{-1} and 860 m^3 ha^{-1}). Soil C stocks were slightly lower (115.5 t ha^{-1}) in the disturbed area when compared to the undisturbed area (134.1 t ha^{-1}; Tab. 2). The difference was mainly due to the lower soil depth at the disturbed area (Tab. 1, Fig. 1). Norway spruce was affected by windthrow and bark beetle whereas beech trees withstood the disturbances. Disturbance reduced the number of standing trees by 28% corresponding to reduction in above ground C stock of approximately 35% (Tab. 2, Fig. 1). Disturbance effects on below ground biomass were assumed to be less pronounced since coarse and fine roots remained in the soil (only one tree was uprooted by windthrow). The reduction in standing trees resulted in roughly 30% decrease in above ground and total biomass increment and a corresponding ~ 30% reduction of litterfall in the disturbed stand area (Tab. 2, Tab. 3). Soil CO_2 efflux showed a clear relationship to soil temperature at both, the disturbed and the undisturbed area and followed the annual course of soil temperature (Fig. 2). Soil CO_2 efflux from disturbed plots was slightly lower during most of the season in 2010, the overall difference being statistically not significant. In 2011, soil CO_2 efflux was significantly ($p = 0.0145$) lower in the disturbed area (cumulative 7.0 ± 0.5 t C ha^{-1} y^{-1}) than in the undisturbed area (8.7 ± 0.6 t C ha^{-1} y^{-1}). The difference in soil CO_2 efflux was most pronounced during late-summer and autumn (Fig. 2). Late summer and autumn was the time during which the contribution of autotrophic CO_2 efflux was highest (Fig. 3). The annual average contribution of autotrophic soil respiration was lower (24%) in the disturbed stand area, when compared with the undisturbed stand area (29%) during 2011. The heterotrophic CO_2 efflux, or in other words the loss of soil C was lower in the disturbed stand area (5.37 t ha^{-1}; Tab. 3) as in the undisturbed area (6.17 t ha^{-1}) in 2011. The 2011 annual NEP (= increment + above ground litterfall – heterotrophic soil CO_2 efflux) was 0.14 t C ha^{-1} at the undisturbed and - 0.10 t C ha^{-1} at the disturbed stand area.

Discussion

Our hypothesis that the disturbance caused a substantial reduction in the NEP of the forest stand was not verified – both, disturbed and undisturbed stand areas were nearly C neutral. The hypothesized decrease in stand productivity came as expected as the number of trees was reduced by ~ 30% resulting in a corresponding decrease in biomass increment. Soil heterotrophic respiration was, in contrary to our hypothesis, lower in the disturbed area. Regarding the NEP, this lowered C loss from the soil largely compensated the lower C uptake by the biomass increment.

We had expected that soil temperatures in the gaps were higher as beneath the closed canopy of the undisturbed forest thereby favoring the decomposition of SOM (Kramer *et al.*, 2004). However, whereas soil temperature in the gap areas was slightly higher when direct sunlight reached the soil surface, soil cooled out more pronounced due to the higher nocturnal radiation. Overall, mean daily soil temperatures at the disturbed and undisturbed stand areas were almost similar (Fig. 2). Since the actual disturbances happened 2 - 4 years prior to the study period in 2011, initially higher CO_2 efflux from the soil cannot be excluded. During the first year after windthrow, the contribution of fine debris (needle, fine roots) to the soil CO_2 efflux can be high, especially when logs and residues are left on site (Knohl *et al.*, 2002; Köster *et al.*, 2011). Almost similar soil CO_2 efflux rates from disturbed and undisturbed plots in 2010 point towards an initially higher C loss from the disturbed stand when compared to 2011. Although logs were removed as a measure to prevent further bark beetle infestation, other residues such as branches and needles remained at the site and together with root decomposition of the killed trees likely have added to the soil CO_2 efflux prior to our comparison year 2011 (Díaz-Pinés *et al.*, 2010). In 2011, however, both, heterotrophic and autotrophic soil respiration were lower in the disturbed than in the undisturbed area. Lower autotrophic soil respiration rates can be explained by decreased or ceased activity of the killed tree fine roots. Lower heterotrophic soil respiration rates were likely caused by substrate limitation due to shortfall in easily decomposable residues combined with less fresh litter input due to the decreased number of trees.

Overall, biomass increment and heterotrophic soil respiration decreased simultaneously, leaving the NEP of the stand largely unaffected by the disturbance. Similar observations were made by Moore *et al.* (2013) who found comparable declines in gross primary production and respiration on a decadal timescale after a beetle outbreak in a subalpine forest. The real biomass increment at our disturbed stand may have been even higher as our conservative estimate. Annual biomass increment was estimated based on a period between two inventories in 2003 and 2012. The mean value which was used to estimate the 2011 increment therefore included pre and post-disturbance data. The post-disturbance increment however could have been higher as the remaining trees found favoring preconditions in terms of light and nutrients. The importance of management practices after disturbances was shown by Mathys *et al.* (2013) who found that the C uptake by the trees which survived a bark beetle attack retained the C sink function of the forest during the growing season while a nearby clear-cut stand turned into a considerable C source. Our results indicate that the immediate removal of the beetle infested and neighboring trees did not reduce the C-sink strength of the affected forest.

It has to be noted that individual stock and flux data hold large uncertainties as they were not measured but estimated using simple biomass equations. Largest uncertainty is associated to fine root data and belowground litterfall which were not accurately assessed in this study. In return, we assessed the autotrophic and heterotrophic components of the soil CO_2 efflux, which usually is measured in bulk. This allowed us to estimate the root prone CO_2 efflux and of the CO_2 which was released by SOM decomposition. For our attempt to estimate the effects on C cycling, a quantification of these fluxes was of high relevance. The applied "trenching" method however has some weaknesses (Hanson *et al.*, 2000). Soil moisture is mostly higher in the trenched plots when compared to the control plots and thereby can lead to an over or under estimation of the autotrophic component (Schindlbacher *et al.*, 2009). If such confounding effects had appeared, the implications had been the same at the disturbed and undisturbed stand areas and therefore would not affect the overall outcome of the study. We further did not quantify the disturbance effects on the leaching of dissolved organic carbon (DOC). This flux however is comparatively small (~ 0.03 t C ha^{-1} y^{-1}; Kobler, unpublished data) in magnitude. Therefore potential disturbance effects on DOC leaching should have been minor when compared to the gaseous C efflux (Schindlbacher *et al.*, 2009).

Our C cycle assessment was a point in time analysis of a single event affecting a single stand and cannot be extrapolated to longer timescales, differently structured stands or other tree species. To get a complete picture of the disturbance effects all the fluxes need to be studied and the time-scale needs to be extended to decadal range. For instance, upcoming gap regeneration will affect the above and belowground C-cycling of the disturbed stand (Kolari *et al.*, 2004; Amiro *et al.*, 2010). Continued monitoring at the LTER site has the potential to provide insights in the longer-term effects of the disturbance and applied management measures.

Conclusions

Disturbance by windthrow or bark beetle attack are common in Austrian mountain forests. Although forest management may not avoid large scale storm damage, several measures are undertaken to prevent the outbreak of bark beetle infestations. Common practice is to immediately remove beetle infested and surrounding trees once the infestation is recognized, thus causing a patchy structure of the remaining stand. As spruce bark beetle populations are supposed to increase in Europe with increasing temperature, small-scale disturbances like in this study will become increasingly important with regard to the forest C-cycling – also in the light of Kyoto reporting. Our study showed that the NEP of a mature Norway spruce forest 2-4 years post-disturbance was hardly affected since the decrease in plant productivity went hand in hand with a decrease in heterotrophic soil respiration.

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Tables

Table 1: Tree and stand characteristics of the disturbed and undisturbed area. Mean tree parameters (± SD) from the monitoring plots as well as soil depths are presented. Relevant parameters were summed to represent hectare (ha) values. Disturbance shows parameters of trees which were killed by wind or bark beetle. Killed-tree number and dbh (diameter at breast height) were measured; other parameters were estimated.

	Undisturbed area		**Disturbed area**		**Disturbance**	
Coniferous trees	Plot	ha	Plot	ha	Plot	ha
Tree number		393		221		136
Tree height (m)	28 (4.8)		28 (3.2)		29 (4.1)	
dbh (cm)	42 (11.5)		44 (8.7)		45 (12.4)	
Basal area (m^2)	0.15 (0.08)	58.7	0.16 (0.06)	34.8	0.17 (0.10)	22.7
Standing volume (m^3)	2.2 (1.39)	866.1	2.3 (1.12)	510.0	2.6 (1.79)	350.9
Deciduous trees						
Tree number		36		126		
Tree height (m)	25 (5.1)		22 (5.9)			
dbh (cm)	36 (15.3)		27 (12.6)			
Basal area (m^2)	0.12 (0.08)	4.3	0.07 (0.06)	8.6		
Standing volume (m^3)	1.6 (1.26)	58.1	0.9 (0.99)	113.7		
All trees						
Tree number		429		347		136
Tree height (m)	27 (4.90)		26 (5.26)		29 (4.1)	
dbh (cm)	42 (11.91)		38 (13.14)		45 (12.4)	
Basal area (m^2)	0.15 (0.08)	63.0	0.12 (0.08)	43.4	0.17 (0.10)	22.7
Standing volume (m^3)	2.15 (1.38)	924.2	1.79 (1.27)	623.7	2.6 (1.79)	350.9
Soil depth (cm)	70 (23.2)		57.2 (30.3)*			

* Significant difference between disturbed and undisturbed

Table 2: Estimated C pools of above and belowground forest stand compartments as well as soil C stocks (tons C ha^{-1}). "Prior to disturbance" values provide an estimate of the theoretical C pool (in 2011) of the disturbed area considering that the killed trees were still alive.

C - Pools	**Undisturbed**	**Disturbed**	**Prior to disturb.**
Stem wood	153.3	108.7	164.7
Branches	21.6	19.5	27.7
Needles/Foliage	7.9	6.6	10.3
Coarse Roots	31.2	20.5 – 32.6*	32.6
Fine Roots	1.6	1.0 – 1.6*	1.6
Abovegr. biomass	182.8	134.8	202.7
Total biomass	**215.6**	**156.3 – 169.0**	**236.9**
Litter	11.4	10.4	
Soil 0-20cm	84.6	67.5	
Soil 0-50 cm	118.0	105.7	
Soil 0-Max	**134.1**	**115.4**	

*minimal value (all dead roots decomposed) – maximum value (no dead roots decomposed)

Table 3: Estimated increment (tons C ha^{-1}), measured aboveground litterfall and estimated belowground litterfall and soil CO_2 efflux (mean (± SE, n=9) during 2011 "Prior to disturbance" values provide an estimate of the theoretical increment (in 2011) at the disturbed area considering that the killed trees were still alive.

	Undisturbed	Disturbed	Prior to disturbance
Increment			
Stem wood	3.10	2.42	3.41
Branches	0.15	0.26	0.32
Needles/Foliage	0.03	0.05	0.07
Coarse Roots	0.36	0.33	0.51
Fine Roots	0.02	0.02	0.03
Aboveground biomass	**3.28**	**2.73**	**3.80**
Total biomass	**3.66**	**3.08**	**4.34**
Aboveground litterfall	2.65	2.19	3.04
Belowground litterfall*	> 1.60	> 1.00	> 1.60
Soil respiration (Rs)	8.68 (0.55)	7.05 (0.48)	
Autotrophic soil respiration (Ra)	2.51 (0.16)	1.69 (0.33)	
Heterotrophic soil respiration (Rh)	6.17 (0.30)	5.37 (0.26)	
NEP (NPP-Rh)	0.14	-0.10	

*Fine roots biomass was estimated as 5% of coarse roots and assumed to have less than one year turnover time. The estimate represents a minimal value for the site conditions.

Figures

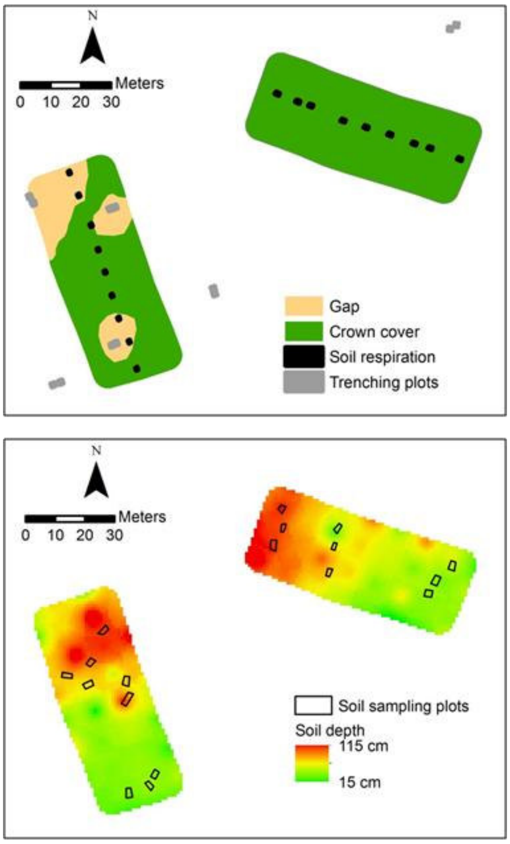

Figure 1: Position of soil respiration chambers, trenching plots and extension of crown cover at unaffected and disturbed plots (upper panel). Soil depth and soil sampling locations (lower panel).

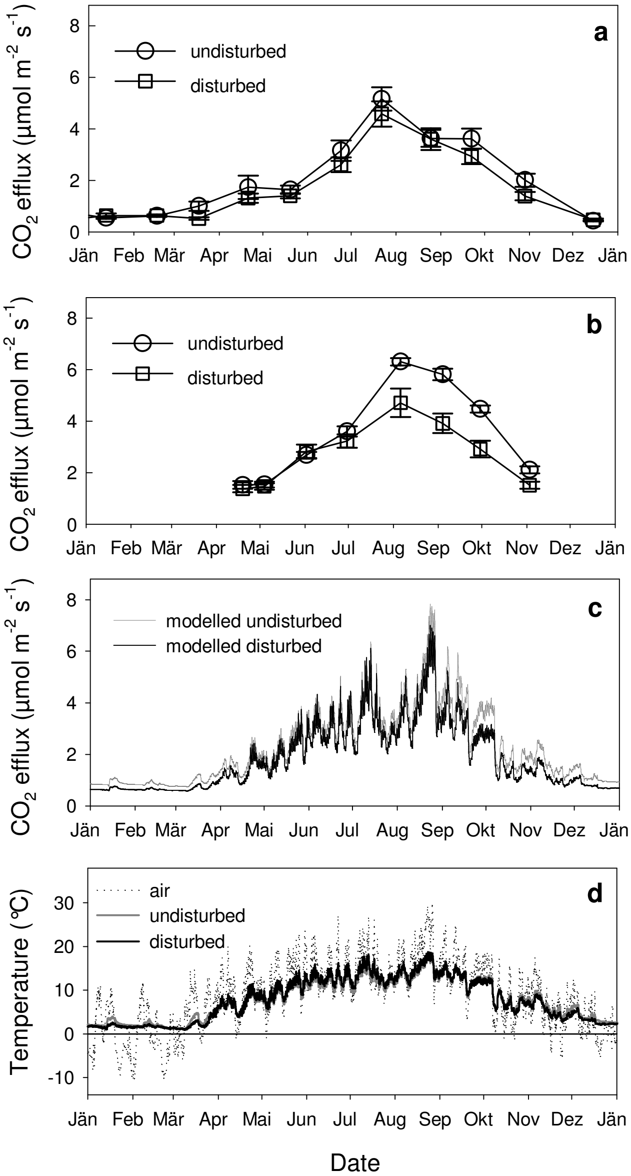

Figure 2: Soil CO_2 efflux (± SE, n = 9) from two transects through the disturbed and undisturbed stand area during 2010 (a) and 2011 (b). Modeled CO_2 efflux during the comparison year 2011 (c). Air and soil temperatures at the disturbed and undisturbed stand area during 2011 (d).

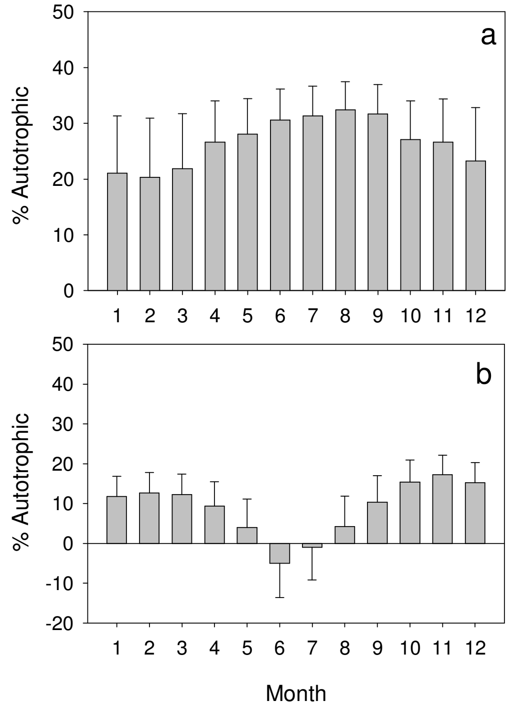

Figure 3: Contribution of autotrophic soil respiration to the total soil CO_2 efflux (± SE, n = 3) in undisturbed stand (a) and in the center of gaps (b) during the year 2011. The autotrophic contribution was derived as the difference in soil CO_2 efflux between trenched (roots cut) and adjacent control plots. Negative values indicate the occurrence of confounding moisture effects which were related to the trenching method.