StartClim2012.C

Disturbance of forest stands and humus loss

Störungen im Waldsystem und Humusverlust

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Kurzfassung

Der Boden ist der weltweit größte, und langfristigste, aktive Speicher für organischen Kohlenstoff. Die gespeicherte Menge ergibt sich als Bilanz aus Eintrag von abgestorbenen Blättern, Ästen und Wurzeln sowie Verlusten, die auf Mineralisation zurückzuführen sind. Mineralisation ist der Vorgang der Zersetzung von organischem Material durch Bodenmikroben. Die Entfernung oder das Absterben eines Baumes reduziert einerseits den Kohlenstoffeintrag und erhöht andererseits die Mineralisation. Die Zunahme der Mineralisation ist durch die Bodenfeuchte und -temperatur und deren Einfluss auf die mikrobielle Aktivität reguliert. Aber auch eine Abnahme der Mykorrizenaktivität lässt eine höhere Aktivität der Saprotrophen zu und dadurch auch eine Zunahme der Mineralisation. Die Untersuchungen wurden an Windwurfflächen von 2007 und 2009 in den Kalkalpen in Oberösterreich durchgeführt. Die Biomasse von Exktomykorrhizenhyphen wurde mittels sandgefüllten Einwuchsbeuteln bestimmt, die im September 2012 in den Boden der ungestörten Wald und Windwurfflächen eingesetzt wurden. Um den Einfluss von Windwurf zu simulieren und die autotrophische Atmung der Wurzeln und Mykorrhizen von der heterotrophischen Atmung des Bodens zu trennen, wurden ‘Trenching-‘ und ‘Clippingplots‘ im September 2012 eingerichtet. Die Einwuchsbeutel wurden im Juli 2013 geerntet, und die Hyphenbiomasse mittels optischer Einschätzung und durch Bestimmung von Ergosterol ermittelt. In der ungestörten Wald- und 2009 Windwurffläche entspricht die autotrophische Atmung ca. 30% der Gesamtatmung. Nur an der 2009 Windwurffläche wurde eine niedrige Hyphenbiomasse gemessen im Vergleich zu den anderen Flächen. Zwischen der ungestörten Wald- und der 2007 Windwurffläche wurden keine Unterschiede in der Hyphenbiomasse festgestellt. Durch Erosion wurde ein Großteil des Bodens weggewaschen, Messungen von Hyphenbiomasse und Bodenatmung an den Restflächen deuten jedoch darauf hin, dass die Bodenfunktion sich wieder erholt hat.

Abstract

Forest soils are world-wide the largest and longest storage pools for organic carbon. In temperate forests ca. 50% of the total C is stored in the soil. The amount stored in the soil is a balance between inputs from leaf and root litter, and outputs which are controlled by the rate at which soil organic matter is broken down by the soil microbial biomass, known as mineralisation. Removal or death of the tree from disturbance results, in the long term, in a decrease in litter inputs, but also results in an increase in mineralisation. The increase in mineralisation is due to changes in soil water content, and soil temperature which control microbial activity but also, a decrease in mycorrhizal fungal activity allows the activity of saprotrophic fungi to increase and hence can also increases soil organic matter mineralisation. The investigation was carried out on a site in the calcareous Alps of Upper Austria. *Picea abies* stands at the site were affected by large windthrows in 2007 and 2009. To determine the hyphal biomass of ectomycorrhizas, sand filled ingrowth bags were inserted into the undisturbed forest and the windthrow areas in September 2012. To simulate the effects of windthrow and to allow a separation of soil autotrophic respiration from the roots and mycorrhizal hyphae, and heterotrophic respiration from soil organic matter mineralisation, a series of trenching and clipping plots were established in September 2012. The ingrowth bags were removed in July 2013, and the biomass of the mycelium in the ingrowth bags was estimated by visual inspection and egrosterol analysis. The autotrophic respiration was about 30% of the total respiration in the stand and a slightly less in the 2009 windthrow. Only in the 2009 windthrow was a lower amount of mycelium found in the ingrowth bags. Between the intact forest and the 2007 windthrow no difference was found. Both measurements of hyphal biomass and soil CO_2 emissions suggest that the 2007 windthrow has recovered function, however a considerable amount of the soil area has been lost to erosion.

C-1 Introduction

Worldwide approximately half of the terrestrial organic carbon (OC) is stored in forests (1,146 Pg = Gigaton), and of this amount over 60% is retained in soil C pools (Nave et al., 2010). Forest soils are world-wide the largest and longest-lasting storage pools for organic carbon. Organic matter (OM) stored in forest soils is a particularly important part of the global C cycle as these soils are characterized by high OC concentrations and large soil organic C stocks (Christophel et al., 2013 and references within). In Europe, the largest OC concentrations of forest soils are found in the mostly shallow soils of the European Alps (Baritz et al., 2010), where low air temperatures retard the decomposition of organic material, resulting in pronounced accumulation of OM. The C amount stored in the soil is a balance between litter inputs, and outputs controlled by the mineralisation rate of soil organic matter by soil microbes and the related CO_2 losses by heterotrophic respiration (Allison et al., 2010), as well as carbon translocation by downward relocation of dissolved organic carbon (DOC), and particulate organic matter (POC) by erosion (Wang et al., 2013). On an annual basis, detrital C inputs often exceed respiratory or translocation C losses from soils, resulting in C storage. However, since the net C balance of forest soils (whether sequestering or losing C) is generally caused by a small difference between two large fluxes, a relatively minor change in either term has major impacts on forests C budget. In forests, both trees and ground vegetation have fungal symbionts on their root called mycorrhizas. The fine hyphae of these mycorrhizas form a large biomass pool in the soil (Ekblåd et al., 2013). Recently it has been shown that the input of biomass from mycorrhizal fungal hyphae is also a major source of C for the formation of soil organic carbon (Godbold et al., 2006, Wilson et al., 2009 Clemmensen et al., 2013). Thus, the interaction between plants and mycorrhizal fungi represents a major link between atmospheric and soil C.

Soil C is important not only because of its role in the global C cycle (Kirschbaum, 1995), but also because of its direct effect on forest productivity (Grigal and Vance, 2000) and stability and subsequent secondary effects on ecosystem services. Since C is the source of energy for the nutrient-recycling activities of heterotrophic soil organisms, soil C stocks are essential for sustainable forest nutrition (Attiwill and Adams, 1993). Furthermore, soil C is the major component of soil OM, which also contains significant amounts of water and nitrogen and is thus a major player in other global biogeochemistry cycles, energy and water budgets. Therefore, detailed information on the factors underlying forest soil C storage (or net loss) is decisive for predicting current and future forest ecosystem-services such as timber and non–timber forest products, groundwater recharge, or greenhouse gas mitigation. Beside this, international negotiations and treaties to limit greenhouse gases such as the Kyoto protocol require an understanding of the current and potential future forest C emissions and sequestration in managed, unmanaged and disturbed forests (Pan et al., 2011).

The main abiotic disturbances in Europe are fire, wind, flooding and drought, all of which may be affected by climate change (Lindner et al., 2010). Wind continuously affects the structure and functioning of forest ecosystems, causing significant economic losses in European forestry (Peltola et al., 2010); over half of the damage caused by natural disturbances to European forests is associated with storms (Gardiner et al., 2010). Thus, wind throw by storms is the most important natural disturbance of forests ecosystems in Europe today, and storms and hurricanes are expected to increase in frequency and severity with climate change (Dale et al., 2001, Peltola et al., 2010). A clear increase in storm-damage timber has been already recorded in Central Europe in the 20th century. This trend is not only caused by stronger storms (Usbeck et al., 2010) but also by human impacts on forests and soils, by increased stock and forested area, and partially by enhanced storm damage awareness (Schelhaas et al., 2003). For example, in the years 1990 and 1999 a total of 100 and 175 Mm^3 of timber were blown over in winter storms throughout Europe, respectively. In January 2007 and 2009, about 100 and 50 Mm^3 of tree logs were damaged in Central and Southern Europe respectively. Various studies have assigned a high storm exposure to summits in mountain ranges (Hofherr and Kunz, 2010). Future cyclone activity is expected to change under global warming conditions, while its regional effects will be highly variable (Ulbrich et al., 2009, Wernli et al., 2003), forest in mountainous regions will likely be affected above-average by increases of storm frequencies and severities due to topography and rather shallow soils. Furthermore coniferous trees, as present in mountainous regions, are in general more sensitive to storm damage than deciduous trees or mixed forest (Polomski and Kuhn, 2001, Klaus et al., 2011). Reasons for this include the higher wind load, superficial rooting, higher stocking, lower diameter at breast height and higher height to diameter ratio of coniferous trees as compared to deciduous trees, especially during the high storm seasons when deciduous trees are defoliated (Klaus et al., 2011).

Wind throw events which cause massive loss of tree cover, but also other disturbances such as bark beetle attacks and wild fires, change the carbon dynamics of forest ecosystems. Disturbances leading to tree mortality, crown damage, formation of gaps in the canopy cover, with subsequent changes in understory, affect the carbon balance directly, by modifying amount, timing and quality of litterfall carbon inputs (pulse input may be followed by decline in litterfall), and indirectly, by altering the soil microclimate (temperature and moisture regime). The microclimate influences decomposition and respiration of soil organic carbon as well as hydrologic losses of dissolved organic carbon (DOC) through leaching. Physiologically, the effect of wind throw on carbon exchange is a reduction in assimilation capacity and an increase in heterotrophic respiration, leading to a reduction in net ecosystem productivity (NEP) (Lindroth et al., 2009). NEP changes depend on the number of trees blown down, and whether or not logs and residual debris are removed, as well as on indirect factors mentioned above such as changing microclimate and site hydrology following disturbance. Furthermore, all processes may change simultaneously, albeit at different rates, and the challenge in understanding short and long term effects of disturbance on C dynamics and sequestration lies in being able to quantify the magnitude and duration of process changes both in absolute terms and relative to one another, as well as the change in process rates over time (Van Miegroet and Olsson, 2011). While some information on the stand level exist on the exchange of carbon dioxide (CO_2) between the atmosphere and forests after wind throw events, e.g. a Russian forest was investigated using the eddy covariance technique (Knohl et al., 2002), information on soil respiration after wind throw and the underlying factors is scarce. To assess the contribution of microenvironments to overall soil respiration after experimental hurricane blowdown, summer CO_2 effluxes were measured by Millikin and Bowden (1996) on pit, mound, and undisturbed microsites. CO_2 effluxes were 45.4, 80.1, and 99.0 mg C m^{-2} h^{-1} for pit, mound, and control, respectively. Millikin and Bowden (1996) concluded that measurements excluding or neglecting site heterogeneity cause a systematic overestimate of forest soil respiration. Mountainous forest sites with calcareous bedrock, such as in the Northern Limestone Alps, are highly heterogeneous due to their hydrogeological karst formations; the heterogeneity is likely increased further by any disturbance events.

In summary, soils at windthrow sites are subjected to rapid changes because of the abrupt alterations in the conditions for humus formation. The seminal study by Covington (1981) on a chronosequence after clear cut suggested a rapid, 50% SOC loss from the forest floor within 20 years after disturbance. More recently, Rusch et al. (2009) investigated the effect of storms Vivian (1990) and Lothar (1999) on forest sites across a range of elevations in Switzerland. Ten years after storm Lothar, which impacted mostly lower elevation mixed forests, an average loss of 4.3 Mg C ha^{-1} was measured. The loss was spread almost equally between forest floor and the upper 10 cm of the mineral soil, and representing around 9% of the C stored in the OM (Rusch et al., 2009). Twenty years after storm Vivian, which affected conifer sites at higher elevations characterized by thick organic litter layers, C losses were six-time higher (approx. 25 Mg C ha^{-1}) (Rusch et al., 2009). Similarly, preliminary results from Tirol and the Salzburgerland have shown that 10 years after a windthrow event soil organic C storage decrease to almost 25% of the pre-disturbance levels (Darabant et al., 2009). The development of the soil cover and the re-established shrub layer largely determine the amount and quality of vegetation debris and litter (Lüscher, 2002). Furthermore, after removal of tree logs and when vegetation recovery is sparse, forest soils on extreme sites such as steep slopes are highly endangered by erosion processes. A previous study in the Höllengebirge revealed an increase of 4% of bare rock within three years after wind throw and drastic translocation of SOM by erosion processes (Hollhaus, 2012).

Windthrow events alter the soil microclimate, but reported changes in microclimate and the subsequent effects on decomposition rates are not uniform across studies or within sites, reflecting the variability in post-disturbance vegetation cover and soil surface disturbances, as well as regional climatic context. Opening in canopy cover eliminates the attenuating effects of over-story trees via crown interception, water use and shading and exposes the soil to external influences more directly. The absence of the tree layer means that soil temperature extremes and average soil temperature rise, causing more rapid mineralisation under sufficient moisture conditions. For example, Kramer et al. (2004) showed for an Alaskan site that the loss of forest floor H-layer, associated with an increase in the quantity and quality (i.e. lower C:N ratio) of the fresh litter material, was attributed to accelerated microbial decomposition with warmer and drier site conditions. Superimposed to this is soil disturbance and mixing due to the falling trees, creating a distinct pit and mound micro-topography and increasing spatial heterogeneity in soil conditions (Van Miegroet and Olsson, 2011 and references within). In addition, as mycorrhizas are dependent on a C supply from the host trees, the death of the trees strongly decreases the activity of mycorrhizal fungi. A decrease in mycorrhizal fungal activity allows the activity of saprotrophic fungi to increase and hence can also increases soil organic matter mineralisation. Gadgil and Gadgil (1971), (1975) found that when ectomycorrhizal roots were excluded from *Pinus radiata* litter, the rate of litter decomposition increased drastically over a 12-month period. This ‘Gadgil effect’ was attributed to stimulated colonization and exploitation of litter by ectomycorrhizal fungi at the expense of litter decomposing saprotroph. The Gadgil effect, is considered to be an important mechanism behind the increase in mineralization. However, attempts to confirm the Gadgil effect in more recent studies have met with a variety of results. Koide and Wu (2003), for example, concluded that the negative effect of ectomycorrhizas on decomposition could be mediated by extraction of water, particularly in relatively dry soils, supressing saprophytic activity rather indirectly than by direct competition between ectomycorrhizas and saprophytes as proposed by Gadgil and Gadgil and others. Further studies are required to understand the mechanism(s) underlying the Gadgil effect and its effect on C mineralization.

C-2 Study aims

Studies dealing explicitly with the effects of windthrow events on forests' C balance are scarce in general and especially rare in Europe; subsequently studies conducted outside Europe have been heavily relied on (Van Miegroet and Olsson, 2011). Furthermore, detailed studies on soil respiration and C quantity and quality after wind throws, taking spatial heterogeneity into account, are virtually absent. Thus, the general aim of the subproject StartClim2012C is to investigate the mechanisms behind the loss and quality change of soil organic C after wind throws in mountain forests of the Alps.

In detail the following questions will be addressed:

1) Does the humus thickness and the quality of C change between windthrow sites and remaining forest plots?
2) Is the biomass of ectomycorrhizas lower on wind throw sites?
3) Which mechanisms are underlying any potential loss of carbon, and do the contributing factors change with time after a wind throw disturbance?

C-3 Material and Methods

C-3.1 Research Site

The investigation was carried out on a site in the Northern Calcareous Alps of Upper Austria in the Höllengebirge mountain range, using the established sites of the EU-Interreg project 'SicAlp'.

Climate is oceanic with cool and humid conditions, characterised by a distinctive precipitation maximum during the summer. Precipitation minima are commonly observed in spring and fall (Kilian et al. 1994). Annual precipitation is around 1400 to 1500 mm and annual average air temperature around 5 °C (ZAMG, 2012). Elevation of the site ranges from 950-1100 m a.s.l. with an exposition of south to south-west and an average slope of 25%. Parent bedrock is dominated by limestone ('Wettersteinkalk') in paragenesis with dolomite ('Wettersteindolomit'). Soil types are Folic Histosols, Rendzic Leptosols and Chromic Cambisols (WRB 2007), which occur in a highly interlocked pattern. The Northern Calcareous Alps are often characterized by such heterogeneous soil patterns, where mosaics of different soil types can be detected within few metres (Koeck et al., 2001). The organic soil types Folic Histosol and Rendzic Leptosol tend to occur more on exposed and steeper locations and Chromic Cambisols are dominating flatter areas and depressions. Humus types were Mull, Moder and Tangel (Zanella et al., 2011).

The sites are or were formerly dominated by spruce (*Picea abies*), beech (*Fagus silvatica*), and fir (*Abies alba*) trees. A catastrophic windthrow event with subsequent bark beetle attacks affected the site in 2007 (subsequently referred to as W07), followed by several smaller windthrow events in 2009 (subsequently denoted by W09). In sum, almost 30 ha of the tree layer was either blown over or broken. Spruce saplings from a pre-disturbance understory tree layer sparsely remained at the windthrow area from 2007. Most of the woody debris, predominantly the stem fraction was removed by cable yard and helicopter logging operations right after the respective disturbance events. Logging residues, mainly consisting of tree branches and twigs, remained at the site and covered around 15 to 20% of the soil surface in 2012. Ground vegetation on the windthrow areas comprised grasses (dominantly *Calamagrostis varia*) and herbaceous plants (*Adenostyles glabra, Eupatorium cannabinum, Cirsium arvense, Urtica dioica*).

An adjacent, undisturbed mature mixed stand was used as a control (denoted as CS). The control stand is dominated by beech (*Fagus sylvatica*), spruce (*Picea abies*) and fir (*Abies alba*), and sporadic intermixed were ash (*Fraxinus excelsior*) and maple (*Acer pseudoplatanus*) outside our research plots. The age of the stand is approximately 220 years. Pre-disturbance tree communities at W07 and W09 were similar to that of the undisturbed CS.

The presence of two windthrows (W07 and W09) differing in age, as well as an unaffected forest stand (CS) with the same site conditions, provided a pseudo chronosequence of disturbance. This approach allows the investigation of temporal changes after large-scale forest disturbance with respect to soil carbon and humus dynamics. The disturbed areas W07 and W09, and the control stand CS will be designated as treatments in the following report.

C-3.2 Experimental set-up

To simulate the effects of windthrow on different soil parameters and to allow a separation of soil CO_2 efflux from the roots and fungal biomass (autotrophic respiration), and from breakdown of soil organic matter mineralisation (heterotrophic respiration), 64 sampling locations were established across the three treatments (W07, W09, and CS) in September 2012.

In the control stand (CS) a trenching experiment was conducted. Ten soil monoliths of 1 m^2 each were isolated by trenching and subsequent installation of a 4 mm-thick plastic sheet down to 50 cm depth. This procedure eliminates the autotrophic respiration by momentarily severing the direct C supply by tree roots into the soil monoliths, and prevents the future ingrowth of roots. In addition, four older trenching plots from 2011 were used. Ten plots were established outside of the trenched areas to measure soil respiration und soil properties under undisturbed forest conditions.

To include a wide range of soil and vegetation parameters at the disturbed sites, four grass vegetation plots, four herbaceous vegetation plots and four bare soil plots (no vegetation) were selected at both W07 and W09. To decrease the rooting density of grass and herbaceous vegetation, and thus autotrophic respiration, the aboveground vegetation was clipped at eight additional plots (four with grass and four with herbaceous vegetation) at both W07 and W09 sites. Clipping was performed during the plot establishment in September 2012, followed by repeated clipping in spring and summer 2013, removing the aboveground plant organs on 1 m^2 around the centre of the plot with scissors.

For disturbance-free soil respiration measurements, a 5 cm-high plastic collar (10 cm inner diameter) was installed on each sampling location in September 2012; the plastic collar was inserted 3 cm into the soil surface (including litter layer). In addition, two mycorrhiza ingrowth bags, filled with 13 g of quartz sand, were installed at 5 cm soil depth and in close vicinity to the plastic collars to determine ectomycorrhizal biomass. Only one ingrowth bag was installed at each treatment on the W09 plots, and in the trenched plots of the intact forest.

C-3.3 Field campaign

C-3.3.1 Soil respiration and soil climate measurements

Soil respiration measurements were conducted prior to soil coring during a two day field campaign (08.-09.07.2013). Efflux from the soil surface was measured by means of a 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). Measurements were taken by connecting the chamber to the installed collars. The temporal CO_2 increase inside the chamber headspace was measured for either 2 minutes or an increase in CO_2 concentration of 50 ppm. The recording interval of CO_2 efflux [ppm] was 4.8- 5 seconds; a CO_2 flux was calculated automatically by the instrument software. For each sampling location either two (if the difference between the measurements was ≤0.05 µmol CO_2 m^{-2} sec^{-1}) or three (>0.05 µmol CO_2 m^{-2} sec^{-1}) efflux measurements were taken and the respective average was calculated for further analysis.

At time of measurements, soil temperature was measured at soil depths of 5 cm and 10 cm (including litter layer) with a handheld puncture thermometer. Volumetric soil water content was determined for 0–7 cm soil depth (including litter layer) by means of time domain reflectometry (TDR). Measurements were performed with a Field Scout TDR Soil Moisture Meter (Spectrum Technologies Inc., Plainfield, IL, USA). Both measurements were taken at an approximate distance to the collar of 15 cm to avoid disturbance. A prior calibration of the TDR instrument to characteristic humus types of the Northern Calcareous Alps was performed (C. Delaney, pers. comm.).

Soil respiration rates were standardized for temperature, using site specific Q_{10} functions (Janssens and Pilegaard, 2003) which were determined during previous investigations. Respective functions were available for each treatment and stratification (e.g. grass vegetation, bare soil, trenched plots). Because the volumetric soil water content showed a homogeneous pattern between treatments and sampling locations and was neither very low nor distinctly high, no standardization was necessary.

C-3.3.2 Soil and mycorrhiza ingrowth bag sampling and site description

Immediately after the soil respiration measurement, a soil sample was taken inside the plastic collar using an 8-cm-wide soil corer. The corer was inserted either down to the bedrock or to a maximum depth of 40 cm. For each soil core, the thickness of different horizons was measured by means of a measurement tape. In addition, the length of the extracted soil core was compared with the depth of the hole to calculate a compression factor. Soil core samples were divided into 10 cm parts (soil depth: 0-10 cm, 10-20 cm etc.) and stored in sealed plastic bags. The mycorrhiza ingrowth bags were dug out. In the field, both soil samples and ingrowth bags were kept in cooling boxes before they were stored at 4°C until further processing took place.

To describe the site conditions, the distance of closest tree to the sampling location and the number of young trees within 2 m around the location was measured. Vegetation cover-abundance was estimated within a 1 m^2 area around the soil respiration collar using the Braun-Blanquet method, distinguishing grass vegetation, herbaceous vegetation and bare soil.

C-3.4 Laboratory analysis

C-3.4.1 Soil and root analysis

The soil samples were sieved fresh through 4 mm sieves and roots were collected with tweezers. The sieved soil was divided into three parts; one part was dried, one third was kept in the fridge (4°C) and one part was frozen (-20°C) for later analysis. Roots were visually separated into tree and grass/herb roots using a stereo microscope (10-40x), dried at 70°C (48h) and weighed to determine the root mass per m^2.

For drying the soil sample was dried at 105°C and weighed to calculate the volumetric water content. After grinding and homogenisation, 300 mg of dried soil were weighed into tin capsules and total carbon and nitrogen contents were measured with a with a CHN-2000 analyser (Leco Corp., St Joseph, MI.) with flash combustion technique. C:N ratios were calculated from this analysis.

Fresh soil material was used to determine pH values and dissolvable C (DOC) and N (TDN). Soil pH was determined in 1:1 (v/v) soil:H_2O extracts. To measure the dissolved C (DOC) and N (DON) in the humus, 2.5 g of fresh soil was shaken in 25 mL distilled water for 1h at 20°C (Jones and Willett, 2006). The extract was frozen until concentrations of DOC and total dissolved N (TDN) were determined with a Shimadzu TOC-TN analyser (Shimadzu Corp., Kyoto, Japan).

The frozen soil was extracted for PLFA to estimate microbial biomass and to determine changes in the microbial community. The amount of the phospholipid fatty acid $18.2\omega 6,9$ was used as an indicator of ectomycorrhiza (EM) and saprophytic fungi and PLFA and NFLA $16:1\omega 5$ AM was used to estimate arbuscular mycorrhiza (AM) in the soil samples. The method of lipid extraction followed Frostegård et al. (1991). Extracted lipids were fractionated into neutral lipids, glycolipids and polar lipids on silicic acid columns (100-200 mesh, Unisil) by successively eluting with chloroform, acetone and methanol. The chloroform and methanol fractions (containing the neutral respectively phospholipids) was subjected to mild alkaline methanolysis to transform the fatty acids into free methyl esters. These were analysed on a GC according to the method of Frostegård et al. (1993). A conversion factor of 2 nmol PLFA $18:2\omega 6,9$ mg^{-1} fungal biomass was used to estimate the biomass of EM mycelium in the soil (Olsson, 1998) and the amount of NFLA and PLFA $16:1\omega 5$ was used to estimate the amount of AM mycelia in the soil (Olsson, 1999). The total amount of PLFAs was also analysed to enable the estimation of the total microbial biomass and detect changes in the microbial community (Frostegård et al., 1993).

C-3.4.2 Visual assessment of hyphae abundance and Ergosterol analysis

The mycorrhiza ingrowth bags were cut open and the content studied under a stereo microscope to estimate the occurrence of hyphae. The presence of hyphae was estimated in 5 classes according to Wallander et al. (2004):

0. No hyphae,

1. Occasionally hyphae present,

2. Sparse mycelia present,

4. Mycelia present but no aggregation of soil particles, and

5. Plenty of mycelia and some aggregation of mycelia.

For more precise analysis of the amount of mycelia, the sand was extracted and analysed for ergosterol, which is a biomarker for fungi (Nylund and Wallander, 1992). Five grams of the sand from each bag were extracted in 10% KOH in methanol, and the sterols transferred to cyclohexane, which was then evaporated. The pellet was dissolved in methanol, and ergosterol analysed on a HPLC with a RF C18 5µm column with 95% methanol 5% water as carrier (Agilent 1100) (Nylund and Wallander, 1992).

C-3.5 Statistics

To test for differences between treatments we used one-way ANOVA and two-way ANOVA followed by Tukey post-hoc test. Significance levels of $P < 0.05$ or lower were used. All statistical analysis was performed with the R statistical package for Windows 7 or SPSS 20 for Mac.

C-4 Results

C-4.1 Sampling site and soil parameters

C-4.1.2 Number of tree seedling around sampling sites

Numbers of tree seedlings at the 2007 wind throw site are clearly higher than at the 2009 windthrow site (Fig. C-1). No seedlings were found around the sampling sites in the undisturbed forest stand.

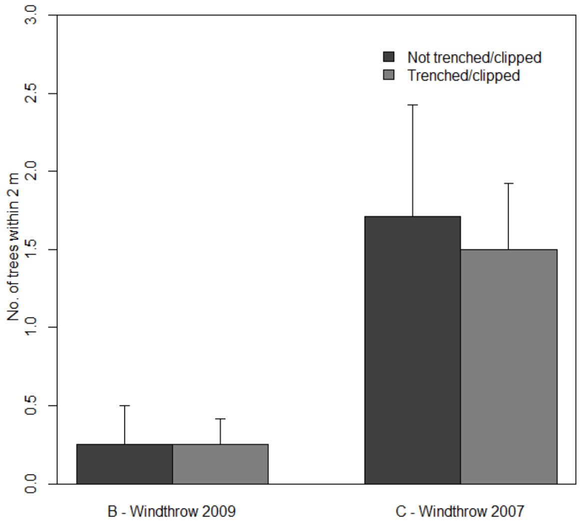


Fig. C-1: Number of tree seedlings within 2 meters of the non- clipped/non-trenched, clipped/ trenched plots at treatment sites WS07 (Windthrow 2007) and WS09 (Windthrow 2009) (Mean±SE).

C-4.1.2 Humus thickness

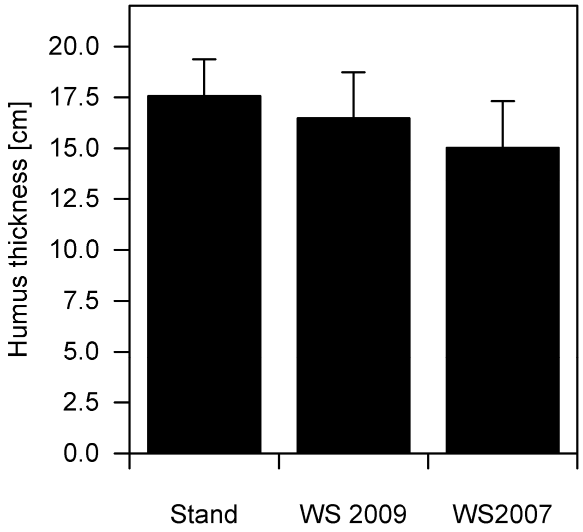


Fig. C-2: Thickness of the humus layer in the control stand (CS), wind throw 2009 (WS2009), and wind throw 2007 (WS2007) (Mean±SE).

In the soil patches that remain at the site, the humus layer thickness at measurement sites was greatest in the undisturbed forest and thinnest on the wind throw 2007 site. The humus layer at windthrow 2009 is of intermediate thickness (Fig. C-2). Although there is a clear decline in thickness due to the high variability between sites, no significant differences could be shown. In addition, the remaining soil patches are only a fraction of the total site area, and are interspersed in large areas of bare rock with no soil layer. On the bare rock sites, the soil cover has been lost by erosion. Thus these soil depth measurements are not representative of the whole site, but are indicative for soil organic matter loss in the remaining soil patches.

C-4.1.3 Soil pH(H_2O)

Using the pooled mean of the treatments, soil pH(H_2O) at soil depth 0-10 cm and 10-20 cm was shown to be significantly lower in the forest stand than in wind throw 2009 and the wind throw 2007. There was no significant difference between treatments (Fig. C-3, Tab. C-1,

Tab. C-2). At 0-10 cm, the pH increased from 4.28 in the undisturbed forest to 4.88 and 5.29 on the 2009 and 2007 windthrows, respectively. Similarly, at 10-20 cm the increase was from 4.41 to 5.17 and 5.12, respectively.

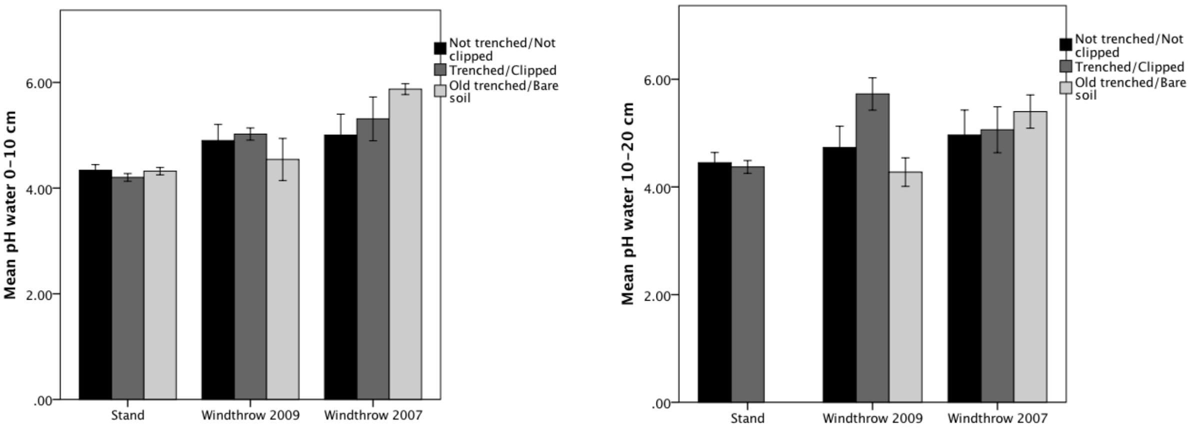
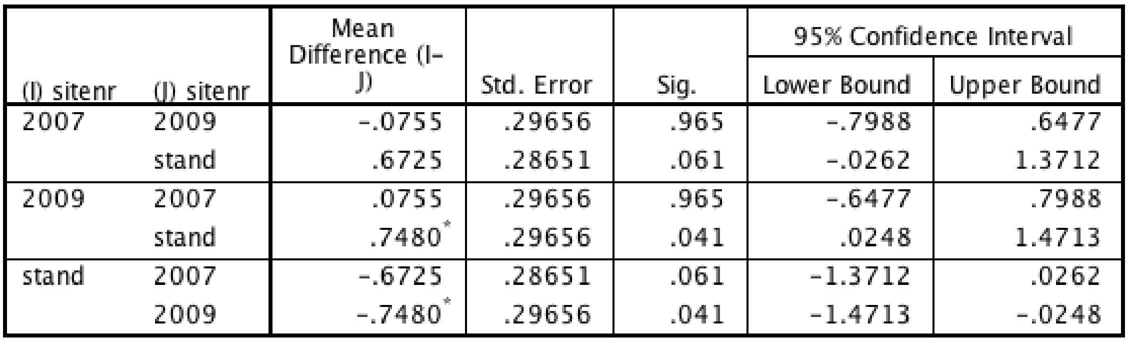


Fig. C-3: pH (H_20) values of the soil depths 0-10 cm and 10-20 cm of the treatments WS07 (Windthrow 2007), WS09 (Windthrow 2009) and the control stand (CS) divided into clipped/new trench, vegetation and bare soil sites (Mean±SE). In the old trenching in the stand not enough soil cores could be taken to a depth of 20 cm to get a representative value.

Tab. C-1: Multiple compression of site (Tukey test) in a two-way ANOVA with site and treatment as independent parameters of the pH values at soil depth 0-10 cm between the treatments WS07 (Windthrow 2007), WS09 (Windthrow 2009) and the control stand (CS).

(I) sitenr	(J) sitenr	Mean Difference (I-J)	Std. Error	Sig.	95% Confidence Interval	
					Lower Bound	Upper Bound
2007	2009	.4076	.22660	.180	-.1388	.9539
	stand	1.0060*	.21747	.000	.4816	1.5303
2009	2007	-.4076	.22660	.180	-.9539	.1388
	stand	.5984*	.21116	.018	.0892	1.1076
stand	2007	-1.0060*	.21747	.000	-1.5303	-.4816
	2009	-.5984*	.21116	.018	-1.1076	-.0892

Tab. C-2: Multiple compression of site (Tukey test) in a two-way ANOVA with site and treatment as independent parameters of the pH values at soil depth 10-20 cm between the treatments WS07 (Windthrow 2007), WS09 (Windthrow 2009) and the control stand (CS).



(I) sitenr	(J) sitenr	Mean Difference (I-J)	Std. Error	Sig.	95% Confidence Interval	
					Lower Bound	Upper Bound
2007	2009	-.0755	.29656	.965	-.7988	.6477
	stand	.6725	.28651	.061	-.0262	1.3712
2009	2007	.0755	.29656	.965	-.6477	.7988
	stand	.7480*	.29656	.041	.0248	1.4713
stand	2007	-.6725	.28651	.061	-1.3712	.0262
	2009	-.7480*	.29656	.041	-1.4713	-.0248

C-4.2 Soil carbon and nitrogen

C-4.2.1 Carbon content in the soil

The relative carbon content of soil at depth 0-10 cm is very heterogeneous, and can be clearly seen in the large standard errors of the treatment bars in Figure C-4. The lowest value was found at clipped plots at windthrow 2007, while the soil under bare soil patches on the same stand hold the most carbon per g d.wt. Between these two treatments there was a significant difference. The pooled treatment means for the sites were not significantly different and the C content was between 36 to 41 % of the organic matter dry weight.

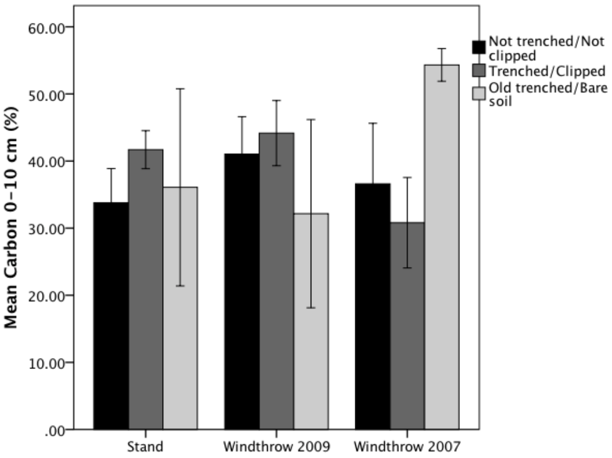


Fig. C-4: Percentage carbon in soil samples of the depth 0-10 cm on non-clipped/non-trenched, clipped/trenched, and old trenched/bare soil plots at the undisturbed stand (Control), wind throw 2009 and wind throw 2007 (mean±SE).

C-4.2.2 Soil C:N ratio at depth 0-10 cm

The C:N ratio differed significantly between the sites was higher in the stand (18.1) than in the 2009 windthrow (16.5) and the 2007 windthrow (15.8) No significant differences were found between (non-)trenched/clipped and bare soil plots (Tab. C-3).

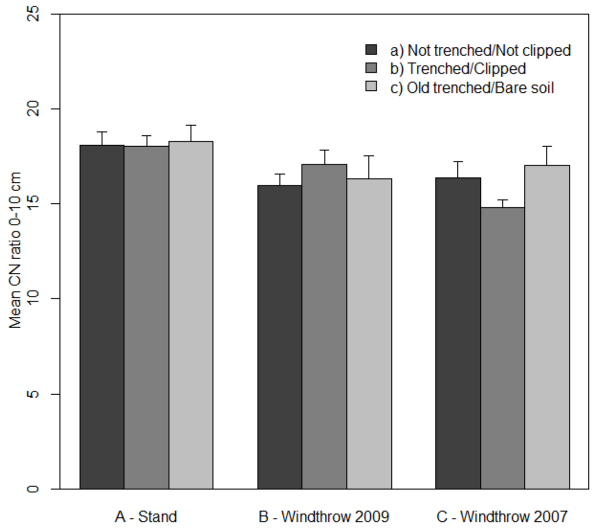
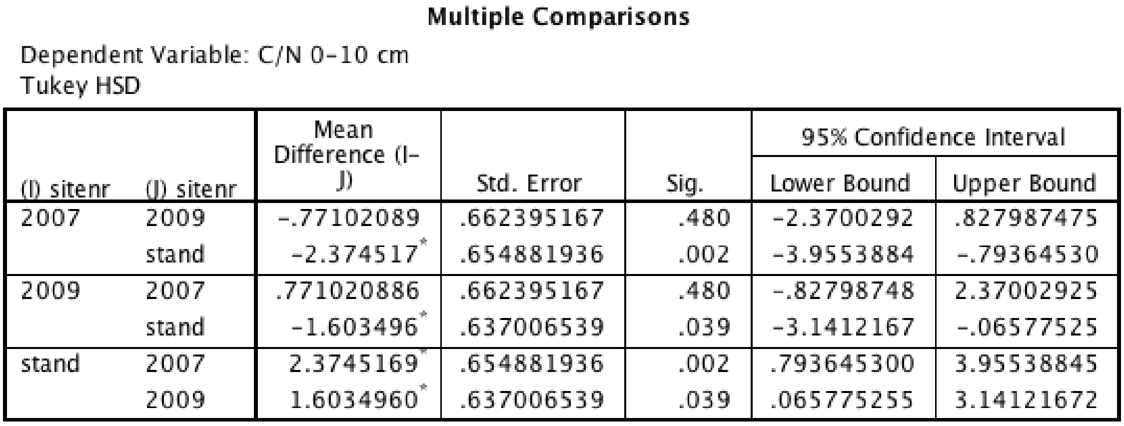


Fig. C-5: C:N ratio at soil depth 0-10 cm on non-clipped/non-trenched, clipped/trenched, and old trenched/bare soil plots at the treatment sites Stand (Control), wind throw 2009 and wind throw 2007 (mean+SE).

Tab. C-3: Multiple compression of site (Tukey test) in a two-way ANOVA with site and treatment as independent parameters of the C:N ratio at soil depth 0-10 cm between the treatments WS07 (Windthrow 2007), WS09 (Windthrow 2009) and the control stand (CS). There are no significant differences between treatments.



Multiple Comparisons

Dependent Variable: C/N 0-10 cm
Tukey HSD

(I) sitenr	(J) sitenr	Mean Difference (I-J)	Std. Error	Sig.	95% Confidence Interval	
					Lower Bound	Upper Bound
2007	2009	-.77102089	.662395167	.480	-2.3700292	.827987475
	stand	-2.374517*	.654881936	.002	-3.9553884	-.79364530
2009	2007	.771020886	.662395167	.480	-.82798748	2.37002925
	stand	-1.603496*	.637006539	.039	-3.1412167	-.06577525
stand	2007	2.3745169*	.654881936	.002	.793645300	3.95538845
	2009	1.6034960*	.637006539	.039	.065775255	3.14121672

C-4.2.3 Extractable dissolved organic carbon

The dissolved organic carbon (DOC) per mg soil was found to be significantly (Tukey test, P < 0.01) different between the 2007 windthrow and 2009 windthrow, the value in the soil of 2009 windthrow were significantly higher (Fig. C-6). The DOC value at the undisturbed forest stand lies between the values of the two windthrow sites and did not significantly differ from them.

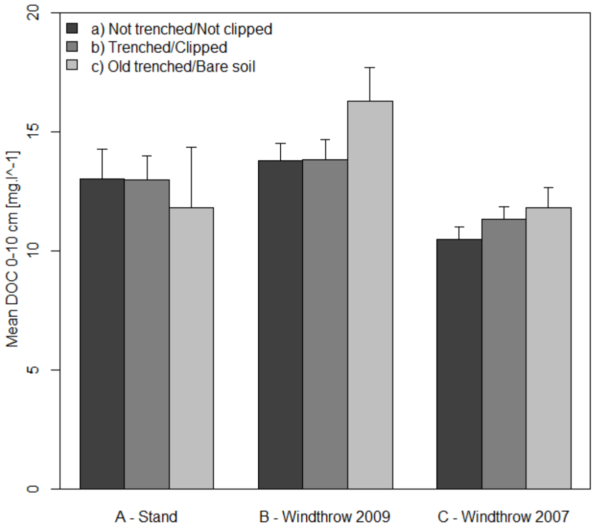


Fig. C-6: Extractable dissolved organic carbon (DOC) on non-clipped/non-trenched, clipped/trenched, and old trenched/bare soil plots at the treatment sites Stand (Control), wind throw 2009 and wind throw 2007 (mean+95% CI).

C-4.3 Tree root mass

The highest total tree root mass (i.e. both living and dead tree roots) was found at the undisturbed stand (679g m^{-2}) followed by 2009 windthrow (279g m^{-2}), and the lowest values were found at 2007 windthrow (175 g m^{-2}) (Fig. C-6). The differences were statistically significant. Tree root masses on trenched, clipped and bare soil plots were constantly lower than on non-trenched or non-clipped plots. However, this difference was not statistically significant.

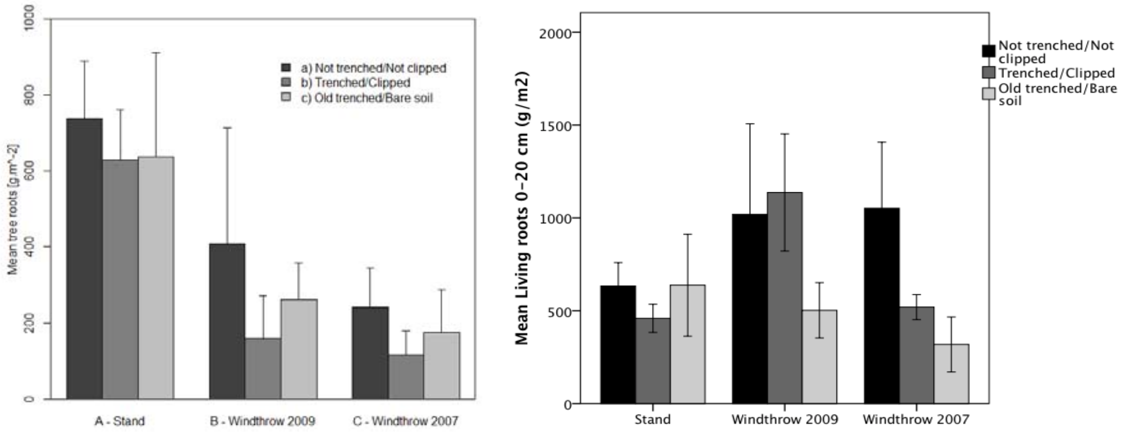


Fig. C-7: Tree fine root (left panel) and total living fine root biomass (right panel) on non-clipped/non-trenched, clipped/trenched, and old trenched/bare soil plots at the treatment sites Stand (Control), wind throw 2009 and wind throw 2007 (mean+95% CI).

The total fine root biomass of both trees and ground vegetation is shown in Figure C-7 right. In no trenched plots the total fine root biomass was higher on the 2009 and 2007 windthrows than the intact stand. This demonstrates the large amount of grass and herbaceous plant roots on the windthrows. Only on the 2007 windthrow did trenching affect the total fine root biomass.

C-4.4 Mycorrhiza

Mycorrhiza hyphal production, measured as Ergosterol in sand-filled ingrowth bags after 10 months incubation at 5 cm soil depth, was significantly lower in the trenched plots than in the non-trenched in the intact stand ($p<0.05$). The small amounts of ergosterol found in the mesh bags in the trenched plots can be assumed to be from saprophytic fungi. After subtraction of the amount of ergosterol found in the trenched plots from the other values, the biomass of mycorrhizal hyphae in the non-trenched plots mycorrhizal hyphal production can be calculated. Hyphal production was higher in the intact stand than in the non-clipped plots on the 2009 and 2007 windthrows (Fig. C-8, Tab. C-4). The clipping of grass and herbs on the 2007 and 2009 wind-throw did not affect the mycelia production. When looking at all three treatments the mycorrhizal production was higher in the 2007 windthrow (0.57 µg g^{-1}) than in the 2009 windthrow, which had in mean no ingrowth. The visual estimates followed in general the same pattern Figure C-9.

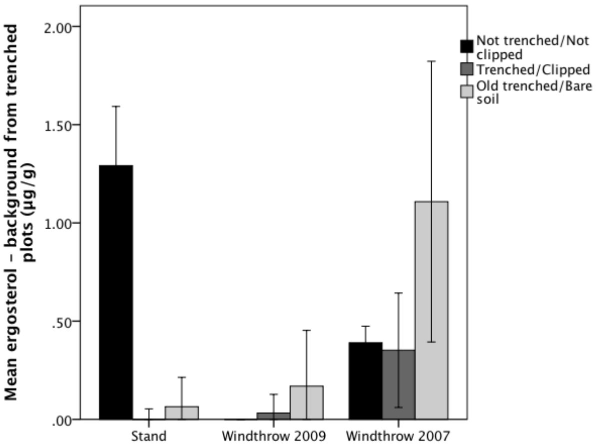


Fig. C-8: Corrected Ergosterol values on non-clipped/non-trenched, clipped/trenched, and old trenched/bare soil plots at the treatment sites Stand (Control), wind throw 2009 and wind throw 2007 (mean+SE).

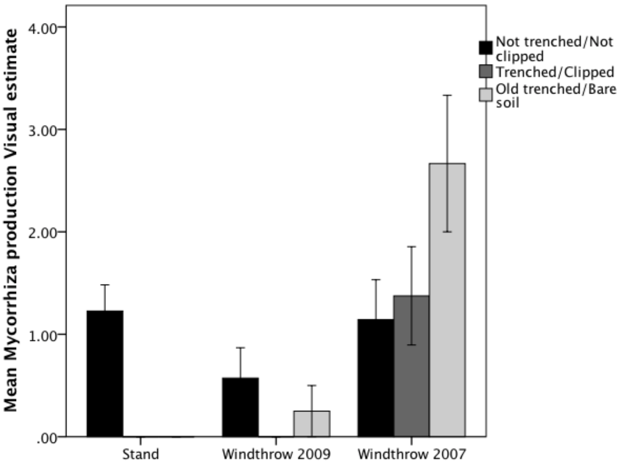
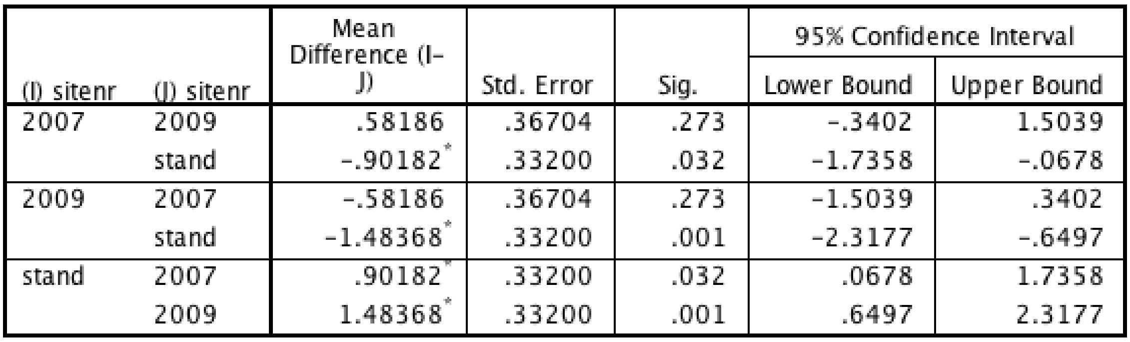


Fig. C-9: Visual estimate of the hyphal biomass on non-clipped/non-trenched, clipped/trenched, and old trenched/bare soil plots at the treatment sites Stand (Control), wind throw 2009 and wind throw 2007 (mean+SE). No hyphae (i.e. class 0) were found on trenched plots; see Material and Methods for description of classes (0-5).

Tab. C-4: Pairwise comparison (Tukey test) of the Ergosterol values in the non-trenched plots at soil depth 0-10 cm between the treatment sites WS07 (Windthrow 2007), WS09 (Windthrow 2009) and the control stand (CS).



(I) sitenr	(J) sitenr	Mean Difference (I-J)	Std. Error	Sig.	95% Confidence Interval	
					Lower Bound	Upper Bound
2007	2009	.58186	.36704	.273	-.3402	1.5039
	stand	-.90182*	.33200	.032	-1.7358	-.0678
2009	2007	-.58186	.36704	.273	-1.5039	.3402
	stand	-1.48368*	.33200	.001	-2.3177	-.6497
stand	2007	.90182*	.33200	.032	.0678	1.7358
	2009	1.48368*	.33200	.001	.6497	2.3177

C-4.5 Respiration

Soil respiration decreased in the trenched plots and clipped plots in the intact forest and the windthrows (Fig. C-10). A comparison of the mean values of the non-trenched and trenched plots indicates that autotrophic respiration is about 30 % of the total soil respiration in the stand, and a little less in the 2009 windthrow.

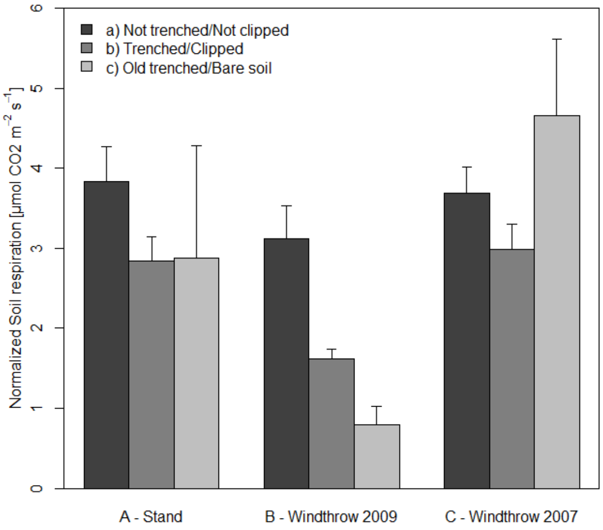


Fig. C-10: Soil CO_2 efflux in intact and trenched/clipped pots in a forest stand and windthrows from 2007 and 2009.

C-5 Discussion

The intensity and frequency of large-scale natural disturbances have are increasing worldwide, windthrow events representing part of them. Environmental conditions on the affected areas are greatly changed, often resulting in a high spatial variability (Bormann et al., 1995, Ulanova, 2000). Predictions of the C and nutrient cycles on windthrow sites, mediated by soil microorganisms, vegetation dynamics and subsequently forest reestablishment are difficult due to scarcity of studies. Thus, detailed studies are urgently needed to correctly predict the geochemical and vegetative developments after wind throws.

C-5.1 Does the thickness of the remaining humus patches and the C quality change after windthrow?

Forest floor soil organic carbon (SOC) has been found to be most vulnerable, with the fastest SOC loss directly after the disturbance. For example, at two Podzol chronosequences in Eastern Germany, 14–16% SOC loss was detected after a regular forest harvest (clear cut) in the forest floor and 0–40 cm mineral soil within 3.5 years (Heinsdorf et al., 1986). Similar, Mattson and Swank, (1989) measured an approximate loss of 26% forest floor SOC within 3.5 years after clear cut and log removal in the Southern Appalachian Mountains. In this study, clear evidence for decreasing humus layer thickness with time after the disturbance event (Fig. C-2) was found, although the changes were not statistically significant. The measurements were made on patches of humus remaining after erosion losses. If the soil material lost by the rapid erosion after the windthrow is taken into account, then the total organic matter loss is greatly in excess of the values shown here.

In the remaining humus patches the concentration of total carbon (i.e. g g d.wt.$^{-1}$) is not reduced on both disturbed sites compared to the control stand (Fig. C-5). Increased organic carbon contents (%) were previously found at spruce wind throws with and without removed tree logs in the Tatra mountains two years after the disturbance event compared to a stand unaffected by the storm (Gömöryová et al., 2008), organic carbon contents on disturbed sites were approximately 55-60% higher than control. Don et al. (2012) showed no loss in soil organic carbon (SOC) stocks at two windthrow sites in the Tatra Mountains with three inventories within 3.5 years after the storm event. However, they found shifts within the organic layers and the mineral soil toward more decomposed organic matter. Furthermore, they concluded that increasing C/N ratios at the harvested windthrow site indicate that newly established herbaceous vegetation compensated for the decline in tree litter input. At the Höllengebirge, the C:N ratio at soil depth 0-10 cm in the intact forest was significantly higher than on both wind throw sites (Fig. C-5). This suggests that either the input of new litter from the herbaceous has a lower C/N ratio than the tree litter from the spruce and beech overstorey, or that the organic matter contains a higher percentage of material from microbial inputs (Ekblad et al 2013), both of which will result in a lower C/N ratio. In addition, N release from decaying roots is an important nutrient flux pathway the first two years following forest harvest (Fahey et al., 1988). At the windthrow sites there is a clear loss of tree roots compared to the intact forest, which is compensated for by an increase in the amount of living roots from the grass and herbaceous vegetation. Dissolved organic carbon (DOC) is an important pool of C in forest soils (Neff and Asner, 2001), and also an major flux pathway for C loss. Cronan et al. (1992) found that concentrations of water-extractable dissolved organic carbon (DOC) after root trenching were approximately twice as high as DOC under undisturbed conditions. In the 2009 windthrow, the amount of extractable DOC was elevated compared to the intact forest and the 2007 windthrow. This suggests that at the 2009 windthrow, C is still being lost as DOC, but this the lost has stabilized in the 2007 windthrow.

C-5.2 Ectomycorrhizal development on windthrow sites four and six years after the disturbance event.

Many studies of windthrow have focused on the changes in physical and chemical properties of soil and specific processes, mainly perturbation caused by uprooting, changes of water and temperature regimes, erosion, and nutrient leaching (Ulanova, 2000). However, information about the soil biota, especially soil microorganisms, at windthrow-affected sites is rare (Gömöryová et al., 2011). Ectomycorrhizal fungi are dependent on the carbohydrates produced by higher plants. Their main energy source is lost immediately if the higher plant is eliminated, e.g. as the result of windthrow. Laessig et al. (1995) found that four years after the windthrow events on 20 areas in the subalpine zone of the Northern Swiss Alp there was sufficient mycorrhizas in the upper soil layers for successful inoculations of spruce tree seedlings. Similar, Egli et al. (2002) found that ten years after a windthrow event, the number of infective ectomycorrhizal fungi in the soil of the windthrow plot was significantly smaller than in the adjacent forest. However, the remaining species were still able to fully mycorrhizal *Picea abies* seedlings. Similar, the diversity of ectomycorrhiza colonizing seedlings was found to be consistently greater in the undisturbed forest than in the windthrow area (Cowden and Peterson, 2013). At the Höllengebirge sites, the level of mycorrhizal hyphae is similar in the intact forest and on the 2007 windthrow, but lower on the 2009 windthrow. This corresponds to an increase in the number of tree seedlings at the 2007 windthrow, and suggests that the mycorrhizas of the seedling make a large contribution to the hyphal biomass. The relatively high amount of mycorrhizal production in the windthrow considering the low tree cover is in accordance with the findings of Wallander et al. (2010) who showed that young trees have more mycorrhiza production than mature stands. In addition, the higher levels of mycorrhizal hyphal biomass are associated with lower amounts of extractable DOC.

C-5.3 Which mechanisms underlie the loss of carbon?

The study by Kramer, Sollins and Sletten (2004) in Alaska provides the best evidence of prolonged (approximately 95 years) post-disturbance impact of windthrow on the amount, distribution and quality of SOC. Increased mixing of the soil, reflected in pit and mound topography, was associated with a significant decline (approximately 27%) in total SOC pool, from 216 Mg ha−1 in the control watershed to 157 Mg ha−1 in the case of complete stand loss. This was mainly due to a decrease in the SOC stock of the H (designated as Oa) and Bh horizons, but following two different pathways. The loss of forest floor H-layer, associated with an increase in the quantity and quality (lower carbon-to-nitrogen ratio) of the fresh litter material (L-layer, designated as Oi), was attributed to accelerated microbial decomposition with warmer and drier site conditions (especially on the mounds). Soil respiration is closely related to soil temperature and moisture. At the same time, soil respiration is also associated with the soil organic matter content and availability (Wright and Coleman, 2002). Gömöryová et al. (2008) found in the Tatra mountains an increased soil respiration on wind thrown spruce stands compared to control stands, two years after the disturbance event. At the Höllengebirge total soil CO_2 efflux was similar at all three sites. The attempt to separate total respiration into autotrophic and heterotrophic respiration by trenching and clipping indicates that heterotrophic respiration is lowest on the 2009 windthrow. However, measurements of heterotrophic respiration using clipping or trenching techniques are confounded by inputs of fresh root litter. On all of the plots, the old trenched/bare soil treatment was used as an estimate of the heterotrophic respiration without inputs from dead or dying roots. This treatment clearly shows a lower heterotrophic respiration on the 2009 windthrow. As DOC is used as a substrate for heterotrophic respiration (Van Hees et al 2006), the higher levels of extractable DOC found at the 2009 windthrow are more likely a consequence of the lower rates of microbial activity rather than higher rates of decomposition. However, this clearly needs further investigation.

In the 0-10 cm soil layer, soil pH increased from the intact stands to the 2007 windthrow. A similar significant increase of soil pH, compared to non-affected stands, was previous found in wind throw spruce stand in the Tatra mountains (Gömöryová et al., 2008). The increase in pH maybe due to mixing of carbonate material from the calcareous bedrock, or a decrease in acidic litter inputs from the tree canopy. An increase in soil pH often results in higher rates of decomposition, but also in a shift from the importance of fungi to bacteria in the decomposition process (Rousk et al 2011). In a previous investigation at the Höllengebirge sites, the highest microbial activity was found on disturbed plots (Mayer unpublished). Such a trend was also observed the Tatra mountains for basal respiration, substrate-induced respiration, and catalase activity (Gömöryová et al., 2008). There are clearly anomalies between the point measurements of soil respiration and the expected or measured changes in microbial activity at the Höllengebirge sites. Measurements of the temporal dynamics of soil respiration are currently being carried out (Mayer unpublished).

C-6 Conclusion

With this study we studied the soil humus dynamics of a disturbed forest stand on a typical calcareous site in the calcareous Alps compared to an undisturbed stands in close vicinity.

The work was carried out on patches of soil that had not been lost by erosion. As hypothesised there are clear fluctuations in the ectomycorrhizal biomass after windthrow, but the biomass recovers after several years and successful colonisation by tree seedlings. Loss of activity of the mycorrhizal hyphae and the onset of the postulated Gadgil effect cannot clearly be shown, as there are a number of parallel changes such as changes in litter input and soil pH which may mask any direct biological effects. However, the work clearly shows that rapid regeneration of vegetation at the site, particularly tree seedlings, is vital for soil protection and restoration of soil biological activity. In addition, it is vital that measures are undertaken to prevent the initial loss of soil due to erosion before vegetation can regrow.

Literature

Allison SD, Wallenstein MD, Bradford MA. 2010. Soil-carbon response to warming dependent on microbial physiology. *Nature Geoscience,* 3: 336-340.

Attiwill PM, Adams MA. 1993. Nutrient cycling in forests. *New Phytologist,* 124: 561-582.

Baritz R, Seufert G, Montanarella L, Van Ranst E. 2010. Carbon concentrations and stocks in forest soils of Europe. *Forest Ecology and Management,* 260: 262-277.

Bormann B, Spaltenstein H, McClellan M, Ugolini F, Cromack Jr K, Nay S. 1995. Rapid soil development after windthrow disturbance in pristine forests. *Journal of Ecology*: 747-757.

Christophel D, Spengler S, Schmidt B, Ewald J, Prietzel J. 2013. Customary selective harvesting has considerably decreased organic carbon and nitrogen stocks in forest soils of the Bavarian Limestone Alps. *Forest Ecology and Management,* 305: 167-176.

Clemmensen KE,. Bahr A, Ovaskainen O,. Dahlberg A, Ekblad A, Wallander H, Stenlid J, Finlay RD, Wardle DA, Lindahl B D, 2013. Roots and Associated Fungi Drive Long-Term Carbon Sequestration in Boreal Forest. Science 339:1615-1618.

Covington WW. 1981. Changes in forest floor organic matter and nutrient content following clear cutting in northern hardwoods. *Ecology,* 62 (1): 41-48.

Cowden CC, Peterson CJ. 2013. Annual and seasonal dynamics of ectomycorrhizal fungi colonizing white pine (Pinus strobus) seedlings following catastrophic windthrow in northern Georgia, USA. *Canadian Journal of Forest Research,* 43: 215-223.

Cronan CS, Lakshman S, Patterson HH. 1992. Effects of disturbance and soil amendments on dissolved organic carbon and organic acidity in red pine forest floors. *Journal of Environmental Quality,* 21: 457-463.

Dale VH, Joyce LA, McNulty S, Neilson RP, Ayres MP, Flannigan MD, Hanson PJ, Irland LC, Lugo AE, Peterson CJ. 2001. Climate change and forest disturbances: Climate change can affect forests by altering the frequency, intensity, duration, and timing of fire, drought, introduced species, insect and pathogen outbreaks, hurricanes, windstorms, ice storms, or landslides. *Bioscience,* 51: 723-734.

Darabant A, Katzensteiner K, Gratzer G, Dorji S. 2009. Pilotstudie: Resilienz von Schutzwäldern in den Nördlichen Kalkalpen. *Forschungsbericht.* Vienna, Austria, ÖBF, Ämter d. Stmk., Tiroler und Salzburger Landesregierungen, Gemeinde Wien.

Don A, Bärwolff M, Kalbitz K, Andruschkewitsch R, Jungkunst HF, Schulze E-D. 2012. No rapid soil carbon loss after a windthrow event in the High Tatra. *Forest Ecology and Management,* 276: 239-246.

Egli S, Peter M, Falcato S. 2002. Dynamics of ectomycorrhizal fungi after windthrow. *Forest, Snow and Landscape Research,* 77: 81-88.

Ekblad A, Wallander H, Godbold DL, Cruz C, Johnson D, Baldrian P, Björk RG,

Epron D, Kieliszewska-Rokicka B, Kjöller R, Kraigher H, Matzner E, Neumann J, Plassard C 2013. The production and turnover of extramatrical mycelium of ectomycorrhizal fungi in forest soils: role in carbon cycling. Marchner Review Plant and Soil 366:1–27

Fahey TJ, Hughes JW, Pu M, Arthur MA. 1988. Root decomposition and nutrient flux following whole-tree harvest of northern hardwood forest. *Forest Science,* 34: 744-768.

Frostegård Å, Tunlid A, Bååth E. 1991. Microbial biomass measured as total lipid phosphate in soils of different organic content. *Journal of Microbiological Methods,* 14: 239-245.

Frostegård Å, Tunlid A, Bååth E. 1993. Phospholipid fatty acid composition, biomass and activity of microbial communities from two soil types experimentally exposed to different heavy metals. *Applied and Environmental Microbiology,* 28: 55-63.

Gadgil RL, Gadgil PD. 1971. Mycorrhiza and litter decomposition. *Nature,* 233: 133.

Gadgil RL, Gadgil PD. 1975. Supression of litter decomposition by mycorrhizal roots of *Pinus radiata*. *New Zealand Journal of Forestry Science,* 5: 33-41.

Gardiner B, Blennow K, Carnus JM, Fleischer P, Ingemarson F, Landmann G, Lindner M, Marzano M, Nicoll B, Orazio C. 2010. *Destructive storms in European forests: past and forthcoming impacts,* Joensuu, Finnland, European Forest Institute.

Godbold DL , Hoosbeek MR, Lukac M, Cotrufo MF, Janssens IA, Ceulemans R, Polle A, Velthorst EJ, Scarascia-Mugnozza G, De Angelis P, Miglietta F, Peressotti A. 2006. Mycorrhizal hyphal turnover as a dominant process for carbon input to soil organic matter. Plant Soil 281: 15-24

Gömöryová E, Střelcová K, Fleischer P, Gömöry D. 2011. Soil microbial characteristics at the monitoring plots on windthrow areas of the Tatra National Park (Slovakia): their assessment as environmental indicators. *Environmental Monitoring and Assessment,* 174: 31-45.

Gömöryová E, Střelcová K, Škvarenina J, Bebej J, Gömöry D. 2008. The impact of windthrow and fire disturbances on selected soil properties in the Tatra National Park. *Soil & Water Research,* 3: S74-S80.

Grigal DF, Vance ED. 2000. Influence of soil organic matter on forest productivity. *Conventional systems for bioenergy. IEA Bioenergy Task 18 workshop, Charleston, South Carolina, USA, 19-25 September 1999.*, New Zealand Forest Research Institute.

Heinsdorf D, Kraus HH, Tolle H. 1986. Entwicklung der C- und N-Vorräte nach Kahlschlag auf armen anhydromorphen Sandböden unter Kiefer. *Beiträge für die Forstwirtschaft,* 20: 8-13.

Hofherr T, Kunz M. 2010. Extreme wind climatology of winter storms in Germany. *Climate research,* 41: 105.

Hollhaus AR. 2012. *Evaluation of methods estimating soil loss after coarse-scale disturbance on a montane mixed forest site in the Northern Limestone Alps,* Master, University of Natural Resources and Life Sciences, Vienna, Vienna, Austria.

Janssens IA, Pilegaard K. 2003. Large seasonal changes in Q10 of soil respiration in a beech forest. *Global Change Biology,* 9: 911-918.

Jones D, Willett V. 2006. Experimental evaluation of methods to quantify dissolved organic nitrogen (DON) and dissolved organic carbon (DOC) in soil. *Soil Biology and Biochemistry,* 38: 991-999.

Kirschbaum MUF. 1995. The temperature-dependence of soil organic-matter decomposition, and the effect of global warming on soil organic-C storage. *Soil Biology & Biochemistry,* 27: 753-760.

Klaus M, Holsten A, Hostert P, Kropp JP. 2011. Integrated methodology to assess windthrow impacts on forest stands under climate change. *Forest Ecology and Management,* 261: 1799-1810.

Knohl A, Kolle O, Minayeva TY, Milyukova IM, Vygodskaya NN, Foken T, Schulze E-D. 2002. Carbon dioxide exchange of a Russian boreal forest after disturbance by wind throw. *Global Change Biology,* 8: 231-246.

Koeck R, Mrkvicka A, Weidinger H. 2001. *Bericht zur Forstlichen Standortskartierung im Revier Rax [In German],* Vienna, Austria, Forstverwaltung Nasswald der Quellenschutzwälder der Stadt Wien, Forstamt und Landwirtschaftsbetriebe der Stadt Wien.

Koide RT, Wu T. 2003. Ectomycorrhizas and retarded decomposition in a Pinus resinosa plantation. *New Phytologist,* 158: 401-407.

Kramer MG, Sollins P, Sletten RS. 2004. Soil carbon dynamics across a windthrow disturbance sequence in southeast Alaska. *Ecology,* 85: 2230-2244.

Laessig R, Egli S, Odermatt O, Schoenenberger W, Stoeckli B, Wohlgemuth T. 1995. Beginning of reforestation of windthrow areas [In German]. *Schweizerische Zeitschrift für Forstwesen,* 146: 893-911.

Lindner M, Maroschek M, Netherer S, Kremer A, Barbati A, Garcia-Gonzalo J, Seidl R, Delzon S, Corona P, Kolström M, Lexer MJ, Marchetti M. 2010. Climate change impacts, adaptive capacity, and vulnerability of European forest ecosystems. *Forest Ecology and Management,* 259: 698-709.

Lindroth A, Lagergren F, Grelle A, Klemedtsson L, Langvall OLA, Weslien PER, Tuulik J. 2009. Storms can cause Europe-wide reduction in forest carbon sink. *Global Change Biology,* 15: 346-355.

Lüscher P. 2002. Humus dynamics and changes in rooting patterns in windthrow areas. *Forest Snow and Landscape Research,* 77: 2.

Mattson KG, Swank WT. 1989. Soil and detrital carbon dynamics following forest cutting in the southern Appalachians. *Biology and Fertility of Soils,* 7: 247-253.

Millikin CS, Bowden RD. 1996. Soil respiration in pits and mounds following an experimental forest blowdown. *Soil Science Society of America Journal,* 60: 1951-1953.

Nave LE, Vance ED, Swanston CW, Curtis PS. 2010. Harvest impacts on soil carbon storage in temperate forests. *Forest Ecology and Management,* 259: 857-866.

Neff JC, Asner GP. 2001. Dissolved Organic Carbon in Terrestrial Ecosystems: Synthesis and a Model. *Ecosystems,* 4: 29-48.

Nylund J-E, Wallander H. 1992. Ergosterol analysis as a means of quantifying mycorrhizal biomass. In: Norris JR, Read DJ, Varma AK eds. *Methods in microbiology.* London, Academic Press.

Olsson PA. 1998. *The external mycorrhizal mycelium*, Lund university, Lund.

Olsson PA. 1999. Signature fatty acids provide tools for determination of the distribution and interactions of mycorrhizal fungi in soil. *FEMS Microbiology Ecology,* 29: 303-310.

Pan Y, Birdsey RA, Fang J, Houghton R, Kauppi PE, Kurz WA, Phillips OL, Shvidenko A, Lewis SL, Canadell JG, Ciais P, Jackson RB, Pacala SW, McGuire AD, Piao S, Rautiainen A, Sitch S, Hayes D. 2011. A large and persistent carbon sink in the world's forests. *Science,* 333: 988-993.

Peltola H, Ikonen V-P, Gregow H, Strandman H, Kilpeläinen A, Venäläinen A, Kellomäki S. 2010. Impacts of climate change on timber production and regional risks of wind-induced damage to forests in Finland. *Forest Ecology and Management,* 260: 833-845.

Polomski J, Kuhn N. 2001. Wurzelhabitus und Standfestigkeit der Waldbäume. *Forstwissenschaftliches Centralblatt vereinigt mit Tharandter forstliches Jahrbuch,* 120: 303-317.

Rousk J, Brookes PC, Baath E 2011. Fungal and bacterial growth responses toNfertilization-tionand pH in the150-year 'Park Grass'UK grassland experiment. FEMS Microbiol Ecology 76: 89–99.

Rusch S, Hagedorn F, Zimmermann S, Lüscher P. 2009. *Bodenkohlenstoff nach Windwurf - eine CO2-Quelle? ,* Zurich, Switzerland, Swiss Federal Institute for Forest Snow and Landscape Research (WSL) and Swiss Federal Office for the Environment.

Schelhaas M-J, Nabuurs G-J, Schuck A. 2003. Natural disturbances in the European forests in the 19th and 20th centuries. *Global Change Biology,* 9: 1620-1633.

Ulanova NG. 2000. The effects of windthrow on forests at different spatial scales: a review. *Forest Ecology and Management,* 135: 155-167.

Ulbrich U, Leckebusch GC, Pinto JG. 2009. Extra-tropical cyclones in the present and future climate: a review. *Theoretical and Applied Climatology,* 96: 117-131.

Usbeck T, Wohlgemuth T, Dobbertin M, Pfister C, Bürgi A, Rebetez M. 2010. Increasing storm damage to forests in Switzerland from 1858 to 2007. *Plant Journal,* 150: 47-55.

van Hees PAW, Jones DL, Finlay R, Godbold DL, Lundström US. 2005.The carbon we do not see: The impact of low molecular weight compounds on carbon dynamics and respiration in forest soils - A review Soil Biol. Biochem. 37: 1-13.

Van Miegroet H, Olsson M. 2011. Ecosystem disturbance and soil organic carbon—a review. In: Jandl R, Rodeghiero M, Olsson M eds. *Soil carbon in sensitive European ecosystems: From science to land management.* 1 ed. Chichester, UK, Wiley.

Wallander H, Göransson H, Rosengren U. 2004. Production, standing biomass and ∂^{15}N/ ∂^{13}C abundance of ectomycorrhizal mycelia at different soil depths in spruce forests and mixed (spruce-oak) forests in southern Sweden. *Oecologia (Berlin),* 139: 89-97.

Wallander, H., Johanssson, U., E, S., Brandström, D.M., Lindahl, B.D., 2010. Production of ectomycorrhizal mycelium peaks during canopy closure in Norway spruce forests. New Phytologist 187, 1124-1134.

Wang X, Cammeraat E, Romeijn P, Kalbitz K. 2013. Soil redistribution and dynamics of organic carbon. *EGU General Assembly Conference Abstracts.* Vienna, Austria.

Wernli H, Bader S, Hächler P. 2003. Winterstürme. In: Hohmann R ed. *Extremereignisse und Klimaänderungen.* Bern, Switzerland, Organe consultatif sur les changements climatiques (OcCC).

Wilson GW, Rice CW, Rillig MC, Springer A, Hartnett DC. 2009. Soil aggregation and carbon sequestration are tightly correlated with the abundance of arbuscular mycorrhizal fungi: results from long-term field experiments. *Ecology Letters,* 12: 452-461.

Wright CJ, Coleman DC. 2002. Responses of soil microbial biomass, nematode trophic groups, N-mineralization, and litter decomposition to disturbance events in the southern Appalachians. *Soil Biology and Biochemistry,* 34: 13-25.

ZAMG. 2012. *Klimadaten der Stationen 'Feuerkogel' und 'Bad Ischl',* Vienna, Austria, Zentralanstalt für Meteorologie and Geodynamik.

Zanella A, Jabiol B, Ponge JF, Sartori G, De Waal R, Van Delft B, Graefe UN, Cools N, Katzensteiner K, Hager H, Englisch M, Brethes A, Broll G, Gobat JM, Brun JJ, Milbert G, Kolb E, Wolf U, Frizzera L, Galvan P, Kolli R, Baritz R, Kemmers R, Vacca A, Serra G, Banas D, Garlato A, Chersich S, Klimo E, Langohr R. 2011. *European humus forms reference base. hal-005496, version 2,* URL: http://hal.archives-ouvertes.fr/hal-00541496 [Accessed 26.08.2013].

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