

Windthrows increase soil carbon stocks

L. T. dos Santos et al.

This discussion paper is/has been under review for the journal Biogeosciences (BG).
Please refer to the corresponding final paper in BG if available.

Windthrows increase soil carbon stocks in a Central Amazon forest

L. T. dos Santos¹, D. Magnabosco Marra^{1,2,3}, S. Trumbore², P. B. Camargo⁴,
J. Q. Chambers⁵, R. I. Negrón-Juárez⁵, A. J. N. Lima¹, G. H. P. M. Ribeiro¹,
J. dos Santos¹, and N. Higuchi¹

¹Laboratório de Manejo Florestal, Instituto Nacional de Pesquisas da Amazônia, Manaus, Brazil

²Biogeochemical Processes Department, Max-Planck-Institute for Biogeochemistry, Jena, Germany

³AG Spezielle Botanik und Funktionelle Biodiversität, Universität Leipzig, Germany

⁴Centro de Energia Nuclear na Agricultura, Piracicaba, Brazil

⁵Climate Sciences Department, Lawrence Berkeley National Laboratory, USA

Received: 15 September 2015 – Accepted: 16 November 2015 – Published: 7 December 2015

Correspondence to: D. Magnabosco Marra (dmarra@bgc-jena.mpg.de)

Published by Copernicus Publications on behalf of the European Geosciences Union.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures



Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



Abstract

Windthrows change forest structure and species composition in Central Amazon forests. However, the effects of widespread tree mortality associated with wind-disturbances on soil properties have not yet been described. In this study, we investigated short-term effects (seven years after disturbance) of a windthrow event on soil carbon stocks and concentrations in a Central Amazon *terra firme* forest. The soil carbon stock (averaged over a 0–30 cm depth profile) in disturbed plots ($61.4 \pm 4.18 \text{ Mg ha}^{-1}$, mean \pm standard error) was marginally higher ($p = 0.009$) than that from undisturbed plots ($47.7 \pm 6.95 \text{ Mg ha}^{-1}$). The soil organic carbon concentration in disturbed plots ($2.0 \pm 0.08 \%$) was significantly higher ($p < 0.001$) than that from undisturbed plots ($1.36 \pm 0.12 \%$). Moreover, soil carbon stocks were positively correlated with soil clay content ($r = 0.575$ and $p = 0.019$) and with tree mortality intensity ($r = 0.493$ and $p = 0.045$). Our results indicate that large inputs of plant litter associated with large windthrow events cause a short-term increase in soil carbon content, and the degree of increase is related to soil clay content and tree mortality intensity. Higher nutrient availability in soils from large canopy gaps created by wind disturbance may increase vegetation resilience and favor forest recovery.

1 Introduction

Tropical forests contain about 44 % (383 PgC) of the approximately 860 PgC stored in forests worldwide, with soils accounting for 32 % of the total carbon stocks (Queré et al., 2009; Lal, 2004). Global emissions due to changes in land use and soil cultivation are estimated to be 136 PgC since the industrial revolution (Lal, 2004; Houghton, 1999). However, there are few estimates of emissions by the decomposition and mineralization of organic carbon in soils following natural disturbances (Lal, 2004), presumably because we assume there is a balance between rapid losses that follow disturbance and recovery between disturbances at the larger spatial scales. The effects of large

BGD

12, 19351–19372, 2015

Windthrows increase soil carbon stocks

L. T. dos Santos et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

◀

▶

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



scale wind disturbances on carbon stocks and cycling due to the increase of litter inputs promoted by widespread tree mortality, the fraction of this carbon that persists in soil organic matter, and how long it is stabilized, are poorly known. In Amazonian forests, where windthrows are a major natural disturbance (Nelson et al., 1994; Chambers et al., 2013), such effects have not yet been investigated.

Wind disturbances are frequent in the West and Central Amazon, (Nelson et al., 1994; Espírito Santo et al., 2010; Negrón-Juárez et al., 2010). In this large region, windthrows are associated with torrential rains and very strong winds (16 m s^{-1}) known as downbursts (Nelson et al., 1994; Garstang et al., 1998). The widespread tree mortality creates canopy gaps with a wide range of sizes (from few square meters up to thousands of hectares) (Nelson et al., 1994; Negrón-Juarez et al., 2010, 2011; Marra et al., 2014) and affect forests at the landscape level (Marra et al., 2014). It has been reported that these large gaps have a potential effect on carbon cycling (Chambers et al., 2013) and can promote tree species diversity by allowing a diverse cohort of species with a broad range of life history strategies requirements (Chambers et al., 2009; Marra et al., 2014) and allometry (Ribeiro et al., 2014).

Treefall gaps can change microclimate conditions such as light intensity and create a variety of microsites, which can be separated into canopy, trunk and root/uprooted sites (Schaetzl et al., 1989; Denslow et al., 1998). These microsites have important features that drive soil and vegetation recovery after disturbance (Schaetzl et al., 1989; Vitousek and Denslow, 1986). They can differ in microbial activity (Batjes, 1996) and enhance the colonization of fast growing species that help in the assimilation of nutrients and soil carbon, which in turn can contribute to quickly restore the forest canopy through succession (Putz, 1983). Winds break and uproot trees causing strong soil disturbances (e.g. increasing litter [leaves and wood debris] or, changing morphology and nutrient availability) (Schaetzl et al., 1989; Lugo et al., 2008). However, in tropical ecosystems these changes, together with other attributes, including vegetation recovery patterns, species-specific chemistry and floristic composition changes along succession (Chambers et al., 2009; Marra et al., 2014), may lead to adaptive responses

Windthrows increase soil carbon stocks

L. T. dos Santos et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures



Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



Windthrows increase soil carbon stocks

L. T. dos Santos et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

◀

▶

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



(Schaetzl et al., 1989). The rapid recycling of nutrients enhances ecosystem resilience (Schaetzl et al., 1989; Ostertag et al., 2003; Lugo et al., 2008). Although changes in key ecosystem processes seem to be related to adaptive responses, it is not clear how complex tropical forests such as the Amazon will respond in a scenario of higher frequency of strong wind storms disturbance events (Chambers et al., 2009, 2013; Marra et al., 2014).

We assessed the effects of wind disturbances on soils of a *terra firme* forest in Central Amazon. We hypothesized that windthrows forming large canopy gaps ($> 2000 \text{ m}^2$) affect the soil carbon content via litter and wood debris deposition and decomposition, and that the soil carbon content is controlled by the interaction of tree mortality intensity, clay content and depth. To test our hypothesis we addressed the following questions: (1) What is the importance of soil texture on soil organic carbon content in wind disturbed areas? (2) Are there differences in soil carbon stocks between disturbed and undisturbed areas and, how do possible variations compare to other tropical forests worldwide? (3) Does tree mortality intensity influence soil carbon stocks?

2 Methods

2.1 Study area

This study was conducted in a large *terra firme* forest, adjacent to the Ramal-ZF2 road and contiguous area at the Estação Experimental de Silvicultura Tropical (EEST) of the Instituto Nacional de Pesquisas da Amazônia (INPA). The study area is located $\sim 55 \text{ km}$ north of Manaus, Amazonas, Brazil (Fig. 1). The forest adjacent to the Ramal-ZF2 road is owned and administered by the Superintendência da Zona Franca de Manaus (SUFRAMA). Mean annual temperature in this region is about 26°C and rainfall averages to 2600 mm yr^{-1} (Sombroek, 2001) with annual peaks of up to 3450 mm (Silva et al., 2002). From July to September there is a distinct dry season with usually less than 100 mm of rain per month. The *terra firme* forests at the studied region are charac-

terized by a closed canopy, high tree species diversity and a dense understory (Braga, 1979).

The soils of the Amazon region are old and complex, with type and texture influenced by local topographical variations. At the studied region, the relief is undulating with altitude ranging from 40–180 m a.s.l. Soils on upland plateaus and the upper portions of slopes have high clay content (Oxisols), while soils on slope bottoms and valleys have high sand content (Spodosols) and are subject to seasonal flooding (Telles et al., 2003). The yellow Oxisols are found primarily on plateaus and slopes. In general, the soils are well drained and have low fertility, low pH, low cation exchange capacity, high aluminum concentration and low organic carbon (Ferraz et al., 1998; Telles et al., 2003).

2.2 Tree mortality estimates

In January of 2005, a single squall line event propagating across the Amazon caused widespread tree mortality over large areas (Negrón-Juárez et al., 2010), including ~ 250 ha of *terra firme* forest in the study area (Fig. 1). Tree mortality directly caused by this event was quantified at landscape level through the correlation of plot-based measurements and changes on the fractions of green vegetation (GV) and non-photosynthetic vegetation (NPV) calculated from Landsat images – see Negrón-Juárez et al. (2010) for a detailed method description. This metric, validated by Negrón-Juárez et al. (2011), allowed us to sample soils across an extent tree mortality gradient 0–70 %, including patches of old-growth forest not affected by the 2005 squall line event (Marra et al., 2014).

2.3 Soil sampling

We sampled soils in the disturbed forest during the dry season (July-September) of 2012 (seven years after disturbance) according to the degree of disturbance intensity measured as tree mortality (%). In total, 16 plots with dimensions of 25 m × 10 m were

BGD

12, 19351–19372, 2015

Windthrows increase soil carbon stocks

L. T. dos Santos et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

◀

▶

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



selected along three pairs of transects, with 200 m (E1), 600 m (E2) and 1000 m (E3) length (Fig. 1). These transects cross several toposequences and include local variations of soils and forest structure among plateaus, slopes and valleys. In this study, we only considered plots established on plateaus, which were more severely affected by the 2005 squall line event (Marra et al., 2014). Although our samples covered soil types from Oxisols to Spodosols we reduce soil attribute variations related to topography by excluding slope and valley areas.

In each of our 16 selected plots, we sampled six soil profiles five meters from each other. We took samples, from three depths (0–10 cm, 10–20 cm and 20–30 cm) using an auger. For soil bulk density, samples were also collected in the three depths in one or two profiles per plot using five centimeters tall cylinders with a volume of 98 cm³. Altogether we collected, 288 soil samples for carbon analysis (16 plots × 6 depth profiles × 3 depths) and 63 samples for density (21 depth profiles × 3 depths) (Fig. 1).

2.4 Soil analysis

Before performing soil analyses, we removed leaves, twigs and roots from our samples. Samples were then sieved, dried and homogenized by grinding (< 2 mm). The carbon content was determined in a combustion analyzer at the Center for Nuclear Studies for Agriculture (CENA), Piracicaba, Brazil. Bulk density samples, were dried at 105 °C to constant weight and weighed. The soil carbon stock (SCS) for each depth was calculated by multiplying the soil organic carbon content (SOC) by bulk density (BD) and depth (*D*), using the formula:

$$\text{SCS} = (\text{SOC} \times \text{BD} \times D) / (10) \quad (1)$$

where SCS is the soil carbon stock (Mg ha⁻¹), SOC is soil organic carbon content (g kg⁻¹), BD is bulk density (g cm⁻³) and *D* is soil depth (cm). The soil clay content was determined by texture analysis using the pipetting method, with data from two depth profiles sampled in each plot.

BGD

12, 19351–19372, 2015

Windthrows increase soil carbon stocks

L. T. dos Santos et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

◀

▶

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



2.5 Statistical analysis

Analysis of variance of three factors was used to determine differences between the soil organic carbon content. Categorical predictive variables were: strata, class of disturbance and soil depth. Before performing statistical tests, we tested our dataset for normality and homoscedasticity. To address our first question we use factorial ANOVA and compared undisturbed/low-disturbance plots (tree mortality < 5 %, hereafter referred as undisturbed plots) with those that experienced higher disturbance intensities (tree mortality \geq 5 %, hereafter referred as disturbed plots). To address our second question, we compared the soil organic carbon content from our study with those from different old-growth tropical forests. We addressed our third question using linear regression to correlate soil carbon stock to soil clay content and tree mortality intensity. We performed all analysis in R 3.0.1 platform (R Core Team, 2014).

3 Results

The soil clay content in the entire study area ranged from 2.0 to 71.5 % averaged over 0–30 cm depth. This large variation in soil texture led to a large variation in the concentration of soil organic carbon (SOC) and soil carbon stocks (SCS). The SOC in the upper samples (0–10 cm) had values ranging from 0.29 to 6.62 % and mean of 2.57 ± 0.13 % (mean \pm standard error). For the same depth interval, values of SCS ranged from 3.79 to 48.53 Mg ha⁻¹ with a mean value of 23.34 ± 2.01 Mg ha⁻¹. Overall, bulk density increased with depth, while SOC and SCS decreased (Table 1). We found no difference comparing soil clay content between disturbed and undisturbed plots, according to ANOVA ($p = 0.108$ and $F = 2.648$). The fact that there is no difference between the two types of forest confirms our hypothesis that the tree mortality is the major vector of the changes we observe.

Soils from disturbed plots had higher mean values of SOC and SCS than the undisturbed plots for all three depths we sampled (Table 1). Summed over the 0–30 cm

BGD

12, 19351–19372, 2015

Windthrows increase soil carbon stocks

L. T. dos Santos et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

◀

▶

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



Windthrows increase soil carbon stocks

L. T. dos Santos et al.

[Title Page](#)[Abstract](#)[Introduction](#)[Conclusions](#)[References](#)[Tables](#)[Figures](#)[I◀](#)[▶I](#)[◀](#)[▶](#)[Back](#)[Close](#)[Full Screen / Esc](#)[Printer-friendly Version](#)[Interactive Discussion](#)

interval, the mean values of SOC and SCS were higher in disturbed than in the undisturbed plot (Fig. 2). The SCS values for the same interval were $61.44 \pm 4.18 \text{ Mg ha}^{-1}$ for disturbed plot and $47.73 \pm 6.95 \text{ Mg ha}^{-1}$ for undisturbed plot ($p = 0.09$) (Fig. 2a). SOC values averaged over 0–30 cm were $2.0 \pm 0.08 \%$ for disturbed plot and $1.36 \pm 0.12 \%$ for undisturbed plot ($p < 0.001$) (Fig. 2b).

The SCS was positively correlated with soil clay content ($r = 0.575$, $p = 0.019$) (Fig. 3a) and tree mortality intensity ($r = 0.493$, $p = 0.045$) (Fig. 3b). When constraining the tree mortality gradient into three disturbance categories defined as tree mortality intensity (%), we found no differences in SCS ($p = 0.226$) (Fig. 4a). However, SCS was $61.10 \pm 6.11 \text{ Mg ha}^{-1}$ in category 3 (tree mortality $> 50 \%$), while in category 1 (tree mortality $< 5 \%$) was $43.08 \pm 8.78 \text{ Mg ha}^{-1}$. The SOC in category 2 was marginally higher than that from category 1 (Tukey HSD, $p = 0.066$) (Fig. 4b).

4 Discussion

4.1 Estimates of soil carbon stocks

The soils from the undisturbed plot, in both 0–10 cm and 0–30 cm depth profiles, had an overall lower SCS when compared to other undisturbed tropical forest (Table 2). Rainforest from Senegal had lower values as our undisturbed plots at 0–30 cm depth profile (Table 2). As expected, our results were between those values found in the two soils types (oxisols and spodosols) in nearby study of undisturbed forest also from the EEST (Telles et al., 2003), in which SCS values for 0–10 cm were reported as $14.9 \pm 3.18 \text{ Mg ha}^{-1}$ (Table 2). However, the overall SCS values ($23.3 \pm 2.01 \text{ Mg ha}^{-1}$) as well those only from disturbed plots ($25.9 \pm 2.06 \text{ Mg ha}^{-1}$) we investigated in our study, were greater than those reported by Telles et al. (2003). Such differences indicate an increasing in SOC and SCS seven years following disturbance.

The soils from our study area also had different SCS values from those reported for other old-growth tropical forests in the Brazilian Amazon (Table 2). For the 0–10 cm

depth profile, the mean SCS were similar in disturbed and lower in undisturbed plots reported for similar forest types in the Pará state (Trumbore et al., 1995; Camargo et al., 1999). At 0–30 cm depth profile, the SCS values of undisturbed plot are similar but greater in disturbed plot to other Amazon states (Table 2).

4.2 Changes in carbon stocks and clay concentration in the soil

The SOC can be influenced by soil type, texture and mineral composition (Powers and Veldkamp, 2005; López-Ulloa et al., 2005; Neumann-Cosel et al., 2011). Different SOC rates are related to important factor such as geology, climate and soil formation (Adams, 1990; Batjes, 1996). When compared to other Amazonian regions, the values of SCS reported in this and other studies conducted in Brazilian forests (as shown in Table 2), might reflect a particular geology and variations of soil type (Quesada et al., 2010 and 2011).

Soil clay content was positively correlated with the SOC ($r = 0.907$) at 0–30 cm depth profile and consequently with SCS ($r = 0.575$, $p = 0.019$) (Fig. 3a). This relationship between SOC and clay content it is already known and was shown in many other studies (Powers and Schlesinger, 2002; Kahle et al., 2002). The soil organic matter can form aggregates stabilizing the clay surface. Telles et al. (2003) also showed that the age of soil C at the same soil depth increases with clay content. However, some authors (Torn et al., 1997; Powers and Schlesinger, 2002; Telles et al., 2003) pointed out that clay content is not always a good predictor of SOC. Thus, the method we applied in this study should better be applied in studies involving the same type and soil origin. In other situations, the mineralogical composition (i.e. including the type of clays) may be a better predictor of SOC than just the percentage of clay itself.

Due to the proximity of our plots we assume climatic and geological aspects to be constant. Thus, the importance of soil texture on carbon stocks in our study area reflects a local pattern. For the 0–10 cm depth profile, samples with clay content greater than 45% were nearly 10 Mgha^{-1} higher than those with clay content lower than 45% ($27.37 \pm 3.0 \text{ Mgha}^{-1}$ against $17.96 \pm 1.83 \text{ Mgha}^{-1}$, respectively). However, soils

Windthrows increase soil carbon stocks

L. T. dos Santos et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

◀

▶

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



from the disturbed plots that had clay content higher than 45% has a SCS value of $31.03 \pm 3.39 \text{ Mg ha}^{-1}$. This indicates the widespread tree mortality caused by wind disturbance increased SCS in our study area.

4.3 Intensity of disturbance and soil carbon stocks

Although we observed an increase in SCS in areas affected by the storm, it is notable that the fresh necromass produced by widespread tree mortality events is not fully incorporated into the soil. The fast decomposition of carbon stored in roots and other woody material probably contributes most to the observed increases in SCS. Carbon inputs from below-ground material, which is already incorporated to the soil, might be specially related to the increase of SCS in the 10–20 and 20–30 cm depth profiles.

Seven years after the windthrow event, the SCS at 30 cm depth was approximately 13.7 Mg ha^{-1} greater in the disturbed plots compared to the undisturbed plots. This number is equivalent to 8.3% of the total carbon stored in the aboveground biomass ($\sim 164.0 \text{ Mg ha}^{-1}$) of the studied forest (Higuchi et al., 2004), which indicates an average rate of soil carbon accumulation of $1.8 \text{ Mg ha}^{-1} \text{ year}^{-1}$. Still, the amount of SCS in our disturbed plots is probably underestimated due to the large amount of carbon stored in below-ground from roots and wood $> 2 \text{ mm}$ which were not included in our samples. Part of this coarse material is not incorporated into the soil. Instead, it is decomposed at the surface (Chambers et al., 2000, 2004), though some is leached into the soil or carried out by detritivores.

The observed organic carbon enrichment derived from widespread tree mortality might also be related to the fast establishment and growth of pioneer species in heavily disturbed areas (Chambers et al., 2009; Marra et al., 2014). The highest frequency and intensity of wind disturbances in plateau areas also suggest that higher carbon stocks in these portions of the relief, besides then related to soil texture and other abiotic factors (e.g. topography), might also reflect differences of vegetation dynamics.

In contrast, according to Lin et al. (2003), the Fushan Experimental Forest, which has experienced frequent windstorms, did not regain any nutrient following disturbance.

Windthrows increase soil carbon stocks

L. T. dos Santos et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures



Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



Windthrows increase soil carbon stocks

L. T. dos Santos et al.

[Title Page](#)[Abstract](#)[Introduction](#)[Conclusions](#)[References](#)[Tables](#)[Figures](#)[I ◀](#)[▶ I](#)[◀](#)[▶](#)[Back](#)[Close](#)[Full Screen / Esc](#)[Printer-friendly Version](#)[Interactive Discussion](#)

This in turn, have limited local tree growth (shown as lower canopy height), and consequently, decreased carbon input into the soil. Thus, more intense mortality regime can also be expected to change forest dynamics, and eventually decrease SCS and nutrient cycling. The effects might depend on forest stature and successional stage (i.e. floristic composition and forest structure attributes such as tree density, basal area and biomass). In our study area, fast vegetation regeneration could even reduce short-term losses of carbon associated with the 2005 squall line event, which had an estimated emission (assuming the carbon from all felled trees emitted to the atmosphere at once) of ~ 0.076 PgC, equivalent to 50 % of the deforestation during that same year (Higuchi et al., 2011; Negrón-Juárez et al., 2010).

Soil carbon content in old-growth upland plateaus is related to soil clay content, but wind disturbances causing widespread tree mortality can increase carbon stocks, even when clay content is not changed. Higher carbon contents in wind-disturbed areas are related to the inputs from deposition and decomposing of the above- and below-ground necromass associated with tree mortality intensity, often controlled by the speed and duration of wind gusts (Lugo et al., 1983; Garstang et al., 1998). The nutrients released in this process might have an important feedback on vegetation resilience and recovery following disturbance. Since wind is a major disturbance agent in West and Central Amazon, more precise estimates of soil carbon stocks need to consider and reflect differences in tree mortality regimes at the landscape level.

Acknowledgements. We gratefully acknowledge the workers from the Estação Experimental de Silvicultura Tropical (EEST) of the Instituto Nacional de Pesquisas da Amazônia (INPA) for giving support with the fieldwork, and the lab team of Centro de Energia Nuclear na Agricultura (CENA) and the Laboratório Temático de Solos e Plantas (LTSP) of the INPA for giving support with the soil analyses. We also acknowledge the Superintendência da Zona Franca de Manaus (SUFRAMA) for allowing us to access part of the study area (Ramal-ZF2). This study was financed by the Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq) within the project SAWI (Chamada Universal MCTI/N°14/2012, Proc. 473357/2012-7) and the INCT - Madeiras da Amazônia. It has also been supported by the Tree Assimilation and Carbon Allocation Physiology Experiment (TACAPE), an initiative from the Biogeochemistry Processes

References

- 5 Adams, J. M., Faure, H., Faure-Denard, L., McGlade, J. M., and Woodward, F. I.: Increases in terrestrial carbon storage from the last glacial maximum to the present, *Nature*, 348, 711–714, 1990.
- Batjes, N. H.: Total carbon and nitrogen in the soils of the world, *Eur. J. Soil Sci.*, 47, 151–163, 1996.
- 10 Batjes, N. H.: Options for increasing carbon sequestration in West African soils: an exploratory study with special focus on Senegal, *Land Degrad. Dev.*, 12, 131–142, 2001.
- Braga, P. I. S.: Subdivisão fitogeográfica, tipos de vegetação, conservação e inventário florístico da floresta amazônica, *Acta Amaz.*, 9, 53–80, 1979.
- 15 Camargo, P. B., Trumbore, S. E., Martinelli, L. A., Davidson, E. A., Nepstad, D. C., and Victoria, R. L.: Soil carbon dynamics in regrowing forest of eastern Amazonia, *Glob. Change Biol.*, 5, 693–702, 1999.
- Chambers, J. Q., Higuchi, N., Schimel, J. P., Ferreira, L. V., and Melack, J. M.: Decomposition and carbon cycling of dead trees in tropical forests on the central Amazon, *Oecologia*, 122, 380–388, 2000.
- 20 Chambers, J. Q., Higuchi, N., Teixeira, L. M., Santos, J., Laurance, S. G., and Trumbore, S. E.: Response of tree biomass and wood litter to disturbance in a central Amazon forest, *Oecologia*, 141, 596–614, 2004.
- Chambers, J. Q., Robertson, A. L., Carneiro, V. M. C., Lima, A. N. L., Smith, M., Plourde, L. C., and Higuchi, N.: Hyperspectral remote detection of niche partitioning among canopy trees driven by blowdown gap disturbances in the Central Amazon, *Oecologia*, 160, 107–117, 2009.
- 25 Chambers, J. Q., Negrón-Juarez, R. I., Marra, D. M., Di Vittorio, A., Tews, J., Roberts, D., Ribeiro, G. H. P. M., Trumbore, S. E., and Higuchi, N.: The steady-state mosaic of disturbance and succession across an old-growth Central Amazon forest landscape, *P. Natl. Acad. Sci. USA*, 110, 3949–54, 2013.

Windthrows increase soil carbon stocks

L. T. dos Santos et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures



Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



Windthrows increase soil carbon stocks

L. T. dos Santos et al.

[Title Page](#)[Abstract](#)[Introduction](#)[Conclusions](#)[References](#)[Tables](#)[Figures](#)[Back](#)[Close](#)[Full Screen / Esc](#)[Printer-friendly Version](#)[Interactive Discussion](#)

da Silva, R., dos Santos, J., Tribuzy, E., Chambers, J., Nakamura, S., and Higuchi, N.: Diameter increment and growth patterns for individual tree growing in Central Amazon, Brazil, *Forest Ecol. Manag.*, 166, 295–301, 2002.

Denslow, J. S., Ellison, A. M., and Sanford, R. E.: Treefall gap size effects on above- and below-ground processes in a tropical wet forest, *J. Ecol.*, 86, 597–609, 1998.

Espírito Santo, F. D., Keller, M., Braswell, B., Nelson, B. W., Frolking, S., and Vicente, G.: Storm intensity and old-growth forest disturbances in the Amazon region, *Geophys. Res. Lett.*, 37, 1–6, 2010.

FAO: World reference base for soil resources, *World Soil Resources Report*, Rome, 60, 1998.

Ferraz, J., Oht, S., and Salles, P. C.: Distribuição dos solos ao longo de dois transectos em floresta primária ao norte de Manaus (AM). In: *Pesquisas Florestais para a Conservação da Floresta e Reabilitação de Áreas Degradadas da Amazônia*, edited by: Higuchi, N., Campos, M. A. A., Sampaio, P. T. B., and dos Santos, J., INPA, Manaus, 111–143, 1998.

Garstang, M., White, S., Shugart, H. H., and Halverson, J.: Convective clouds downdrafts as the cause of large blowdowns in the Amazon Rainforest, *Meteorol. Atmos. Phys.*, 67, 199–212, 1998.

Grimm, R., Behrens, T., Märker, M., and Elsenbeer, H.: Soil organic carbon concentrations and stocks on Barro Colorado Island, Digital soil mapping using random forests analysis, *Geoderma*, 146, 102–113, 2008.

Higuchi, N., Chambers, J. Q., Santos, J., Ribeiro, R. J., Pinto, A. C. M., Silva, R. P., Rocha, R. M., and Tribuzy, E. S.: Dinâmica e balanço do carbono da vegetação primária da Amazônia Central, *Floresta*, 34, 295–304, 2004.

Higuchi, N., Santos, J., Lima, A. J. N., Higuchi, F. G., and Chambers, J. Q. A.: A floresta amazônica e a água da chuva, *Floresta*, 41, 427–434, 2011.

Houghton, R. A.: The annual net flux of carbon to the atmosphere from changes in land use 1850–1990, *Tellus B*, 50, 298–313, 1999.

IBGE: Mapa de vegetação do Brasil. Fundação Instituto Brasileiro de Geografia e Estatística/Ministério da Agricultura/Instituto Brasileiro de Desenvolvimento Florestal, IBGE, Rio de Janeiro, 2004.

Kahle, M., Kleber, M., Torn, M. S., and Jahn, R.: Carbon storage in coarse and fine clay fractions of illitic soils, *Soil Sci. Soc. Am. J.*, 67, 1732–1739, 2002.

Lal, R.: Soil carbon sequestration to mitigate climate change, *Geoderma*, 123, 1–22, 2004.

- Lin, K., Hamburg, S. P., Tang, S., Hsia, Y., and Lin, T.: Typhoon effects on litterfall in a subtropical forest, *Can. J. Forest Res.*, 33, 2184–2192, 2003.
- López-Ulloa, M., Veldkamp, E., and de Koning, G. H. J.: Soil carbon stabilization in converted tropical pastures and forests depends on soil type, *Soil Sci. Soc. Am. J.*, 69, 1110–1117, 2005.
- 5 Lugo, A. E.: Visible and invisible effects of hurricanes on forest ecosystems: an international review, *Austral. Ecol.*, 33, 368–398, 2008.
- Lugo, A. E., Applefield, M., Pool, D., and McDonald, R.: The impact of Hurricane David on the forests of Dominica, *Can. J. Forest Res.*, 13, 201–211, 1983.
- 10 Maia, S. M. F., Ogle, S. M., Cerri, C. E. P., and Cerri, C. C.: Effect of grassland management on soil carbon sequestration in Rondônia and Mato Grosso states, Brazil, *Geoderma*, 149, 84–91, 2009.
- Maia, S. M. F., Ogle, S. M., Cerri, C. C., and Cerri, C. E. P.: Changes in soil organic carbon storage under different agricultural management systems in the Southwest Amazon Region of Brazil, *Soil Till. Res.*, 106, 177–184, 2010.
- 15 Marín-Spiotta, E., Silver, W. L., Swanston, C. W., and Ostertag, R.: Soil organic matter dynamics during 80 years of reforestation of tropical pastures, *Glob. Change Biol.*, 15, 1584–1597, 2009.
- Marra, D. M., Chambers, J. Q., Higuchi, N., Trumbore, S. E., Ribeiro, G. H. P. M., Santos, J. dos, Negrón-Juárez, R. I., Reu, B., and Wirth, C.: Large-Scale Wind Disturbances Promote Tree Diversity in a Central Amazon Forest, *Plos One*, 9, e103711, doi:10.1371/journal.pone.0103711, 2014.
- 20 Negrón-Juárez, R. I., Chambers, J. Q., Guimarães, G., Zeng, H., Raupp, C. F. M., Marra, D. M., Ribeiro, G. H. P. M., Saatchi, S., Nelson, B. W., and Higuchi, N.: Widespread Amazon forest tree mortality from a single cross-basin squall line event, *Geophys. Res. Lett.*, 37, 1–5, 2010.
- 25 Negrón-Juárez, R. I., Chambers, J. Q., Marra, D. M., Ribeiro, G. H. P. M., Rifai, S. W., Higuchi, N., and Roberts, D.: Detection of subpixel treefall gaps with Landsat imagery in Central Amazon forests, *Remote Sens. Environ.*, 115, 3322–3328, 2011.
- Neill, C., Melillo, J. M., Steudler, P. A., Cerri, C. C., de Moraes, J. F. L., Piccolo, M. C., and Brito, M.: Soil carbon and nitrogen stocks following forest clearing for pasture in the south-western Brazilian Amazon, *Ecol. Appl.*, 7, 1216–1225, 1997.
- 30 Nelson, B. W., Kapos, V., Adams, J. B., Oliveira, W. J., and Oscar, P. G. B.: Forest disturbance by large blowdowns in the Brazilian Amazon, *Ecol. Soc. Am.*, 75, 853–858, 1994.

Windthrows increase soil carbon stocks

L. T. dos Santos et al.

[Title Page](#)[Abstract](#)[Introduction](#)[Conclusions](#)[References](#)[Tables](#)[Figures](#)[I◀](#)[▶I](#)[◀](#)[▶](#)[Back](#)[Close](#)[Full Screen / Esc](#)[Printer-friendly Version](#)[Interactive Discussion](#)

Windthrows increase soil carbon stocks

L. T. dos Santos et al.

[Title Page](#)[Abstract](#)[Introduction](#)[Conclusions](#)[References](#)[Tables](#)[Figures](#)[I◀](#)[▶I](#)[◀](#)[▶](#)[Back](#)[Close](#)[Full Screen / Esc](#)[Printer-friendly Version](#)[Interactive Discussion](#)

Neumann-Cosel, L., Zimmermann, B., Jefferson, S., van Breugel, M., and Helmut, E.: Soil carbon dynamics under young tropical secondary forests on former pastures – a case study from Panama, *Forest Ecol. Manag.*, 261, 1625–1633, 2011.

Ngo, K. M., Turner, B. L., Muller-Landau, H. C., Davies, S. J., Larjavaara, M., Nik Hassan, N. F., and Bin Lum, S.: Carbon stocks in primary and secondary tropical forests in Singapore, *Forest Ecol. Manag.*, 296, 81–89, 2013.

Ostertag, R., Scatena, F. N., and Silver, W. L.: Forest floor decomposition following hurricane litter inputs in several Puerto Rican forests, *Ecosystems*, 6, 261–273, 2003.

Powers, J. S. and Schlesinger, W. H.: Relationships among soil carbon distributions and biophysical factors at nested spatial scales in rain forests of northeastern Costa Rica, *Geoderma*, 109, 165–190, 2002.

Powers, J. S. and Veldkamp, E.: Regional variation in soil carbon and $\delta^{13}\text{C}$ in forests and pastures of northeastern Costa Rica, *Biogeochemistry*, 72, 315–336, 2005.

Putz, F. E.: Treefall pits and mounds, buried seeds, and the importance of soil disturbance to pioneer trees on Barro Colorado Island, Panama, *Ecology*, 64, 1069–1074, 1983.

Queré, C. L., Raupach, M. R., Canadell, J. G., and Marland, G.: Trends in the sources and sinks of carbon dioxide, *Nat. Geosci.*, 2, 831–836, 2009.

Quesada, C. A., Lloyd, J., Schwarz, M., Patiño, S., Baker, T. R., Czimczik, C., Fyllas, N. M., Martinelli, L., Nardoto, G. B., Schmerler, J., Santos, A. J. B., Hodnett, M. G., Herrera, R., Luizão, F. J., Arneith, A., Lloyd, G., Dezzeo, N., Hilke, I., Kuhlmann, I., Raessler, M., Brand, W. A., Geilmann, H., Moraes Filho, J. O., Carvalho, F. P., Araujo Filho, R. N., Chaves, J. E., Cruz Junior, O. F., Pimentel, T. P., and Paiva, R.: Variations in chemical and physical properties of Amazon forest soils in relation to their genesis, *Biogeosciences*, 7, 1515–1541, doi:10.5194/bg-7-1515-2010, 2010.

Quesada, C. A., Lloyd, J., Anderson, L. O., Fyllas, N. M., Schwarz, M., and Czimczik, C. I.: Soils of Amazonia with particular reference to the RAINFOR sites, *Biogeosciences*, 8, 1415–1440, doi:10.5194/bg-8-1415-2011, 2011.

R Core Team: R: A language and environment for statistical computing, available at: <http://www.r-project.org> (last access: 1 October 2015), 2014.

Rhoades, C. C., Eckert, G. E., and Coleman, D. C.: Soil carbon differences among forest, agriculture, and secondary vegetation in lower montane Ecuador, *Ecol. Appl.*, 10, 497–505, 2000.

Windthrows increase soil carbon stocks

L. T. dos Santos et al.

[Title Page](#)[Abstract](#)[Introduction](#)[Conclusions](#)[References](#)[Tables](#)[Figures](#)[I◀](#)[▶I](#)[◀](#)[▶](#)[Back](#)[Close](#)[Full Screen / Esc](#)[Printer-friendly Version](#)[Interactive Discussion](#)

- Ribeiro, G. H. P. M., Suwa, R., Marra, D. M., Lima, A. J. N., Kajimoto, T., Ishizuka, M., and Higuchi, N.: Allometry for juvenile trees in an Amazonian forest after wind disturbance, *JARQ*, 48, 213–219, 2014.
- Schaetzl, R. J., Burns, S. F., Johnson, D. L., and Small, T. W.: Tree uprooting: review of impacts on forest ecology, *Vegetatio*, 79, 165–176, 1989.
- Sombroek, W.: Spatial and temporal patterns of Amazon rainfall, *Ambio*, 30, 388–396, 2001.
- Telles, E. de C. C., Camargo, P. B. de, Martinelli, L. A., Trumbore, S. E., Costa, E. S. da, Santos, J. dos, Higuchi, N., and Oliveira Jr., R. C.: Influence of soil texture on carbon dynamics and storage potential in tropical forest soils of Amazonia, *Global Biogeochem. Cy.*, 17, 1040, doi:10.1029/2002GB001953, 2003.
- Torn, M. S., Trumbore, S. E., Chadwick, O. A., Vitousek, P. M., and Hendricks, D. M.: Mineral control of soil organic carbon storage and turnover, *Nature*, 389, 3601–3603, 1997.
- Trumbore, S. E., Davidson, E. A., De Camargo, P. B., Nepstad, D. C., and Martinelli, L. A.: Belowground cycling of carbon in forests and pastures of Eastern Amazonia, *Global Biogeochem. Cy.*, 9, 515–528, 1995.
- Veldkamp, E., Becker, A., Schwendenmann, L., Clark, D. A., and Schulte-Bisping, H.: Substantial labile carbon stocks and microbial activity in deeply weathered soils below a tropical wet forest, *Glob. Change Biol.*, 9, 1171–1184, 2003.
- Vitousek, P. M. and Denslow, J. S.: Nitrogen and phosphorous availability in treefall gaps of a lowland tropical rainforest, *J. Ecol.*, 74, 1167–1178, 1986.

Windthrows increase soil carbon stocks

L. T. dos Santos et al.

Table 1. Average concentrations of soil organic carbon content (SOC), soil carbon stocks (SCS), bulk density (BD) and clay, silt and sand average concentrations in transect 1 (E1), transect 2 (E2) and transect 3 (E3). Values in brackets represent the standard error of the mean.

Trans	Depth (cm)	Disturbed forest		Undisturbed forest		Soil texture			
		SOC (%)	SCS (Mg ha ⁻¹)	SOC (%)	SCS (Mg ha ⁻¹)	BD (g cm ⁻³)	Clay (%)	Silt (%)	Sand (%)
E1	0–10	3.72 (0.28)	31.00 (5.07)	2.48 (0.24)	20.18 (0.75)	0.74	69.42	21.97	8.56
	10–20	2.31 (0.13)	22.82 (1.97)	2.05 (0.22)	19.24 (0.74)	0.97	69.04	22.42	8.54
	20–30	1.79 (0.13)	16.61 (1.76)	1.71 (0.17)	13.06 (0.44)	0.98	68.69	22.78	8.53
E2	0–10	3.27 (0.19)	25.50 (1.42)	–	–	0.89	57.41	19.31	22.25
	10–20	1.79 (0.09)	19.87 (0.84)	–	–	1.15	67.59	22.42	8.54
	20–30	1.36 (0.07)	15.11 (1.59)	–	–	1.31	60.23	19.41	19.34
E3	0–10	2.11 (0.14)	21.52 (1.80)	1.17 (0.14)	11.36 (3.44)	1.24	22.63	10.33	67.04
	10–20	1.31 (0.08)	17.48 (3.08)	0.82 (0.09)	10.69 (2.63)	1.36	57.8	19.1	23.1
	20–30	1.13 (0.10)	16.50 (2.90)	0.75 (0.07)	10.14 (2.63)	1.41	24.78	10.94	63.93
Average	0–10	2.89 (0.13)	25.90 (2.06)	1.58 (0.19)	14.90 (3.18)	0.95	50.55	17.30	32.15
	10–20	1.71 (0.07)	20.05 (1.34)	1.13 (0.13)	14.11 (2.76)	1.16	50.45	17.90	31.65
	20–30	1.37 (0.06)	16.01 (1.27)	0.98 (0.10)	11.31 (1.91)	1.19	51.95	17.51	30.54

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

I ◀

▶ I

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



Windthrows increase soil carbon stocks

L. T. dos Santos et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures



Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion

**Table 2.** Estimates of soil carbon stock (SCS) from this study and in other tropical forests.

Autor	Regions	Forest types	SCS (Mg ha ⁻¹)		Soil type/description
			0–10 cm	0–30 cm	
Trumbore et al. (1995)	Brazilian Amazon	Forest type			
		Pará	26.0		Oxisols
Neill et al. (1997)	Rondônia	Floresta Ombrófila Aberta ^b		36.1	Ultisols ^a
		Rondônia		48.2	Oxisols
Camargo et al. (1999)	Pará	Floresta Ombrófila Aberta	26.0		Oxisols
		Floresta Ombrófila Densa	19.2		Oxisols
Telles et al. (2003)	Amazonas	Floresta Ombrófila Densa	12.5		Spodosols ^a
		Pará	24.6		Oxisols
Maia et al. (2009)	Mato Grosso	Floresta Ombrófila Aberta ^b		45.7	Oxisols
		Floresta Ombrófila Aberta		31.2	Ultisols
		Floresta Ombrófila Aberta		49.7	Oxisols
Maia et al. (2010)	Mato Grosso	Floresta Ombrófila Aberta ^b		46.9	Oxisols
		Rondônia		47.6	Oxisols
This study	Amazonas	Mean values	23.3	56.8	Oxisols/Spodosols
		Disturbed forest	25.9	61.4	Oxisols/Spodosols
		Undisturbed forest	14.9	47.7	Oxisols/Spodosols
		Other tropical forests	0–10 cm	0–30 cm	
Rhoades et al. (2000)	Ecuador	Tropical lower montane forest		95.6	Andic humitropepts
Batjes 2001	Senegal	Equatorial forest		23.0	Orthic Ferralsol ^c
		Equatorial forest		35.0	Plinthic Ferralsol ^c
		Equatorial forest		30.0	Eutric Regosol ^c
Powers and Schlesinger 2002	Costa Rica	Tropical wet forest	34.1	82.2	Trophumults, dystropepts, dystrandeps ^a
Veldkamp et al. (2003)	Costa Rica	Tropical moist forest		64.0	Oxisols
		Tropical moist forest		96.0	Oxisols
Marin-Spiotta et al. (2009)	Puerto Rico	Subtropical wet forest life zone	31.0		Oxisols
Grimm et al. (2008)	Barro Colorado Island	Semi-deciduous moist tropical forest	38.1	69.4	Oxisols, Cambisols
Neumann-cosel et al. (2011)	Panama	Tropical Moist Forest (100 years-old)	34.0		Homogenous, silty clay and clay, pH values from 4.4 to 5.8.
K.M. Ngo et al. (2013)	Singapura	Coastal hill dipterocarp forest	22.1		Very acidic and infertile

^a US Soil Taxonomy.^b IBGE, 2004.^c FAO, World Reference Base for Soil Resources (WRB).

Windthrows increase soil carbon stocks

L. T. dos Santos et al.

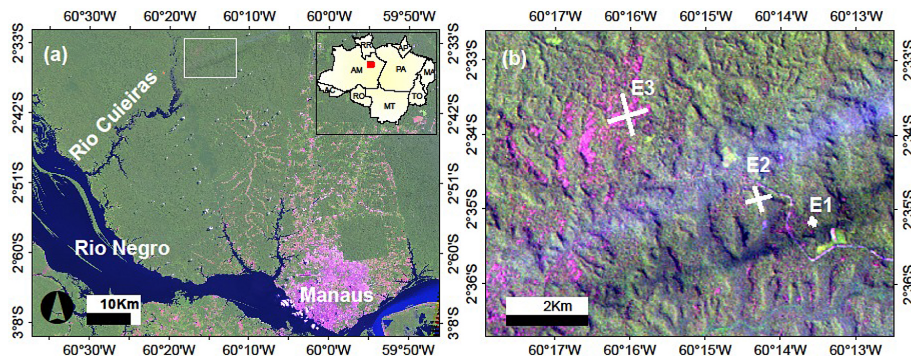


Figure 1. Study area (white inset) on the left side of the Rio Cuieiras, Amazonas, Brazil **(a)**. Sampled transects (white inlet) set along wind-disturbed *terra-firme* forest at the Estação Experimental de Silvicultura Tropical (EEST/INPA) and a contiguous forest (SUFRAMA). The reddish color in **(b)** indicates the high middle-infrared reflectance (dead wood and litter) of wind-disturbed areas. Image: RGB composition (bands 3, 4 and 5) from Landsat 5 TM (p231, r062, from 29 July 2005). Image source: <http://earthexplorer.usgs.gov/>

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

◀

▶

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



Windthrows increase soil carbon stocks

L. T. dos Santos et al.

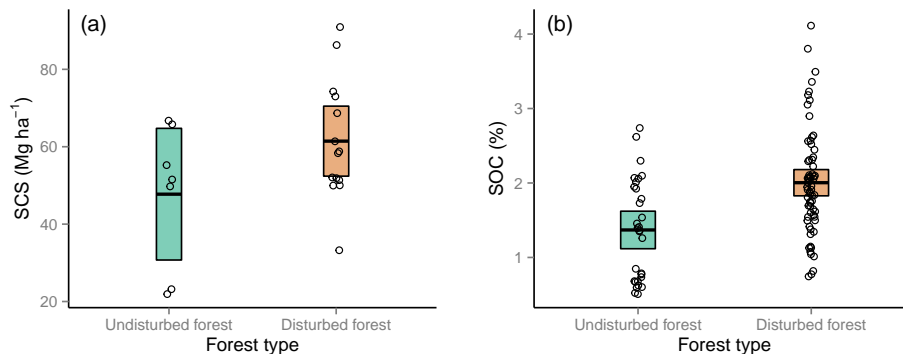


Figure 2. Comparison of the entire 0–30 cm depth profile for (a) soil carbon stock (SCS) and (b) soil organic carbon (SOC) between the disturbed and the undisturbed forest (mean \pm 95 % confidence interval) at 0–30 cm depth profile.

[Title Page](#)[Abstract](#)[Introduction](#)[Conclusions](#)[References](#)[Tables](#)[Figures](#)[I◀](#)[▶I](#)[◀](#)[▶](#)[Back](#)[Close](#)[Full Screen / Esc](#)[Printer-friendly Version](#)[Interactive Discussion](#)

Windthrows increase soil carbon stocks

L. T. dos Santos et al.

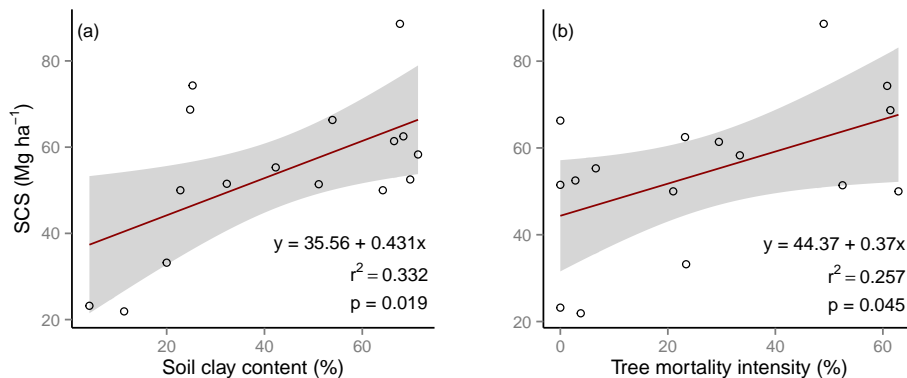


Figure 3. Soil carbon stock (SCS) as a linear function of clay content **(a)** and tree mortality intensity (%) **(b)** at 0–30 cm depth profile.

[Title Page](#)[Abstract](#)[Introduction](#)[Conclusions](#)[References](#)[Tables](#)[Figures](#)[I ◀](#)[▶ I](#)[◀](#)[▶](#)[Back](#)[Close](#)[Full Screen / Esc](#)[Printer-friendly Version](#)[Interactive Discussion](#)

Windthrows increase soil carbon stocks

L. T. dos Santos et al.

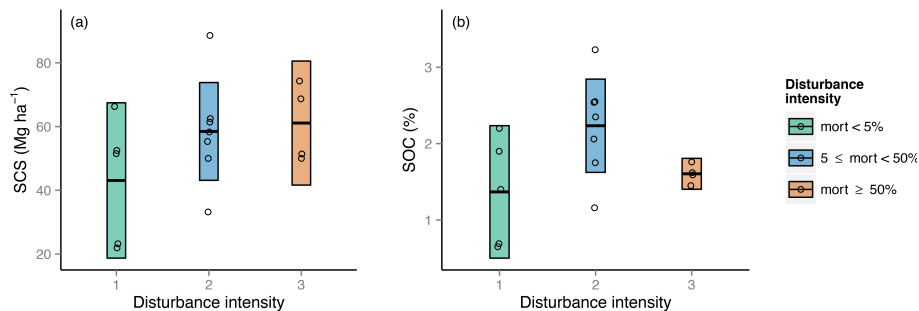


Figure 4. Soil carbon stock (SCS) **(a)** and soil organic carbon (SOC) **(b)** (mean \pm 95 % confidence interval) at 0–30 cm depth profile over disturbance intensity classes defined as tree mortality intensity (%) directly caused by the 2005 squall line event.

[Title Page](#)
[Abstract](#)
[Introduction](#)
[Conclusions](#)
[References](#)
[Tables](#)
[Figures](#)
[◀](#)
[▶](#)
[◀](#)
[▶](#)
[Back](#)
[Close](#)
[Full Screen / Esc](#)
[Printer-friendly Version](#)
[Interactive Discussion](#)
