A permafrost glacial hypothesis to explain atmospheric CO₂ and the ice ages during the Pleistocene

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Received: 26 September 2010 – Accepted: 8 October 2010 – Published: 15 October 2010

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

Over the past several 100 ka glacial-interglacial cycles, the concentration of atmospheric CO$_2$ was closely coupled to global temperature, which indicates the importance of CO$_2$ as a greenhouse gas. The reasons for changes in atmospheric CO$_2$ have mainly been sought in the ocean, yet proxy evidence does not support the notion of increased oceanic carbon storage during glacials. Here we present results from the first permafrost loess sequence in Siberia spanning two glacial cycles (~240 ka), which reveal that permafrost soils repeatedly sequestered huge amounts of terrestrial carbon during glacial periods. This can be explained with permafrost favouring more intensive waterlogging conditions and better preservation of soil organic matter. Terrestrial carbon stored in permafrost soils was released upon warming and provided a powerful feedback mechanism for the glacial terminations. We outline a “permafrost glacial hypothesis” building on integrated annual insolation forcing, which readily explains the observed succession of the ice ages during the Pleistocene, including the mid-Pleistocene transition.

1 Introduction

Antarctic ice cores have revealed that the succession of glacials and interglacials during the past ~1 Ma was intimately linked to the global carbon cycle (Petit et al., 1999; Shackleton, 2000; Luthi et al., 2008). Cold glacial periods were characterized by low concentrations of atmospheric CO$_2$ (~180 to 200 ppm), while interglacials had high concentrations (~280 ppm, preindustrial value). The large size of the carbon pool in the ocean (~40 times the atmospheric carbon) led to the prevailing notion that the oceans were the principal driver and acted as a net carbon sink during the glacials (Broecker, 1982; Sigman et al., 2010). Changes in the Southern Ocean in particular have been proposed to play an important role in controlling atmospheric CO$_2$, because up-welling and ventilation of the deep ocean, which constantly accumulates respired
CO₂ from sinking organic particles, occurs mainly around Antarctica (Toggweiler et al., 2006; Fischer et al., 2010; Sigman et al., 2010). However, it has been impossible so far to find the supposedly large pool of “old” radiocarbon trapped in the glacial deep ocean, which would be required to corroborate the “ocean hypothesis” (Broecker and Barker, 2007; De Pol-Holz et al., 2010). Additionally, carbon models are yet unable to convincingly explain the full range of glacial-interglacial changes in atmospheric CO₂ with physical and biological changes in the ocean (Brovkin et al., 2007; Boer et al., 2010; Fischer et al., 2010). In light of these inconsistencies, we should stay open minded to the possibility of changes in the terrestrial carbon cycle as an alternative.

Terrestrial carbon pools have long been considered to be negligible in comparison to marine reservoirs, and to have acted as sources rather than sinks during glacials. This partly stems from the fact that net production of terrestrial biomass is lower during glacials compared to interglacials, because lower temperatures, lower atmospheric CO₂, and increased glacial aridity are less favorable conditions for plant growth. Revised estimates, however, suggest that the soil carbon pools in northern permafrost regions are much larger than previously thought. They could exceed 1670 Pg (Zimov and Schuur, 2006; Tarnocai et al., 2009), which is more than twice the atmospheric pool. Changes in sizes of these carbon pools could thus have major impacts on atmospheric CO₂ levels. The enormous carbon storage at high-latitudes reflects that apart from biomass productivity, the rate of decomposition is crucial for terrestrial carbon storage. Cold permafrost regions provide very suitable environments for preservation of soil organic matter and long-term carbon storage. In fact, many studies have fueled concerns that today, at times of global warming, CO₂ and methane emissions from thawing and decomposing permafrost soils result in a large positive feedback and accelerate global warming (Zimov and Schuur, 2006; Schuur et al., 2008; Tarnocai et al., 2009).

In order to evaluate the role of permafrost soils in the global carbon cycle, information is needed about their age, formation, and carbon dynamics. So far, the lack of long, continuous outcrops spanning several glacial-interglacial cycles has limited such
insights. We here present results from a unique loess-paleosol sequence, which documents environmental and climate changes over the last \( \sim240\) ka.

2 Material and methods

Our research site is a \( \sim50\) m high permafrost bluff along the Tumara River in the southwestern foreland of the Verkhoyansk Mountains, Northeast Siberia (Fig. 1). The lower part of the bluff exposes Tertiary sands and Quaternary gravels. The upper \( \sim15\) m, referred to as “Tumara Paleosol Sequence”, consist of frozen dark grey loess-like sediments alternating with bright brown soil horizons (Fig. 2). Previous detailed stratigraphical and geochemical analyses (Zech et al., 2007, 2008) have shown that the dark units (B and D) are dominated by silt size particles and have total organic carbon (TOC) contents exceeding 1%. The bright brown units (A, C and E) contain more clay and have much lower TOC (<0.5%). These findings have been interpreted to document the succession of glacials and interglacials, with low temperatures favoring intensive permafrost and water logging conditions and good preservation of soil organic matter, while warmer temperatures favor better drainage, mineralization and weathering (Zech et al., 2007, 2008, 2010a).

Radiocarbon and luminescence ages support this interpretation and the correlation of the organic-rich units B and D with the last (MIS 2 to 4) and penultimate (MIS 6) glacials, respectively (Fig. 2). It must be acknowledged though that obtaining robust and precise age control in arctic, partly reworked and weathered loess is very challenging. Radiocarbon ages can be significantly too old, because soil organic material is exceptionally well preserved in cold, arctic environments, and re-working of sediments can occur through aeolian, fluvial or colluvial processes without mineralization of “old” carbon. On the other hand, the humic acid fraction, which for the above reasons is generally preferred over the refractory humin fraction when dating soils, is more susceptible to translocation, particularly in soils with waterlogging conditions. This can lead to too young radiocarbon ages. Similarly, the IRSL ages can be too old when
the samples have been insufficiently bleached prior to deposition (which might explain the inconsistent IRSL age of 177 ka in unit C), or they can be too young due to signal fading or saturation. For a full discussion of the available numeric ages, the reader is referred to the previous publications (Zech et al., 2010a).

In light of the dating uncertainties, the correlation of the organic-rich units with glacials remained controversial; particularly as palynological and biomarker results became available and documented larch forest cover for unit D (Zech et al., 2010a). This seems to be at odds with its correlation with the penultimate glacial, since larch has traditionally been considered to be an indicator for interglacials in Siberia. Similar inconsistencies are known from Lake El'gygytgyn in NE-Siberia, possibly questioning the validity of using vegetation reconstructions to infer “independent” age control (Brigham-Grette et al., 2007).

In order to circumvent the chronostratigraphical difficulties and to robustly assess the carbon storage and dynamics in the Tumara Paleosol Sequence, we aimed at obtaining direct temperature estimates and measured the deuterium/hydrogen isotopic ratios ($\delta D$) in the long-chain $n$-alkanes C27, C29 and C31. These $n$-alkanes are epicuticular leaf waxes synthesized by plants. They are relatively resistant against degradation and well preserved in paleosols. They can thus be employed to reconstruct the $\delta D$ signal of the water used by the plants during synthesis (Sachse et al., 2006; Hou et al., 2008). Assuming constant metabolic fractionation and limited effects of soil water evaporation, the $n$-alkane signal mainly reflects changes in the isotopic composition of past growth season soil water and thus precipitation. Similar to ice core oxygen and hydrogen isotope records, our leaf wax $\delta D$ record thus allows inferring past temperature changes, with more negative $\delta D$ values indicating lower temperatures.

The laboratory work followed standard procedures. The air-dried soil samples were ground and extracted with DCM/Methanol (9:1) using accelerated solvent extraction. The total lipid extracts were separated over activated silica columns. The alkane fractions were spiked with hexamethyl-benzene for quantification on a GC-FID. Triplicate measurements of the compound-specific deuterium isotope ratios of the alkanes were
performed on a GC-pyrolyses-irMS. Standard deviations (shown in Fig. 2) were 2.3, 1.9 and 1.2‰ on average for C27, 29 and 31. External standards (C27 and 29) were run every 6 measurements and yielded fairly constant isotope values of $-221.2 \pm 2.8$ and $-186.1 \pm 3.0‰$.

3 Results and discussion

3.1 Interpretation of $\delta D$ as temperature record

The $\delta D$ records of the three $n$-alkanes show very similar patterns (Fig. 2). The organic rich units B and D are characterized by values as negative as $-270‰$, while the alkanes in units A, C and E are more enriched and exceed $-240‰$. The similarity between compounds suggests that the overall pattern is robustly recording isotopic changes related to temperature and that the potential effects of changing vegetation cover are negligible. Changing vegetation could theoretically have an effect on the reconstructed isotopic signal, because plants may exhibit specific isotopic leaf water enrichments. In fact, vegetation changes have been reconstructed for the Tumara Paleosol Sequence, employing that fact that C27 and 29 are dominantly produced by trees, whereas C31 can be mainly attributed to grass (Zech et al., 2010a). As all three $n$-alkanes show very similar values and patterns (Fig. 2), we suggest that the effect of changing vegetation on the $\delta D$ signal is negligible.

Evaporation effects are probably also only of second-order importance, because the plants likely could use the soil water close to the thawing front of the active layer, which has not yet experienced the isotopic enrichment that can be expected for the soil water in the uppermost topsoil. If evaporation had an effect on our $\delta D$ record, it would have led to isotopic enrichment during the more arid glacial periods, which would have dampened the observed glacial-interglacial pattern. In fact, this could possibly explain the slightly smaller range of $\delta D$ values in our record ($\sim30‰$) compared to respective
ranges in ice core records (up to 50‰, Fig. 3), and particularly the relatively positive values during MIS 2.

We finally note that a correction could be applied to our record to take global ice volume changes into account. This would consider the fact that the glacial oceans and thus precipitation became more positive and would further increase the glacial-interglacial differences in δD values. However, such a correction would require relatively precise age control, and we prefer to plot the non-manipulated δD record.

In summary, although we acknowledge the need for further research to quantify and correct for the potential effects of changing vegetation, evaporation, global ice volume and water vapor sources, we suggest that our δD record dominantly reflects temperature, and we infer that units B and D were deposited during particularly cold conditions, namely the last and penultimate glacial.

3.2 Regional paleoclimatic and environmental reconstruction

Plotted on an age scale (Fig. 3, see also the Supplement for the construction of the age-depth model), our deuterium record reveals good overall agreement with independent paleoclimate data, for instance the isotope temperature proxies derived from Greenland and Antarctic ice cores (Petit et al., 1999; NGRIP members, 2004), paleoecological evidence from Beringia for warming during MIS 3 (Anderson and Lozhkin, 2001), and peak warmth during MIS 5e (CAPE – Last Interglacial Project Members, 2006; Kienast et al., 2008).

Although the paleoenvironmental reconstruction is not the main focus of this manuscript, we would like to point out two particularly interesting features. First, cold conditions indicated by unit C2 are consistent with various findings documenting substantial cooling and glacial advances within the last interglacial during MIS 5d (Karanbonov et al., 1998; Stauch and Gualtieri, 2008; Zech et al., 2010b).

Second, relatively positive δD values are found for MIS 2. As already mentioned above, this could either indicate extreme arid conditions (evaporation effects), or it documents that the temperatures were relatively modest in NE Siberia. Both
interpretations would corroborate plant macrofossils findings from the Laptev Sea coast, which reveal extremely continental, arid conditions characterized by relatively warm summers during MIS 2 (Kienast et al., 2005). Increasing aridity and continentality during the course of the last glacial probably also explain (i) successively more restricted glacial extents in Siberia (Svendsen et al., 2004; Stauch and Gualtieri, 2008; Zech et al., 2010b), and (ii) the decline in forest cover and expansion of “Mammoth Steppe” (Sher et al., 2005; Zech et al., 2010a). Explanations for this trend may be found in the lowering of sea level and the resultant distance to the Arctic Ocean, combined with rain shadow effects on the lee-side of the growing Fennoscandian and Barents Ice Sheets (Svendsen et al., 2004). However, a compelling observation is that the penultimate glacial apparently developed differently compared to the last glacial. Glaciers seem to have reached their maximum extents in Siberia at the end of the penultimate glacial (Svendsen et al., 2004; Stauch and Gualtieri 2008; Zech et al., 2010b), and although our δD record indicates very low temperatures, trees and even Larch prevailed (Zech et al., 2010a). We therefore speculate that our results may lend support to the controversial hypothesis that the sprawling megafauna itself was responsible for the expansion of the “Mammoth Steppe” and the aridization trend during the last glacial (Zimov et al., 1995).

3.3 The role of permafrost for enhanced carbon sequestration

The by far most important implications of our results are related to the role of permafrost for carbon sequestration. As illustrated in Figs. 2 and 3, more negative δD values (i.e. lower temperatures) correlate with higher TOC contents (correlation coefficient $R = -0.61$). Note that this correlation is totally independent of the age model uncertainties. We suggest that the correlation reflects the importance of permafrost (as impermeable layer) in favoring water logging conditions and, in turn, resulting in reduced organic matter mineralization and enhanced carbon storage. Net biomass productivity, which was likely higher during warmer periods, is apparently not be the dominant factor in controlling TOC contents in permafrost soils. Our reasoning is consistent with
studies that indicate that increasing biomass productivity in a warming world doesn’t offset the effect of permafrost thawing and resultant mineralization of soil organic matter (Zimov and Schuur, 2006; Schuur et al., 2008), as well as with modern analogues, for example the fact that tundra soils preserve and accumulate more TOC than (the more productive) taiga or forest-steppe soils further south.

Permafrost loess sequences along the arctic coast, which are referred to as “ice complex deposits”, or “Yedoma”, often have TOC values exceeding 5–10% (Schirrmeister et al., 2002; Wetterich et al., 2008). Most of these sequences, however, span only a few ten thousand years, are discontinuous, and strongly affected by cryoturbation, which limits the possible insights into permafrost loess formation and carbon storage on glacial-interglacial timescales. Apart from the ice-wedge at ∼5 m depth, the Tumara Paleosol Sequence shows no evidence for cryoturbation. It thus provides the first field evidence for the temporal dynamics of carbon storage in permafrost soils, documenting enhanced terrestrial carbon sequestration during glacials and reduced sequestration during interglacials/interstadials.

We acknowledge that more long permafrost sequences should be studied, but we suggest that such permafrost carbon dynamics characterize most of the vast, non-glaciated areas in Siberia (Fig. 1). The reasoning will reach its limits only at extremely cold sites, where TOC contents in soils become production-limited, and at the southern boundary of the Siberian permafrost area, where glacial aridity might offset the water logging effect of permafrost.

3.4 Up-scaling to glacial-interglacial carbon pool changes

Is the permafrost-induced terrestrial carbon storage large enough to affect atmospheric CO₂ levels? The “excess carbon storage” during glacials compared to interglacials can be calculated for the Tumara Paleosol Sequence as follows. Using estimated dry soil densities of 1000 kg/m³, TOC differences of 1%, and soil thicknesses of 3 m, the glacial units B and D each store ∼30 kg/m² excess carbon. When scaled to an estimated expanded extent of Siberian permafrost areas during glacials (∼10 × 10⁶ km², Fig. 1),
this excess carbon storage would be $\sim 300 \text{ Pg}$, equivalent to $\sim 150 \text{ ppm}$ atmospheric CO$_2$ and thus easily exceeding the observed glacial-interglacial difference of $\sim 100 \text{ ppm}$ (ocean uptake will be discussed below).

This simple up-scaling exercise is only meant to illustrate the potential of permafrost carbon dynamics and most likely underestimates the real effects, because Yedoma deposits can have TOC contents much higher than 2.5% and be more than 25 m thick (Zimov and Schuur, 2006; Tarnocai et al., 2009). A more sophisticated up-scaling approach, using a permafrost-soil carbon model, indicates that permafrost soils in Europe and South Siberia may have lost more than 1000 Pg carbon upon warming during the last deglaciation (Zimov et al., 2009), equivalent to $\sim 500 \text{ ppm}$ atmospheric CO$_2$.

The pedological evidence for this carbon storage during the last glacial has mostly been erased due to mineralization. Only where permafrost prevailed and protected the carbon-rich, deeper paleosols even during interglacials, as in the case of the Tumara Paleosol Sequence, the permafrost carbon dynamics left their obvious marks in the sedimentary stratigraphies. This applies also to previous glacial, of course, and combined with the landscape dynamics and intensive erosion related to permafrost thawing likely explains why long, continuous paleosol sequences suitable for paleoenvironmental reconstruction are so scarce.

### 3.5 A revised role for the ocean?

In order to evaluate, to which degree carbon released from permafrost soils during deglaciations would have affected atmosphere CO$_2$ concentrations and global climate, one has to track its further fate. For the most part, the released carbon will be taken up by the ocean as dissolved inorganic carbon, where it leads to “ocean acidification” and carbonate dissolution (carbonate compensation). Only about 10% of the permafrost carbon released during terminations would remain in the atmosphere on millennial timescales (Archer et al., 2004). Estimating the glacial-interglacial permafrost carbon pool changes to 1000 Pg (Zimov et al., 2009), this would be equivalent to 50 ppm atmospheric CO$_2$ – a significant portion of the carbon balance during the ice age cycles. As
roughly another 50 ppm would be a simple amplification effect due to a warming ocean (which holds less dissolved CO$_2$), permafrost carbon dynamics alone might be able to explain the glacial-interglacial atmospheric CO$_2$ differences of $\sim$100 ppm. We acknowledge, that the exact role of permafrost carbon dynamics will have to be investigated in more detail in future studies, but that the major shortcomings of the current global carbon models might stem from not including permafrost soils (Boer et al., 2010).

The above scenario notably contradicts the current notion of the role of the oceans in controlling atmospheric CO$_2$ on glacial-interglacial timescales (Broecker, 1982; Toggweiler et al., 2006; Brovkin et al., 2007; Fischer et al., 2010; Sigman et al., 2010). Based on our findings, we have to conclude that the oceans might have acted as carbon sinks during (rapid) deglaciations, and as carbon sources during (slow) glacial cooling, respectively. In the following, we provide a brief, critical review of “independent” evidence for the ocean versus the permafrost hypotheses.

First, the main reason for the gross underestimation of the terrestrial, permafrost-related carbon dynamics probably has to be sought in the apparent isotopic constraints of global carbon pool changes. More negative deep ocean carbon isotope signals ($\delta^{13}$C) during glacials have long been inferred to document the release of negative, terrestrial carbon (Duplessy et al., 1984; Matsumoto et al., 2002; Curry and Oppo, 2005). However, a persistent, yet unexplained finding is that the upper $\sim$2000 m of the oceans were more $\delta^{13}$C positive during glacials (Matsumoto et al., 2002; Curry and Oppo, 2005). This mystery could now be reconciled with the storage of (negative) carbon on land. In fact, colder tropical and mid-latitudinal oceans should have been less stratified and have allowed the less negative $\delta^{13}$C surface signal to mix to greater depth, which is exactly what is observed. Other processes, such as changes in ocean circulation, the biological pump, and respiration, are probably able to explain the more negative deep ocean $\delta^{13}$C signal. More data will be necessary to robustly quantify the sign and amplitude of the “total” glacial $\delta^{13}$C changes.

Second, carbon isotopic measurements of atmospheric CO$_2$ trapped in ice cores are also in agreement with the notion of permafrost soils storing significant amounts
of (negative) carbon during glacials. As the measured LGM and Holocene $\delta^{13}CO_2$ values are almost identical (Köhler et al., 2010; Lourantou et al., 2010), this reasoning becomes evident when bearing in mind that the pure ocean’s temperature and salinity effect on isotopic fractionation would have caused atmospheric $\delta^{13}CO_2$ values to be $\sim$0.5‰ more negative during glacials. As this was not the case, we can infer that the temperature and salinity effect was offset by terrestrial carbon contributions.

Third, temporally higher-resolution isotope records over the last termination have been suggested to corroborate the ocean hypothesis. Negative carbon isotopic excursions in ice core $\delta^{13}CO_2$ (Lourantou et al., 2010) and many ocean records (Spero and Lea, 2002), as well as the simultaneous drop in $\Delta^{14}C$ (Broecker and Barker, 2007) have been interpreted as evidence of increased deep ocean up-welling and release of old, $\delta^{13}C$-depleted CO$_2$. We point out, however, that all these three isotope signals can also be explained with release of old, $\delta^{13}C$-negative carbon from thawing permafrost soils.

Fourth, and maybe most importantly, it has been impossible so far to find the supposedly large pool of “old” radiocarbon trapped in the glacial deep ocean, which would be required to corroborate the “ocean hypothesis” (Broecker and Barker, 2007; De Pol-Holz et al., 2010). Our record from the Tumara Paleosol Sequence, and the climate-soil carbon model of Zimov et al. (2009), support the idea that large amounts of carbon could have been stored terrestrially in expanding permafrost soils.

### 3.6 Annually integrated insolation forcing of permafrost dynamics

Having shown that permafrost carbon dynamics readily could have affected atmospheric CO$_2$ concentrations and global climate, we now discuss our TOC and deuterium records from the Tumara Paleosol Sequence in a temporal, global context. Major drops in atmospheric CO$_2$, for example at $\sim$190, 110 and 70 ka, coincided with the beginning of excess carbon storage (Fig. 3). Conversely, dramatic increases in atmospheric CO$_2$ during terminations (after $\sim$220, 130, and 15 ka) coincided with reduced
permafrost carbon storage. We suggest that low integrated annual insolation, which is controlled by the orbital parameter obliquity (Huybers, 2006), played a pivotal role in triggering the expansion of permafrost and increased carbon sequestration every \( \sim 40 \text{ ka} \), as for example at \( \sim 190, 110 \) and \( 70 \text{ ka} \) (Fig. 3). High obliquity, on the other hand, favored permafrost thawing, carbon release, and in some cases led to glacial terminations, for example at \( \sim 220, 130 \) and \( 15 \text{ ka} \).

Note that \( 65^\circ \text{N} \) July insolation, which is used in the classical Milankovitch theory of insolation forcing, only controls peak summer temperatures, but has no effect on integrated annual insolation. While peak summer temperatures are most relevant for enhanced methane emissions from arctic/subarctic wetlands and could well explain increased atmospheric methane levels at times of maximum \( 65^\circ \text{N} \) July insolation (Fig. 3), we argue that integrated annual insolation is the key parameter in triggering changes in permafrost extents.

3.7 Towards an overarching permafrost glacial hypothesis

One of the most intriguing observations is that not every obliquity maximum led to a glacial termination during the last \( \sim 200 \text{ ka} \) (Fig. 3). This has been different during the early Pleistocene (\( \sim 1–2 \text{ Ma} \)), which was characterized by \( \sim 40 \text{ ka} \) glacial-interglacial cycles (Raymo and Nisancioglu, 2003; Huybers, 2006) (Fig. 4). Glacial theories have long tried to explain the so-called mid-Pleistocene transition at \( \sim 1 \text{ Ma} \) from the “40 ka world” to longer, approximately 100 ka glacial cycles (e.g., Clark et al., 1999; Tziperman and Gildor, 2003). Our “permafrost glacial hypothesis”, which builds on integrated annual insolation forcing and resultant permafrost extents and terrestrial carbon sequestration, might readily unravel this mystery by providing a surprisingly simple explanation for “skipped obliquity cycles” (Huybers, 2007) (Fig. 4).

The overall long-term cooling trend during the Pleistocene resulted in expansion of permafrost areas as far south as \( \sim 45^\circ \text{N} \) latitudes (Fig. 1). Integrated annual insolation south of \( \sim 45^\circ \text{N} \) shows the opposite signal compared to north of \( \sim 45^\circ \text{N} \), because obliquity (the tilt of the Earth’ axis) basically controls the amount of insolation that reaches
high latitudes rather than the equator (see Supplement). Thus the permafrost dynamics become insensitive to changes in obliquity, once the Earth has cooled enough for permafrost areas to reach mid-latitudes. Permafrost dynamics should then become sensitive to the orbital parameter eccentricity (100 ka cycles), which controls annual integrated insolation at \( \sim 45^\circ \) latitudes and integrated global insolation. As a consequence, obliquity cycles (glacial terminations) were skipped during the Late Pleistocene, when they coincided with decreasing annual insolation at mid-latitudes due to eccentricity. Only the next obliquity maximum that coincided with increasing eccentricity kicked off the warming feedbacks related to thawing permafrost and CO\(_2\) releases. The result are glacial terminations every \( \sim 80 \) or 120 ka during the Late Pleistocene, i.e. exactly the observed succession of ice ages (Huybers, 2007) (Fig. 4).

4 Conclusions

Our study highlights that the high-latitude carbon pools have been hugely underestimated in terms of their size and particularly their temporal dynamics and their role for atmospheric CO\(_2\). Glacial-interglacial changes in terrestrial carbon storage far exceeded the observed changes in atmospheric CO\(_2\). This implies that contrary to the prevailing notion, the oceans had to act as carbon sources rather than sinks during glacials. Some ocean proxies might have to be re-evaluated in view of these findings, and carbon and climate models will have to take permafrost dynamics into account in order to provide more realistic simulations.

Major implications of our study also arise for our understanding of the role of high latitude regions for the carbon cycle today. Many studies have focused on postglacial peatland development since the Holocene (MacDonald et al., 2006; Tarnocai et al., 2009). We acknowledge that part of the total carbon inventory at high latitudes accumulated only since the Holocene, but (i) non-glaciated permafrost regions likely had very different carbon dynamics than formerly glaciated areas, in which many peatlands developed after deglaciation, and (ii) one needs to take into account the loss of
non-glaciated permafrost and peatland regions upon warming, for example after the last glacial maximum, as well as today. The carbon sequestration in the Holocene peatlands does not at all contradict the permafrost glacial hypothesis, but rather supplements it. The initial $\sim$7 ppm drop in atmospheric $\text{CO}_2$ during the Early Holocene has been interpreted to reflect a $\sim$110 Pg carbon sequestration in rapidly developing peatlands (MacDonald et al., 2006). We argue that carbon sequestration in peatlands would have contributed to initiate the next ice age, namely by starting the cooling trend and causing further sequestration of carbon in expanding permafrost soils and peatlands. This feedback would likely have continued during the Holocene, had there not been man-made global warming and increasing anthropogenic emissions (Ruddiman, 2003), reaching $\sim$5 Pg/year during the last century. To put this emission rate into context, the positive feedback due to thawing permafrost now is $\sim$1 Pg/year (Schuur et al., 2008; Tarnocai et al., 2009), while the natural rate of permafrost carbon release during the last deglaciation (1000 Pg over 5 ka) can be estimated to have been only $\sim$0.2 Pg/year. We are thus responsible for rapid and probably unprecedented rates of climate and environmental changes in the Arctic.

Supplementary material related to this article is available online at: http://www.clim-past-discuss.net/6/2199/2010/cpd-6-2199-2010-supplement.zip.

Acknowledgement. We thank J. Russell, E. Thomas and J. Zech for discussions and comments on the manuscript. This work has partially been funded by DFG grant ZE 154/52 to W.Z. and NSF grants 0902805 and 0816739 to Y.H. R.Z. gratefully acknowledges support through the SNF PostDoc fellowship for advanced researchers.
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Fig. 1. Geographic setting of the research site and distribution of permafrost soils. The location of the Tumara Paleosol Sequence is indicated by the red star. Mean annual temperatures (MAT in °C) (New et al., 2002) are draped over a hillshade model. The –5 °C isotherm (red dashed line) approximately marks the southward extent of continuous permafrost today (Tarnocai et al., 2009). Discontinuous permafrost exists at MAT < 0 °C, and the +5 °C isotherm (dashed blue line) indicates the approximate southward expansion of continuous permafrost during glacial conditions assuming a 10 °C temperature reduction.
Fig. 2. Stratigraphy and analytical results for the Tumara Paleosol Sequence. The stratigraphy illustrates the distinction between organic-rich, dark grey units (B and D) and bright brown organic-poor units (A, C and E). Calibrated radiocarbon ages (cal. ka BP) have been obtained for the upper part of the profile (* humic acids, others: humins, macrofossils from within the ice wedge), and infrared stimulated luminescence ages (IRSL) for the lower part (Zech et al., 2010a). TOC is the total organic carbon content, and $\delta D$ shows the deuterium/hydrogen isotope ratios measured on the $n$-alkanes C27, C29 and C31 (in blue, red and green, error bars show standard deviation of triplicate measurements, grey line is the average of all three alkanes). The correlation with marine isotope stages (MIS) is shown to the right.
Fig. 3. The Tumara Paleosol record in its paleoclimatic context. The TOC content and the mean δD values are compared to temperature proxies from Greenland (NGRIP δ¹⁸O) (NGRIP members, 2004) and Antarctica (δD Vostok) (Petit et al., 1999), and to atmospheric carbon dioxide (Petit et al., 1999; Ahn and Brook, 2008) and methane concentrations (Petit et al., 1999). The bottom plots show obliquity (solid line), 65°N July insolation (dashed line) and eccentricity. Blue dots mark cooling and atmospheric CO₂ drops, red dots glacial terminations, and orange dots “skipped obliquity cycles”. The triangles indicate tie points used to establish the age-depth model.
Fig. 4. Outline of the “permafrost glacial hypothesis” explaining the obliquity cycle skipping after the mid-Pleistocene transition. The Tumara Paleosol records (TOC and $\delta D$ mean) are compared to the marine $\delta^{18}O$ stack reflecting changes in global ice volume and temperatures (Lisiecki and Raymo, 2005), obliquity and eccentricity (Berger and Loutre, 1991). Blue lines mark prominent examples where obliquity cycles were skipped, red lines mark subsequent obliquity maxima that coincided with increasing eccentricity and that therefore triggered major terminations.