

# Carbon storage in permafrost and soils of the mammoth tundra-steppe biome: Role in the global carbon budget

N. S. Zimov,<sup>1</sup> S. A. Zimov,<sup>1</sup> A. E. Zimova,<sup>1</sup> G. M. Zimova,<sup>1</sup> V. I. Chuprynin,<sup>1</sup> and F. S. Chapin III<sup>2</sup>

Received 14 October 2008; revised 29 November 2008; accepted 9 December 2008; published 23 January 2009.

[1] During the Last Glacial Maximum (LGM), atmospheric CO<sub>2</sub> concentration was 80–100 ppmv lower than in pre-industrial times. At that time steppe-tundra was the most extensive biome on Earth. Some authors assume that C storage in that biome was very small, similar to today's deserts, and that the terrestrial carbon (C) reservoir increased at the Pleistocene-Holocene transition (PHT) by 400–1300 Gt. To estimate C storage in the entire steppe-tundra biome we used data of C storage in soils of this biome that persisted in permafrost of Siberia and Alaska and developed a model that describes C accumulation in soils and in permafrost. The model shows a slow but consistent C increase in soil when permafrost appears. At the PHT, C-rich frozen loess of Europe and South of Siberia thawed and lost most of its carbon. Soil carbon decreases as tundra-steppe changes to forest, steppes and tundra. As a result, over 1000 Gt C was released to the atmosphere, oceans, and other terrestrial ecosystems. The model results also show that restoring the tundra-steppe ecosystem would enhance soil C storage, while providing other important ecosystem services.

**Citation:** Zimov, N. S., S. A. Zimov, A. E. Zimova, G. M. Zimova, V. I. Chuprynin, and F. S. Chapin III (2009), Carbon storage in permafrost and soils of the mammoth tundra-steppe biome: Role in the global carbon budget, *Geophys. Res. Lett.*, 36, L02502, doi:10.1029/2008GL036332.

## 1. Introduction

[2] During the LGM steppe-tundra extended from present-day France to Canada, and from the arctic islands to China [Adams *et al.*, 1990]. According to some assessments, C storage in this biome was as small as 4–40 Gt [Friedlingstein *et al.*, 2003] and C content of Siberian soils was only 100 g m<sup>-2</sup> [Adams *et al.*, 1990]; these estimates assume zero C present in permafrost. Under these assumptions Holocene forests, tundra, and steppes, which replaced the mammoth ecosystem, must have absorbed from the oceans hundreds of gigatons of C [Sigman and Boyle, 2000], and only few doubt that [Zeng, 2003]. However, even in the high Arctic this LGM ecosystem was not a desert but a mammoth pasture [Schirmer *et al.*, 2002; Sher *et al.*, 2005]. The C-rich soils of this ecosystem have been preserved in permafrost of Siberia and Alaska, providing opportunities to measure directly their LGM C pools.

[3] The North Siberian plains are covered by an ice-rich permafrost that is tens of meters thick, known locally as yedoma. There is little humus but substantial labile C in yedoma. In continental areas, the C concentration of yedoma varies from 1–5% dry mass (maximum of 30%) [Zimov *et al.*, 2006a; Dutta *et al.*, 2006] and in wetter areas from 2–30% [Schirmer *et al.*, 2002]. The average C content of yedoma is ~40 kg m<sup>-3</sup> (from dry weight), equivalent to ~400–500 Gt for the North Siberian plains (1 × 10<sup>6</sup> km<sup>2</sup>) [Zimov *et al.*, 2006b].

[4] In permafrost soils without sedimentation C accumulates only within the active layer, to the depth of the maximum summer soil thaw. Carbon does not move into the permafrost. During periods of active loess (yedoma) accumulation, however, blowing dust accumulates on the ground surface, and the soil surface and upper boundary of permafrost shift upward, as the lower horizons of the active layer become incorporated into permafrost. Yedoma is therefore derived from only the lowest soil horizon of the mammoth ecosystem. To estimate total-C storage of mammoth biome soils we must know the C storage in its active-layer, which have not been preserved to the present. We must also know the C storage in loess soils that formed as yedoma in Europe and South Siberia before they thawed and lost their C in the Holocene. To solve these problems we developed a model that, describes the vertical C distribution in the soils and in permafrost, under various scenarios of sediment deposition.

## 2. Methods

[5] Carbon accumulation in the entire soil profile (one-box model) or in any soil horizon can be defined as the difference between soil C inputs (SCI) and outputs. Carbon inputs to a soil come from root mortality and from C transport from aboveground litter via organic C leaching and mixing by bioturbation or cryoturbation. Output depends mostly on decomposition (respiration). Organic matter consists of various compounds that differ in decomposition rate. We therefore divide it into different pools, for which we estimate the decomposition rate (percent per year) [Krinner *et al.*, 2005]. If we know the input and relative decomposition of organic compounds in each soil layer, we can use these relationships to calculate the vertical distribution of each of these compounds in the soil [Khvorostyanov *et al.*, 2008].

[6] Under conditions of sediment deposition when aeolian dust or river sediments is deposited on the soil surface, each horizon shifts downward relative to the ground surface at a rate that equals the soil accumulation rate. The differential equation describing the C dynamics therefore

<sup>1</sup>North-East Scientific Station, Pacific Institute for Geography, Russian Academy of Sciences, Cherskii, Russia.

<sup>2</sup>Institute of Arctic Biology, University of Alaska Fairbanks, Fairbanks, Alaska, USA.

receives an extra term (for detailed model description see auxiliary material)<sup>1</sup>:

$$\frac{\partial C_i(z, t)}{\partial t} + u(t) \frac{\partial C_i(z, t)}{\partial z} = f_i(z, t) - g_i(z, t) \cdot C_i(z, t)$$

where  $z$  is depth, m;  $t$  is time, yr;  $u(t)$  is soil accumulation rate, m yr<sup>-1</sup>;  $f_i(z, t)$  is soil C input (SCI) of the  $i$  compound, kg m<sup>-3</sup> yr<sup>-1</sup>;  $g_i(z, t)$  is decomposition rate (DR) of the  $i$  compound, yr<sup>-1</sup>; and  $C_i(z, t)$  is C concentration of the  $i$  compound, kg m<sup>-3</sup>.<sup>1</sup>

[7] Figure 1 shows the calculated vertical distribution of organic C in soils and permafrost for different vertical distributions of SCI and DR, for scenarios of no sedimentation, and different accumulation rates. For all scenarios, SCI is divided into 3 components: “very fast” (sugar, protein), 30% of total SCI; “fast” (labile: cellulose, hemicellulose), 45%; and “slow” (non-labile: lignin), 25% [Chapin *et al.*, 2002]. The quantity of the “very fast” component in soils is very small, so we do not show it on the graphs. We also add a “very slow component” that we conditionally call humus. It is absent in plant remains but is produced by microbial turnover during decomposition. We assume that the annual production of humus is 10% of the annual decomposition of the slow component.

[8] In all scenarios, in all soil layers, the DR of the slow component is assumed to be 10-fold less than the fast [Chapin *et al.*, 2002]. Decomposition of the humus is assumed to be 200-fold less than the fast component. We assume that total SCI is mostly determined by vegetation productivity and that its vertical distribution is sensitive to moisture regime. Under wet conditions, roots do not need to grow deeply for water, so most roots grow in the top soil layers, where there is high nutrient availability from decomposing litter. Under dry conditions, the roots penetrate more deeply. In the case of well-drained, well-aerated soils, soil temperature defines DR. Average annual soil temperature does not change substantially with depth in any climate. However, the seasonal amplitude of soil temperature is greatest at the surface. Decomposition depends nonlinearly on temperature, so DR will be greater at the surface than at depth. In the temperate zone, this difference is not very large because during a summer maximum DR is by the surface but during winter top soil layer is frozen while lower soil layers continue to respire.

[9] Permafrost causes a qualitative change in this situation. When permafrost is present, DR is maximal at the surface and decreases rapidly with depth, reaching values close to zero at the roof of the permafrost. Permafrost also significantly alters the soil drainage: lower active layer are saturated in moist climates. These temperature and moisture profiles lead to a decline in DR in lower horizons. Therefore, any organic input there (e.g., from the leaching of dissolved organic C in water) will lead to C accumulation [Karavaeva and Targulian, 1960; Tarnocai, 2004]. This explains the unique property of many permafrost soils—their deeper horizons contain more C than upper horizons [Karavaeva and Targulian, 1960; Tarnocai, 2004; Michaelson *et al.*, 2004; Bockheim, 2007].

[10] We show here calculations for 3 temperature zones: (1) temperate zone (A), with total SCI of 0.4 kg/m<sup>2</sup> yr and DR on the surface 12%/yr; (2) cold zone (B), where both SCI and DR are half the temperate-zone rate; and (3) extra cold zone (C), where SCI and DR are 4 times lower than for the temperate zone (for detailed values of all scenarios see Table S2 in auxiliary material).

[11] For all 3 temperature zones we examine 4 variants of typical SCI distribution with depth corresponding to different soil moisture regimes (Figure 1 and Figure S2).

[12] 1. Dry. Unproductive dry steppe corresponds to this variant. Water is a limiting resource. Therefore, we assume that total SCI here (area of SCI under the curve, Figure 1) is half that in variants 2–4. Lower horizons are always dry, and roots do not penetrate to depth. This pattern is found on the south slopes of loess steppe in northern Siberia in a region where potential evapotranspiration is 2 to 3 times the annual precipitation.

[13] 2. Dry-wet. This is meadow steppe. Roots penetrate to the maximum depth. All soil profiles are periodically moistened by precipitation and dried by plants.

[14] 3. Wet-dry. This is forest-steppe or tundra-steppe. The roots only occasionally penetrate to deep horizons. This and the previous scenarios are not typical of modern North Siberian landscapes.

[15] 4. Wet. This is a boreal forest or tundra. Very few roots penetrate to deep horizons. This type of distribution on permafrost can occur even in arid climates. Unproductive vegetation consisting of plants without roots (mosses and lichens) on poor soils is not able to evaporate all precipitation and dry out the soil [Zimov *et al.*, 1995].

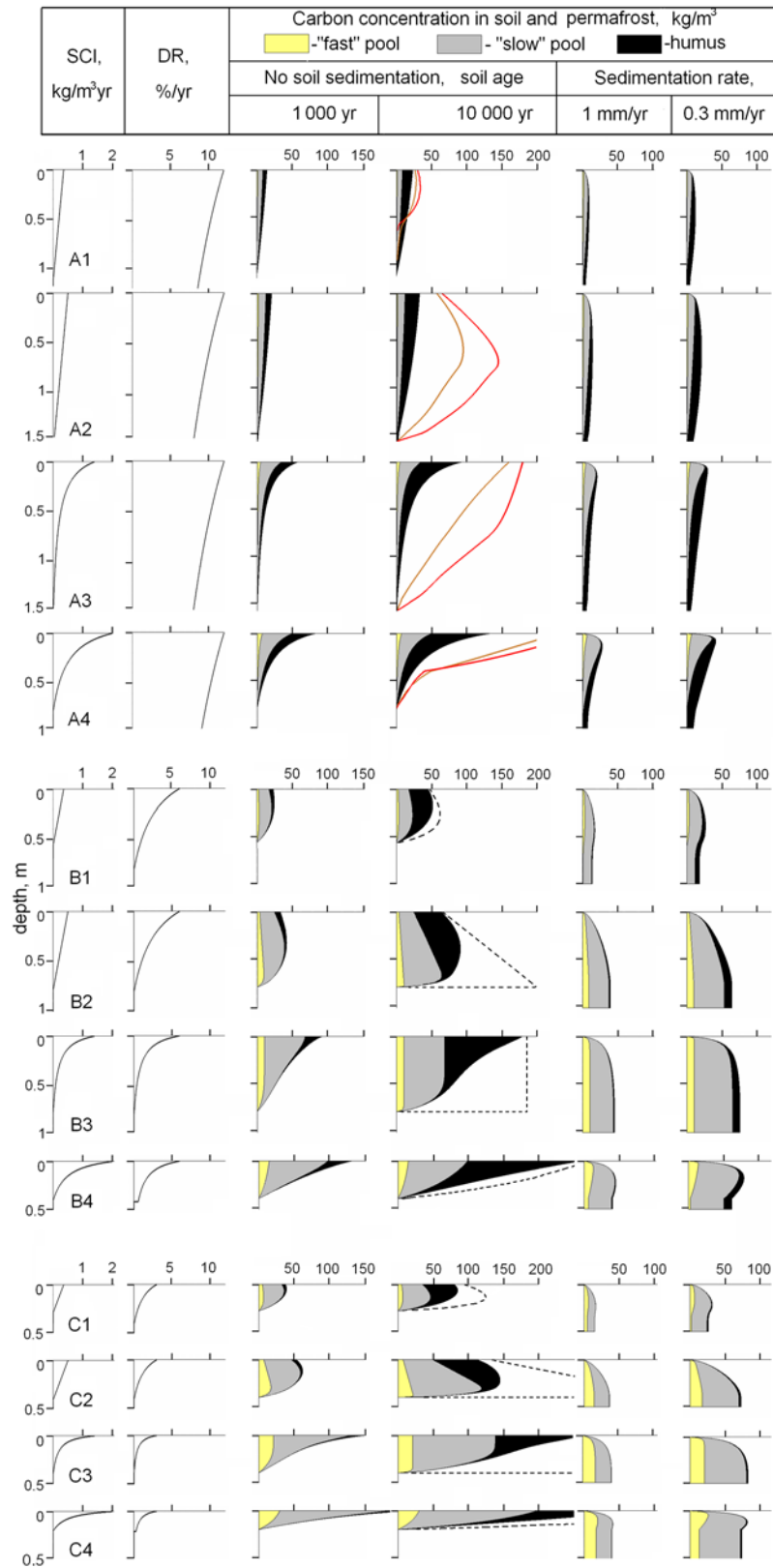
[16] For all 4 temperate-zone scenarios (A1–A4) we assumed same DR vertical profile because at good drainage DR depends only on temperature. In cold and extra-cold scenarios DR profiles of dry and dry-wet scenarios (B1-2 and C1-2) were taken identical. For wet and wet-dry scenarios (B3-4, C3-4) the DR profile is assumed to be more convex, because lower soil horizons are often saturated.

[17] For each temperature zone we also examined a one-box model (Figure 2) in which we assume parameters that are the same as when SCI and DR show no vertical variation. We initiated all simulations (without sedimentation) with soil that contained no organic C (soil age equal 0). Respiration increased through time as soil C accumulated until a point at which it became equal to C input (equilibrium state). After that, soil C concentration did not increase. For the fast pool, a state close to equilibrium required tens of years; for humus –thousands of years.

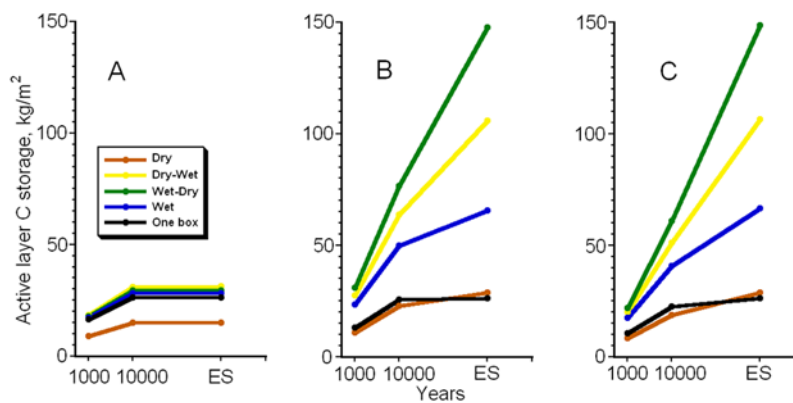
### 3. Results and Discussion

[18] The C content derived from the one-box model did not change substantially with climate cooling (Figure 2). However, in our model the presence of permafrost substantially increased C storage in the soil. At equilibrium, when C content in the model reaches its maximum, there was 3–5.5 times more C than in the one-box model. Under extra-cold conditions, the C concentration was higher than under cold conditions (Figure 1), but C storage at equilibrium was the same (Figure 2). Decomposition in cold soils was so low that peat accumulated at the soil surface and even in lower soil horizons if conditions were aerobic,

<sup>1</sup>Auxiliary materials are available in the HTML. doi:10.1029/2008GL036332.



**Figure 1.** Vertical soil profiles of C input (SCI), decomposition rate (DR), various carbon fractions content in soils and permafrost. A, temperate zone; B, cold zone; and C, extra cold zone; 1, dry conditions; 2, dry-wet; 3, wet-dry; and 4, wet. Dotted line is maximum possible C content in soils. Red and brown lines are possible C storage in European soils at the LGM.



**Figure 2.** Time course of active-layer soil C storage at various moisture regimes (see Figure 1) and for a 1-box model: A, temperate zone; B, cold; and C, extra cold. ES is equilibrium state (maximum possible C content in this soil at assumed conditions).

although the accumulation was very slow. Therefore, C storage in soils of the extra-cold zone was less than in soils of the same age in the cold zone. They had very little humus and much labile organic material. (The low C content in some modern northern soils reflects their relative youth; they are a sink of C.) In yedoma areas where sedimentation rate is  $1 \text{ mm yr}^{-1}$ , organic material remains within the active layer for several hundred years at most. Therefore, soils that enter the permafrost are very young. The C concentration there is less than in the active layer with no sedimentation. Total C concentration in permafrost increases as sedimentation rate declines.

[19] Our model calculation of C distribution matches well with the content and distribution of C and its fractions in soils of the temperate zone: Total C storage is  $30 \text{ kg/m}^2$  at most; the maximum C concentrations are at the surface; and the humus fraction dominates. On the other hand, for cold conditions and a soil sedimentation rate of  $1 \text{ mm/yr}$ , our model predicted C presence in permafrost  $\sim 40 \text{ kg/m}^3$  with very low humus content. That is very typical for massive yedoma sediments. Given the correspondence of model results to observed data, we use this model for paleoanalysis.

[20] Yedoma is characterized by an abundance of thin roots and a high moisture content [Sher *et al.*, 2005; Zimov *et al.*, 2006a]. Their well-preserved state in permafrost indicates that they penetrated to the deepest horizons, indicating favorable water and aerobic conditions in these lower soil horizons. Dry yedoma does not occur. On the other hand, methane occurrence in permafrost, which is indicative of anaerobic conditions, is usually absent in yedoma [Rivkina *et al.*, 2006]. All these observations indicate that the entire profile of tundra-steppe soils is periodically dried out by plants and moistened again (scenarios 2, 3 and rarely 4). Under dry conditions, water released from thawing soil is a source of water for plants. In summer grass roots grow rapidly downward to compete for water as the frozen layer retreats.

[21] In Siberia, precipitation in the yedoma-occupied territory is only 150–200 mm, and the radiative aridity index (potential evapotranspiration relative to precipitation) is 1.5 to 3 [Zimov *et al.*, 1995]. It has been assumed that there was less precipitation in Siberia during the LGM [Schirrmeister *et al.*, 2002; Sher *et al.*, 2005]. To the southwest (in Europe), conditions were warmer with more

precipitation (200–250 mm in the Eastern Europe in the LGM [Morozova *et al.*, 1998] therefore SCI and DR increased in parallel. Consequently, C concentration in frozen loess of Europe should have been similar to amounts currently observed in frozen yedoma in the north of Siberia (in the zones B and C (Figure 1) C concentration in the permafrost is approximately the same). The average C content of yedoma in northern Siberia ( $\sim 40 \text{ kg m}^{-3}$ ) has been estimated from samples that combine the thick sediment layers that had an average sedimentation rate  $\sim 1 \text{ mm yr}^{-1}$  [Schirrmeister *et al.*, 2002; Zimov *et al.*, 2006a]. However, the average rate of loess sedimentation was significantly less in Europe:  $0.07\text{--}0.4 \text{ mm yr}^{-1}$  [Morozova *et al.*, 1998]. The lower sedimentation rate should have led to a higher C content there ( $\sim 75 \text{ kg m}^{-3}$ ), with a humus content of only  $\sim 10 \text{ kg m}^{-3}$  (scenarios B2, B3) This appears realistic, knowing that today this loess still contains  $1.5\text{--}4 \text{ kg C m}^{-3}$  humus [Morozova *et al.*, 1998]. The high porosity of these soils indicates their former highly labile organic content. Taking this into account, our earlier estimate of the C emission from loess thawed during the PHT ( $\sim 500 \text{ Gt}$ ), where we assumed an average C content of  $40 \text{ kg/m}^3$  [Zimov *et al.*, 2006b], should be increased by 50–100%.

[22] At the PHT, about  $10 \times 10^6 \text{ km}^2$  of the steppe-tundra ecosystem with underlying permafrost changed to forest and steppe [Adams *et al.*, 1990]. Scenarios A1–A4 show C storage in these ecosystems. (We did not take into account in our model the biomass losses in upper forest soil horizons resulting from fires (surface soil begins to combust at  $100 \text{ kg C m}^{-3}$ ). This correction could reduce total C storage to a value approximately equal to aboveground biomass storage in the forest). To get C storage in the soils of LGM we need to make calculations starting with the beginning of the glacial period.

[23] As the climate cooled with the onset of glaciation, the lower horizons of soil became incorporated into permafrost even without sedimentation, reducing the depth of the active layer. We assumed in our modeling that the soil profiles were initially the same as in zone A on Figure 1. Later, permafrost and a 1.6 m active layer appeared. The active layer decreased linearly over 10 000 years to 0.8 m. SCI and DR decreased correspondingly. Final profiles are shown on Figure 1 by brown lines. Maximum C storage was



114 kg m<sup>-2</sup> (A3). Red lines show C storage under the same conditions, if we assume a slower cooling over 100 000 years. Maximum C storage is 181 kg m<sup>-2</sup> (A3). The values are 6-fold greater than was previously estimated for the active layer of tundra-steppe soils [Zimov *et al.*, 2006b]. At the PHT, we assume that the temperate climate returned rapidly, and permafrost disappeared. C storage in these profiles decreased by 36 and 46 kg m<sup>-2</sup> within 100 years. Details on this and other scenarios are presented in the auxiliary material.

[24] Thus, C accumulated very slowly under cold (glacial) conditions, but C release occurred quickly with the return to Holocene warm conditions. As a minimum, tens of kg C m<sup>2</sup> were released from steppe-tundra soils after permafrost thawed. Taking into consideration frozen loess, this C release at the Pleistocene-Holocene boundary was greater than 1000 Gt. It is unlikely that other terrestrial ecosystems (e.g., expanding tropical forests [Adams *et al.*, 1990]) could have absorbed this amount of C. We therefore suggest that the ocean consumed several hundreds of Gt C.

[25] Soil organic C has low  $\delta^{13}\text{C}$ , so it may be expected that C release from soil and permafrost would decrease  $\delta^{13}\text{C}$  in the oceanic C reservoir at the PHT. However, observations suggest the opposite. At that time the  $\delta^{13}\text{C}$  in marine dissolved inorganic C (DIC), recorded in shells of benthic foraminifera, increased by 0.35‰. This fact is usually taken as a strong evidence of transfer of 400–700 Gt of isotopically light ocean C into the terrestrial biosphere [Sigman and Boyle, 2000]. However, both the  $\delta^{13}\text{C}$  change [Spero *et al.*, 1997] and its interpretation [Brovkin *et al.*, 2002] can be debated. The size and isotopic composition of the marine reservoir of organic C are similar to those on land, so, if the terrestrial reservoir released the same amount of C as accumulated in the marine organic-C reservoir, the ocean  $\delta^{13}\text{C}$  would not change substantially [Brovkin *et al.*, 2002]. So our scenario is possible only if there was a decline in the ocean organic C reservoir during glacial times and an increase at the PHT. Recent reanalysis of data from marine sediment cores provides information to test this hypothesis [Kohfeld *et al.*, 2005]. A mapping of these data led Kohfeld *et al.* [2005] to conclude that during the middle of the last glaciation biological productivity and C export to ocean sediments were substantially reduced in all oceans. This means that the decline in atmospheric CO<sub>2</sub> concentration by 50 ppm (relative to the interglacial period) was accompanied by a decrease in ocean productivity [Kohfeld *et al.*, 2005]. This is consistent with our hypothesis. However, Kohfeld *et al.* [2005] suggest that, during the LGM, ocean productivity was higher than during the Holocene [Kohfeld *et al.*, 2005, Figure 2c]. This map is difficult to interpret visually because cores of increasing and decreasing productivity frequently coincided. We present auxiliary material provided by Kohfeld *et al.* [2005] in Table S2. These data indicate that reliable productivity increases during the LGM were recorded only for the well studied and relatively small, equatorial Atlantic: increased productivity recorded in 48 cores and decreased in 15, whereas in the larger Pacific Ocean productivity was lower in 43 cores and higher in 19. In summary, the data of Kohfeld *et al.* [2005] do not contradict our hypothesis that ocean organic C reservoir was less in the glacial periods than during the Holocene.

There are also other processes such as changes in ocean ventilation that could have altered marine  $\delta^{13}\text{C}$ .

[26] Our conclusion that terrestrial C decreased at the PHT differs from previous assumptions, but is based on direct measurements of C in Yedoma. Yedoma territory in the LGM was the least productive region. Yedoma is characterized by very fast rates of accumulation but nevertheless, it has a high C content. Other soils of the steppe-tundra biome most likely contained at least this much C.

[27] Our model could also be used to refine the projections of future C losses from northern soils with climate warming. The scenarios we present suggest a rapid release of tens of kg C m<sup>-2</sup> when permafrost disappears. The model also shows that conditions could be modified to cause northern soils to accumulate C. The north of the Eastern Siberia is an arid region. However, unproductive mossy forest and tundra dominates there, causing soil saturation. As climate warms, because of the melting of ground ice wedges and erosion, these ecosystems will be destroyed. If they are replaced by productive grasslands with an abundance of herbivorous animals (scenarios B2 and B3), the high albedo of grass-dominated systems, and the reduced winter insulation of snow trampled by mammals would reduce summer energy input and increase winter heat loss [Zimov, 2005]. If these effects on energy exchange are strong enough, this could reduce permafrost temperature, reduce methane emission to the atmosphere, allowing accumulation tens of kg C m<sup>-2</sup>, in the active layer, where C is protected from fires (shift from B4 scenario to B3; see auxiliary material for details). Given the political challenges of sharply reducing anthropogenic CO<sub>2</sub> emissions to the atmosphere, exploration of ecological processes that sequester C warrant careful consideration.

[28] **Acknowledgments.** This work was supported by the National Science Foundation under grant number NSF-OPP-0732944 (the Polarix Project, [www.thepolarisproject.org](http://www.thepolarisproject.org)).

## References

- Adams, J. M., H. Faure, L. Faure-Denard, J. M. McGlade, and F. I. Woodward (1990), Increases in terrestrial carbon storage from the Last Glacial Maximum to the present, *Nature*, **348**, 711–714.
- Bockheim, J. G. (2007), Importance of cryoturbation in redistributing organic carbon in permafrost-affected soils, *Soil Sci. Soc. Am. J.*, **71**, 1335–1342.
- Brovkin, V., M. Hofmann, J. Bendtsen, and A. Ganopolski (2002), Ocean biology could control atmospheric  $\delta^{13}\text{C}$  during glacial-interglacial cycle, *Geochim. Geophys. Geosyst.*, **3**(5), 1027, doi:10.1029/2001GC000270.
- Chapin, F. S., III, P. A. Matson, and H. A. Mooney (2002), *Principles of Terrestrial Ecosystem Ecology*, Springer, New York.
- Dutta, K., E. A. G. Schuur, J. C. Neff, and S. A. Zimov (2006), Potential carbon release from permafrost soils of northeastern Siberia, *Global Change Biol.*, **12**, 2336–2351.
- Friedlingstein, P., J.-L. Dufresne, P. M. Cox, and P. Rayner (2003), How positive is the feedback between climate change and the carbon cycle?, *Tellus, Ser. B*, **55**, 692–700.
- Karavaeva, N. A., and V. O. Targulian (1960), Osobennosti raspredeleniya organicheskogo veshchestva v pochvakh tundr Vostochnoi Sibiri, *Pochvo-vedenie*, **12**, 36–45.
- Khvorostyanov, D. V., G. Krinner, P. Ciais, M. Heimann, and S. A. Zimov (2008), Vulnerability of permafrost carbon to global warming. Part I: Model description and role of heat generated by organic matter decomposition, *Tellus, Ser. B*, **60**, 250–264.
- Kohfeld, K. E., C. Le Quéré, S. P. Harrison, and R. F. Anderson (2005), Role of marine biology in glacial-interglacial CO<sub>2</sub> cycles, *Science*, **308**, 74–78.
- Krinner, G., N. Viovy, N. de Noblet-Ducoudré, J. Ogée, J. Polcher, P. Friedlingstein, P. Ciais, S. Sitch, and I. C. Prentice (2005), A dynamic global vegetation model for studies of the coupled atmosphere-biosphere

- system, *Global Biogeochem. Cycles*, **19**, GB1015, doi:10.1029/2003GB002199.
- Michaelson, G. J., X. Y. Dai, and C.-L. Ping (2004), Organic matter and bioactivity in cryosols of Arctic Alaska, in *Cryosols: Permafrost-Affected Soils*, edited by J. M. Kimble, pp. 463–477, Springer, Berlin.
- Morozova, T., A. A. Velichko, and K. G. Dlussky (1998), Organic carbon content in the late Pleistocene and Holocene fossil soils (reconstruction for eastern Europe), *Global Planet. Change*, **16–17**, 131–151.
- Rivkina, E. M., G. N. Kraev, K. V. Krivushin, K. S. Laurinavichus, D. G. Fyodorov-Davydov, A. L. Kholodov, V. A. Shcherbakova, and D. A. Gilichinsky (2006), Methane in permafrost of northeastern Arctic, *Kriosfera Zemli*, **10**, 23–41.
- Schirmmeister, L., C. Siegert, T. Kuznetsova, S. Kuzmina, A. Andreev, F. Kienast, H. Meyer, and A. Bobrov (2002), Paleoenvironmental and paleoclimatic records from permafrost deposits in the Arctic region of northern Siberia, *Quat. Int.*, **89**, 97–118.
- Sher, A. V., S. A. Kuzmina, T. V. Kuznetsova, and L. D. Sulerzhitsky (2005), New insights into the Weichselian environment and climate of the East Siberian Arctic, derived from fossil insects, plants, and mammals, *Quat. Sci. Rev.*, **24**, 533–569.
- Sigman, D. M., and E. A. Boyle (2000), Glacial/interglacial variations in atmospheric carbon dioxide, *Nature*, **407**, 859–869.
- Spero, H. J., J. Bijma, D. W. Lea, and B. E. Bemis (1997), Effect of seawater carbonate concentration on foraminiferal carbon and oxygen isotopes, *Nature*, **390**, 497–500.
- Tarnocai, C. (2004), Cryosols of Arctic Canada, in *Cryosols: Permafrost-Affected Soils*, edited by J. M. Kimble, pp. 95–117, Springer, Berlin.
- Zeng, N. (2003), Glacial-interglacial atmospheric CO<sub>2</sub> change: The glacial burial hypothesis, *Adv. Atmos. Sci.*, **20**, 677–693.
- Zimov, S. A. (2005), Pleistocene park: Return of the mammoths ecosystem, *Science*, **308**, 796–798.
- Zimov, S. A., V. I. Chuprynin, A. P. Oreshko, F. S. Chapin III, J. F. Reynolds, and M. C. Chapin (1995), Steppe-tundra transition: An herbivore-driven biome shift at the end of the Pleistocene, *Am. Nat.*, **146**, 765–794.
- Zimov, S. A., S. P. Davydov, G. M. Zimova, A. I. Davydova, E. A. G. Schuur, K. Dutta, and F. S. Chapin III (2006a), Permafrost carbon: Stock and decomposability of a globally significant carbon pool, *Geophys. Res. Lett.*, **33**, L20502, doi:10.1029/2006GL027484.
- Zimov, S. A., E. A. G. Schuur, and F. S. Chapin III (2006b), Permafrost and the global carbon budget, *Science*, **312**, 1612–1613.

F. S. Chapin III, Institute of Arctic Biology, University of Alaska Fairbanks, Fairbanks, AK 99775, USA.

V. I. Chuprynin, N. S. Zimov, S. A. Zimov, A. E. Zimova, and G. M. Zimova, North-East Scientific Station, Pacific Institute for Geography, Russian Academy of Sciences, Cherskii, 678830 Russia. (nzimov@mail.ru)