requires detailed information on the statespecific collision rate and ortho-to-para conversions of H_2 , H_3^+ , and isotopomers. Such information is being provided by means of an ingenious temperature-variable cryogenic ion trap (23)

The Discussion Meeting contained many other exciting reports on H_3^+ and its deuterated species, as well as the related species, H_3 , H_3^- , H_3^{++} , H_5^+ , H_3^+ (H_2)_n, etc. (24). With the 100th anniversary of the discovery of H_3^+ only 5 years away and research forging ahead on many fronts, it is likely that a centennial Discussion Meeting on this most interesting and important molecular ion and its relatives will be timely.

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10.1126/science.1126279

CLIMATE CHANGE

Permafrost and the Global Carbon Budget

Sergey A. Zimov, Edward A. G. Schuur, F. Stuart Chapin III

he carbon content of Earth's atmosphere has increased from ~360 gigatons (Gt)—mainly as CO_2 —during the last glacial maximum to ~560 Gt during preindustrial times and ~730 Gt today. These changes reflect redistributions among the main global carbon reservoirs. The largest such reservoir is the ocean (40,000 Gt, of which 2500 Gt is organic carbon), followed by soils (1500 Gt) and vegetation (650 Gt). There is also a large geological reservoir, from which ~6.5 Gt of carbon are released annually to the atmosphere by burning fossil fuels.

Permafrost (permanently frozen ground) is an additional large carbon reservoir that is rarely incorporated into analyses of changes in global carbon reservoirs. Here we illustrate the importance of permafrost carbon in the global carbon budget by describing the past and potential future dynamics of frozen loess (windblown dust, termed yedoma in Siberia) that was deposited during the glacial age, covering more than 1 million km² of the north plains of Siberia and Central Alaska to an average depth of ~25 m.

The frozen yedoma represents relict soils of the mammoth steppe-tundra ecosystem that occupied this territory during glacial times (1). As windblown or river-borne materials accumulated on the soil surface, the bottom of the previously thawed soil layer became incorporated into permafrost. These sediments contain little of the humus that characterizes modern ecosystems of the region, but they comprise large amounts of grass roots (see the figure) and animal bones, resulting in a carbon content that is much higher than is typical of most thawed mineral soils. Frozen yedoma deposits across Siberia and Alaska typically have average carbon contents from 2% to 5%—roughly 10 to 30 times the amount of carbon generally found in deep, nonpermafrost mineral soils.

Using an overall average carbon concentration for yedoma of ~2.6%, as well as the typical bulk density, average thickness, and icewedge content of the yedoma, we estimate the carbon reservoir in frozen yedoma to be ~500 Gt (2). Another ~400 Gt of carbon are contained in nonyedoma permafrost (excluding peatlands) (3), and 50 to 70 Gt reside in the peatbogs of western Siberia (4). These preliminary estimates indicate that permafrost is a large carbon reservoir, intermediate in size between those of vegetation and soils.

Our laboratory incubations and field experiments show that the organic matter in yedoma decomposes quickly when thawed, resulting in respiration rates of initially 10 to 40 g of carbon per m³ per day, and then 0.5 to 5 g of carbon per m³ per day over several years. These rates are similar to those of productive northern grassland soils. If these rates are sustained in the long term, as field observations suggest, then most carbon in recently thawed yedoma will be released within a century—a striking contrast to the preservation of Climate warming will thaw permafrost, releasing trapped carbon from this highlatitude reservoir and further exacerbating global warming.

carbon for tens of thousands of years when frozen in permafrost.

Some local thawing of yedoma occurs independently of climate change. When permafrost ice wedges thaw, the ground subsides (thermokarst), forming lakes. The abundant thermokarst lakes on yedoma territory migrate across the plains as thawing and subsidence occur along their margins. During the Holocene (the past 10,000 years), about half of the yedoma thawed beneath these migratory lakes and then refroze when the lakes had moved on.

The yedoma carbon beneath the thermokarst lakes is decomposed by microbes under anaerobic conditions, producing methane that is released to the atmosphere primarily by bubbling (5). Near eroding lake shores, methane bubbling is so high that channels through the lake ice remain open all winter. During a thaw/freeze cycle associated with lake migration, ~30% of yedoma carbon is decomposed by microbes and converted to methane. As a potent greenhouse gas, this methane contributes to climate warming.

In response to climate warming, permafrost sediments have already begun to thaw (6), with extreme projections that almost all yedoma will thaw by the end of the 21st century (7). What would happen to the carbon derived from permafrost if high-latitude warming continues?

The unique isotopic signature of permafrost carbon provides clues from past warming episodes, such as the transition from the last glacial maximum to the Holocene. The $^{13}C/^{12}C$ isotope ratio of the permafrost reservoir is similar to that of soil, vegetation, and

S. A. Zimov is at the North-East Scientific Station, Pacific Institute for Geography, Russian Academy of Sciences, Cherskii, Republic of Sakha 678830, Russia. E-mail: sazimov@cher.sakha.ru E. A. G. Schuur is in the Department of Botany, University of Florida, Gainesville, FL 32611, USA. F. S. Chapin III is at the Institute of Arctic Biology, University of Alaska, Fairbanks, AK 99775–7000, USA.

marine biota. Unlike these reservoirs, however, permafrost carbon is depleted in radiocarbon (14 C). Methane, CO₂, and dissolved organic carbon released from thawing yedoma have a radiocarbon age reflecting the time when the yedoma was formed in the glacial age, differentiating the permafrost carbon signal from emissions from other reservoirs that have a modern radiocarbon age.

For example, the release of a large pool of radiocarbon-depleted carbon from permafrost could have contributed to declines in atmospheric km²) of steppe-tundra had a carbon content typical of polar deserts (4 to 40 Gt) (13, 14). The assumed soil carbon content for steppe-tundra in Siberia was only 0.1 kg m⁻² (13).

We can now provide a more accurate estimate of the carbon content of the steppe-tundra based on direct measurements. The carbon content of lowland steppe-tundra soils in Siberia and Alaska is ~2.6% with an active-layer depth of about 1 m, yielding ~42 kg of carbon per m². In mountains, the carbon content is about 50% less, giving an average carbon content for the steppe-

 CO_2 concentration at the last glacial maximum could also explain the reduced ${}^{13}C/{}^{12}C$ ratio of foraminifera (17). Given this estimate of permafrost carbon storage on land, the redistribution of carbon during glacial periods is a fertile area for reassessment.

Permafrost is a globally significant carbon reservoir that responds to climate change in a unique and very simple way: With warming, its spatial extent declines, causing rapid carbon loss; with cooling, the permafrost reservoir refills slowly, a dynamic that mir-



Ancient soils. (Left) Exposed carbon-rich soils from the mammoth steppe-tundra along the Kolyma River in Siberia. The soils are 53 m thick; massive ice wedges are visible. (Right) Soil close-up showing 30,000-year-old grass roots preserved in the permafrost.

radiocarbon during two strong warming events that occurred during the last deglaciation. These radiocarbon changes have previously been attributed to an assumed increase in deep- and midocean venting, because no terrestrial pool that could readily release ancient carbon (such as permafrost carbon) was included in the analysis (δ).

Carbon loss from permafrost may also have contributed to past changes in atmospheric CO₂ concentrations. During the last glacial maximum, permafrost extended south to 45°N in Europe and to 40°N in North America. About 4 m of yedoma-like soils accumulated across 3 million km² in the steppe-tundra ecosystems of Europe and south of West Siberia toward the end of the glacial age and thawed in the early Holocene (9, 10). If this frozen loess initially had a carbon concentration similar to the average for yedoma (2.6% C) and decreased to the carbon concentration of the current soils (0.15%)C), it would have released about 500 Gt of permafrost carbon at the beginning of the Holocene. Additional carbon was presumably released by thawing of nonloess permafrost (river-borne, slope, and glacial sediments).

Most researchers assume that the terrestrial carbon reservoir declined by 300 to 700 Gt at the last glacial maximum as a result of ice sheet formation and a decline in forest area. This terrestrial carbon was assumed to have been transferred to the oceans (11). However, these estimates ignore the soils and peat buried in frozen moraines beneath glaciers (380 Gt) (12) and assume that the broad expanses (~24 million

ZIMOV

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tundra biome of \sim 30 kg per m² and a total carbon content of \sim 720 Gt. Taking into account frozen loess (500 Gt), steppe-tundra soils (720 Gt), sediments beneath ice sheets (380 Gt), and other frozen sediments, we hypothesize that the total terrestrial carbon reservoir did not decrease in glacial times but instead may have even absorbed several hundred gigatons of carbon from the atmosphere and ocean.

The decline in the ¹³C/¹²C ratio in marine dissolved inorganic carbon, recorded in shells of foraminifera, in glacial times is usually taken as strong evidence of transfer of terrestrial carbon to the ocean (11). However, the size and isotopic composition of the marine reservoir of organic carbon are similar to those on land (15), making it difficult to identify changes in the relative sizes of marine and terrestrial organic reservoirs. A decline in marine productivity (perhaps associated with reduced vertical mixing and reduced illumination under ice) might lead to a net release of depleted ¹³C from marine organic carbon reservoirs that could instead have caused the decreased foraminifera isotope ratio. Recent reanalysis of data from marine sediment cores shows that biological productivity and carbon export to ocean sediments were substantially reduced at the middle of the last glacial cycle in all oceans. At the last glacial maximum, biological productivity in the Atlantic Ocean increased, but in the much larger Pacific Ocean it decreased (16). Independent of carbon transfers between land and ocean, the reduction in alkalinity associated with the lower atmospheric

rors the past atmospheric record of CO_2 . In a warmer climate, permafrost carbon is thus likely to become part of more actively cycling carbon reservoirs. Factors inducing high-latitude climate warming should be mitigated to minimize the risk of a potentially large carbon release that would further increase climate warming.

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10.1126/science.1128908

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