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Vulnerability of Permafrost Carbon to Climate Change: Implications for the Global Carbon Cycle

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Thawing permafrost and the resulting microbial decomposition of previously frozen organic carbon (C) is one of the most significant potential feedbacks from terrestrial ecosystems to the atmosphere in a changing climate. In this article we present an overview of the global permafrost C pool and of the processes that might transfer this C into the atmosphere, as well as the associated ecosystem changes that occur with thawing. We show that accounting for C stored deep in the permafrost more than doubles previous high-latitude inventory estimates, with this new estimate equivalent to twice the atmospheric C pool. The thawing of permafrost with warming occurs both gradually and catastrophically, exposing organic C to microbial decomposition. Other aspects of ecosystem dynamics can be altered by climate change along with thawing permafrost, such as growing season length, plant growth rates and species composition, and ecosystem energy exchange. However, these processes do not appear to be able to compensate for C release from thawing permafrost, making it likely that the net effect of widespread permafrost thawing will be a positive feedback to a warming climate.

Keywords: permafrost, carbon, climate change, global carbon cycle, terrestrial ecosystem feedback

Humans alter the global cycle of carbon (C) by burning fossil fuels and modifying the land surface. The addition of billions of tons of C greenhouse gases to the atmosphere is changing its heat-trapping capacity, which, in turn, is changing Earth's climate (IPCC 2007). Although much of the modern increase in the atmospheric C pool results from human activities, the future trajectory of the atmosphere also depends on the response of terrestrial and ocean systems to climate change (Friedlingstein et al. 2006). Natural fluxes of C in and out of terrestrial and ocean reservoirs are an order of magnitude larger annually than the perturbation from fossil fuels and land-use change. Accordingly, relatively small changes in ocean dissolution and biological C cycling processes, such as photosynthesis and decomposition, can have large impacts on the size of the atmospheric C pool (IPCC 2007). The responses of these processes to changes in temperature, precipitation, carbon dioxide (CO_2) levels, and nitrogen (N) deposition have therefore received significant attention by the scientific community (Holland et al. 1997, Nemani et al. 2003, Davidson and Janssens 2006).

Recent attention has also focused on processes and pools in the global C cycle that are less well understood than photosynthesis, decomposition, and ocean dissolution, but could

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be of equal importance in potential feedbacks to atmospheric C and the climate system within this century. Five general mechanisms could move significant quantities of ocean or land C into the atmosphere in response to a changing climate (Gruber et al. 2004). These so-called vulnerable C pools and the processes that affect them include thawing permafrost, wetland drying, fires/land-use change, methane hydrates, and the ocean biological pump (Field and Raupach 2004). These pools and processes may be susceptible to change from the direct and indirect effects of climate change, but the level of risk and the timescale of change is uncertain. In many cases, both the size of the pools and the rates of processes affecting them are only roughly quantified.

In this article, we focus on one of the largest of these pools, organic C stored in permafrost (perennially frozen) ground, and on the vulnerability to change under an increasingly warmer climate. Global climate models project the strongest future warming in the high latitudes, with some models predicting a 7 to 8 degree Celsius (°C) warming over land in these regions by the end of the 21st century (IPCC 2007). As a consequence, thawing permafrost and the resulting microbial decomposition of previously frozen organic C is one of the most significant potential feedbacks from terrestrial ecosystems to the atmosphere. We present an overview of the permafrost C pool, the processes that might transfer this C into the atmosphere, and the associated ecosystem changes that occur with thawing. Our intention is to highlight the threshold dynamics and landscape-level changes resulting from permafrost thawing, which are expected to influence future radiative forcing of the atmosphere and thus the ultimate contribution to climate change. Simply put, permafrost thawing is not just a problem of temperature sensitivity of decomposition rates. Finally, we point to research directions that would improve quantitative predictions of the feedback of permafrost C to climate change.

Size and distribution of the permafrost carbon pool

Permafrost, defined as subsurface earth materials remaining below 0°C for two consecutive years, is widespread in the Arctic and boreal regions of the Northern Hemisphere, where permafrost regions occupy 22% of the exposed land surface area (Zhang et al. 1999). Permafrost also occurs on the continental shelf of the Arctic Ocean and in mountainous regions as far south as the subtropics (figure 1; Brown et al. 1998). In the Southern Hemisphere, permafrost occurs in mountains, in subantarctic islands, and in the Antarctic continent but, because the soil C content is low, it is less important to the C cycle feedbacks discussed here (Bockheim 1995). Permafrost temperature, thickness, and geographic continuity are controlled to a large extent by the surface energy balance and thus vary strongly with latitude. Permafrost thickness spans a wide range; in the continuous permafrost zone of the Northern Hemisphere, permafrost thickness typically ranges between 350 and 650 meters (m) (up to 1450 m in unglaciated areas of Siberia); in the discontinuous zone farther south, it typically ranges from less than 1 m to 50 m (Yershov 1998). In the discontinuous zone, because the regional temperature is not low enough to sustain permafrost everywhere, patterns of permafrost distribution are determined to a large extent by local factors such as topography, hydrology, vegetation, snow cover, and subsurface material properties.

The surface ground layer that thaws during summer and refreezes completely in winter is referred to as the active layer. Active-layer thickness ranges from a few tens of centimeters to more than 2 m in the zone of continuous permafrost, whereas in the zone of discontinuous permafrost, the active layer can be several meters thick. Active-layer thickness is controlled to a large extent by regional climate, but it is also influenced by the same local factors that affect permafrost distribution. Beneath the active layer is the transition zone, an ice-rich layer that separates the active layer from the more stable permafrost below (Shur et al. 2005). Active-layer thickness is important because it influences plant rooting depth, hydrological processes, and the quantity of soil organic matter exposed to above-freezing seasonal temperatures.

Permafrost is defined on thermal and temporal criteria, and therefore the term refers to a variety of materials, including mineral and organic soil, rock, and ice. Both the size of the organic C pool in permafrost and the rate of release to the atmosphere control the overall impact of thawing permafrost on future climate. The ice content of permafrost is also important to future climate impacts because the loss of ground ice can have large consequences for local ecosystem C dynamics. Many permafrost soils contain visible ice inclusions in the form of ice wedges (networks of massive wedge-shaped, foliated ice bodies), segregated ice (layers or lenses), or pore ice (small, interstitial crystals). In some areas ground ice can occupy a large proportion (up to 80%) of the soil volume, and thus thawing can trigger major changes in surface topography and ecosystem dynamics (Brown et al. 1998, Yershov 1998).

The total pool of organic C stored in permafrost is composed of C frozen at depth in peatlands (20% to 60% C) and C intermixed with mineral soils (< 1% to 20% C) (figure 2), each of which dominates different locations in the Northern Hemisphere, depending on physiographic characteristics (Gorham 1991, Romanovsky 1993, Smith et al. 2004). Because organic C in permafrost originates from plant photosynthesis and growth, there is typically higher C density in near-surface permafrost. However, organic C pools can be much larger at depth than previously recognized because of cryogenic (freeze-thaw) mixing and sediment deposition (figure 2a) (Schirrmeister et al. 2002, Zimov et al. 2006b).

The estimated size of the permafrost C pool can vary depending on the regions under consideration and on the depth of permafrost included. We estimate the total soil C in the northern circumpolar permafrost zone to be 1672 petagrams (Pg; 1 Pg = 1 billion metric tons), with 277 Pg of that in peatlands. The peatland C estimate accounts for total peat depth (up to several meters) but not underlying mineral soil C. All permafrost-zone soils estimated to 3 m depth (including peatlands, but with variable depth) contain 1024 Pg C.

Figure 1. Latitudinal zonation of permafrost. Source: Brown and colleagues (1998).

Another 407 Pg is contained in deep loess sediment accumulations below 3 m in Siberia (Zimov et al. 2006b), and the remaining 241 Pg is estimated for deep alluvial sediment accumulations below 3 m in river deltas of the seven major Arctic rivers. Several important accounting assumptions, made in accordance with previous work, were used to arrive at this estimate: (a) All terrain lying within the circumpolar permafrost region (including both the continuous and discontinuous permafrost zones) was used in the estimate, regardless of whether specific locations were known to meet the strict time-temperature definition of permafrost. (b) Extensive northern peatlands store organic C as a result of moisture-related anoxia. Only some of these are underlain by permafrost. The peatland C pool in this estimate includes all those found in the circumpolar permafrost region (Tarnocai 2006).

Still, 1672 Pg could be an underestimate of total soil C pools in the permafrost region, because deep soils were only considered for one area in northeastern Siberia and for river deltas, and because the soil C content in the 2- to 3-m layer of most mineral soil orders was conservatively estimated because of data scarcity. Both the 2- to 3-m layer and the deep soil C estimates should be considered preliminary because a relatively small number of data points are extrapolated to large

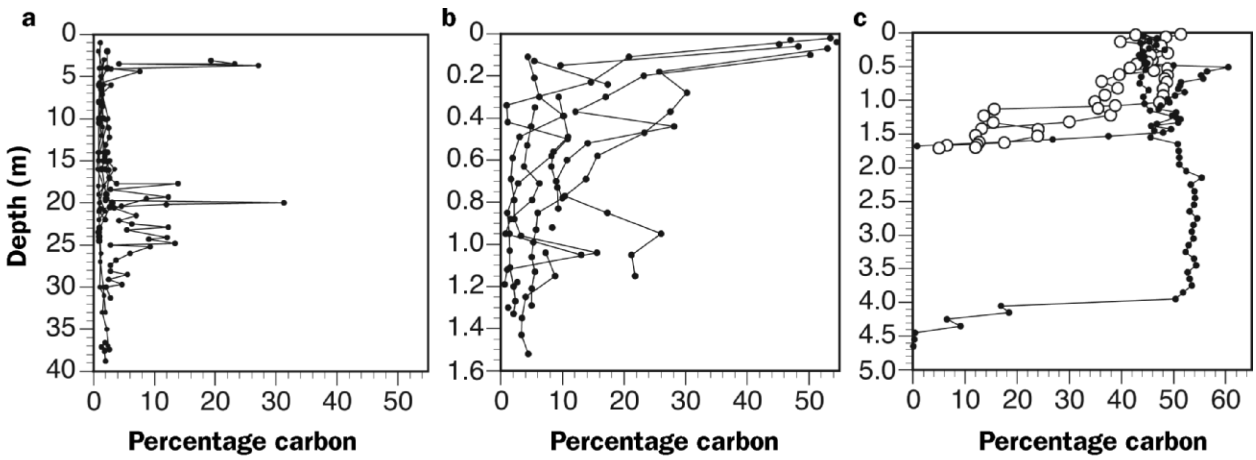

Figure 2. Vertical distribution of soil carbon content in active layer and permafrost from (a) mineral soil sediment deposits in Siberia (data from Zimov et al. 2006a), (b) thaw lakes/thin peat on the North Slope of Alaska (data from Bockheim 2006), and (c) frozen peatlands in Canada (white circles; data from Kuhry 1998) and Russia (black circles; data from Oksanen et al. 2001, 2003).

areas, but this provides a general outline to the size of this deep C pool. Overall, this permafrost C pool estimate is more than twice the size of the entire atmospheric C pool, and it is more than double previous estimates of high-latitude soil C (Gorham 1991, Jobbágy and Jackson 2000). The 0–3 m permafrost-zone soil C estimated here at 1024 Pg represents a large fraction of world soil C stocks; global soil C stocks from 0 to 3 m depth (peatlands not included) have been estimated to be 2300 Pg (Jobbágy and Jackson 2000).

Development of the permafrost carbon pool

Development of soil C pools in northern regions occurs through the action of several processes that are characteristic of permafrost environments. If active layer thickness and energy exchange remain constant, a vertical increase in the elevation of the soil surface (e.g., through sedimentation or peat formation) results in upward growth of the permafrost surface, a process known as syngenetic permafrost growth. In poorly drained areas, vertical peat accumulation on the order of approximately 0.5 millimeters (mm) per year occurs in response to impeded microbial decomposition and the presence of *Sphagnum* mosses (figure 3a; Gorham 1991). Soil accretion can also occur in areas subject to active aeolian or alluvial sedimentation. Mineral soil deposited over time can cause the elevation of the ground surface to increase vertically approximately 0.7 mm per year (figure 3b; Schirrmeister et al. 2002). Silt deposition over decades to millennia, especially during the dustier cold phases of glacial periods, has resulted in large deposits of loess and alluvial soil tens of meters thick that are patchily distributed across the Northern Hemisphere in areas not covered by Pleistocene ice sheets, including large parts of Alaska, Yukon, and Siberia (Walter et al. 2007). In these regions of organic and mineral soil accumulation, organic C at the bottom of the active layer becomes incorporated into permafrost as the permafrost surface rises over time.

A second mechanism for incorporating soil C into permafrost is cryoturbation, the mixing of soil layers in response to repeated freeze-thaw cycles. Cryoturbation can redistribute organic C away from the surface to greater depth in the soil profile (figure 3c; Michaelson et al. 1996). The most common form of cryoturbation is related to frost heave (seasonal expansion) as water freezes in the fall and occupies a greater volume of the soil, and thaw settlement, the reverse process that occurs during spring when the ice melts (Walker et al. 2004). The net result is exchange of soil material between the surface and the base of the active layer and downward movement of organic C (Bockheim 2007). Organic C buried by this mechanism can eventually be incorporated into permafrost, especially if accretion of mineral or organic soil at the surface occurs simultaneously. Cryoturbation is particularly strong in locations experiencing two-sided freezing in the early winter, downward from the surface and upward from the permafrost surface. The unfrozen layer between the freezing fronts is exposed to pressure because of increased volume displacement, as liquid water becomes ice. This pressure is released when the unfrozen layer is squeezed upward through cracks in the frozen soil surface, and results in soil mixing. Cryoturbated areas can be distributed in patches around a landscape or may be nearly continuous geographically, depending on the temperature of the permafrost, ground vegetation cover characteristics, and soil texture and moisture content (Walker et al. 2004). Both cryoturbation and syngenetic growth of permafrost interact with biological processes, such as the rooting depth of plants (e.g., Mack et al. 2004), which determine the depth distribution of new C inputs into the soil available for incorporation into permafrost.

The genesis of the current permafrost C pool was highly dependent on the changing distribution of permafrost during the last glacial/interglacial cycle. During the last glacial maximum (LGM) (20 thousand years [ky] BP), permafrost underlay more land area than today, including nonglaciated parts of Europe, northern Eurasia, and North America (Dawson 1992). After the LGM, permafrost started to thaw rapidly at its southernmost limits, and by the time of the Holocene Optimum (5–9 ky BP), permafrost had completely disappeared from most of Europe and the continental United States, from northern Kazakhstan, and from significant portions of western Siberia in northern Eurasia (Yershov 1998). During this time, the zonal distribution of permafrost was relatively stable in north-central Siberia, northeastern Siberia, and the Russian Far East, although rapid development of thaw lakes during this period caused localized thaw (MacDonald et al. 2006). There were several relatively cold periods during the Mid and Late Holocene, of which the most recent and perhaps coldest was the Little Ice Age (1650–1850 CE). New permafrost appeared in some parts of the landscape within the present-day sporadic and discontinuous permafrost zones during cold intervals, and began to disappear during warmer periods. During the Little Ice Age, shallow permafrost (15 to 25 m) formed in places that were predominantly unfrozen for most of the Holocene (Romanovsky et al. 1992). Recent warming trends appear to have initiated thawing of this Little Ice Age permafrost (Jorgenson et al. 2001).

Permafrost C accumulation in high latitudes has generally followed these warming and cooling trends. The western Siberian peatlands started to develop between 11.5 and 9 ky BP (Smith et al. 2004), while Canadian peatlands expanded during the period from 6 ky BP to the present (Gorham 1991, Kuhry and Turunen 2006). Many boreal and subarctic peatlands developed initially under permafrost-free conditions during the Holocene Optimum, with permafrost aggrading subsequently (epigenetic permafrost growth) at these locations during the Late Holocene (Oksanen et al. 2001, Zoltai 1995). Loess deposits in unglaciated Siberia and Alaska developed over the past 50 ky BP or more, during the glacial/interglacial intervals of the Pleistocene (Romanovsky 1993, Schirrmeister et al. 2002, Zimov et al. 2006b).

Thaw and removal of carbon from the permafrost pool

Under a warming climate, release of C from permafrost to the atmosphere will occur primarily through accelerated microbial decomposition of organic matter. However, the rate and form of this C release is contingent on landscape-level processes that are only beginning to be understood quantitatively (figure 4). To understand how C moves from permafrost to the atmosphere, it is necessary to consider the processes that remove C from the permafrost pool. By definition, this involves a temperature above 0°C for part of the year. This defines a pool of soil organic C referred to here as thawed permafrost C (although we recognize that, as such, it is now part of the continuum of soil organic C already in the active layer or thawed elsewhere on the landscape). It is our contention that processes that move permafrost C from the frozen to the thawed state rapidly increase the C pool size available for decomposition at rates an order of magnitude higher, and thus for determining total C emissions may be as

Figure 3. Photographs of typical permafrost profiles. (a) Frozen peatland soil from the Hudson Bay Lowlands, Canada; the shovel is approximately 100 centimeters (cm). (b) Mineral soil sediment deposit in Siberia. Massive ice wedges are white in color; mineral soil, with visible roots and other organic matter fragments, is frozen between ice wedges. The unfrozen active layer (approximately 80 cm) is visible at the soil surface above the permafrost. (c) Cryoturbated soil from the North Slope of Alaska; the rod is approximately 15 cm. Photographs: a, Peter Kuhry; b, Edward A. G. Schuur; c, James Bockheim.

important as—or more important than—the direct effects of temperature sensitivity on the decomposition of organic matter.

The freezing point of water is a change of physical state that causes orders-of-magnitude threshold changes in biotic processes, including decomposition rates (Monson et al. 2006). It is important to recognize, however, that microbial decomposition of organic C occurs below 0°C in films of liquid water (Price and Sowers 2004). Subzero increases in permafrost temperature can, in theory, have impacts on C losses to the atmosphere, albeit at lower levels. The phase change from water to ice also controls thresholds in abiotic processes. Although permafrost thawing can occur gradually as the thickness of the active layer increases, it can also occur more abruptly through development of thermokarst (ground surface subsidence caused by thaw of ice-rich permafrost) and erosion. The extent and rate of these processes depend highly on initial ground-ice content and other landscape attributes (Osterkamp et al. 2000). They have major impacts on whole-ecosystem C cycling and on the fate of thawed permafrost C because erosion and river transport are significant C loss pathways at regional scales (Berhe et al. 2007). Although the thawing of permafrost and the resulting release of C is an ongoing process, contemporary climate change has the potential to increase rates of thawing and of transfers of C out of the permafrost pool. Figure 4 illustrates what may be the relative strength of these thawing mechanisms in a warming world. Even though actual magnitudes are unknown, this schematic illustrates both the continuous and threshold nature of permafrost thawing.

The simplest form of permafrost thawing to consider from a conceptual and modeling standpoint is active-layer thickening, which leads to thawing of C contained in the uppermost permafrost. Increases in active-layer thickness can occur directly as a result of higher summer air temperatures and the infiltration of precipitation (Nelson et al. 1997, Hinzman et al. 1998), with the latter increasing soil heat content and thermal conductivity. Changes in winter temperature and precipitation also can have an indirect but significant impact on active-layer thickness and permafrost thawing. Low winter air temperatures are responsible for maintaining permafrost, but

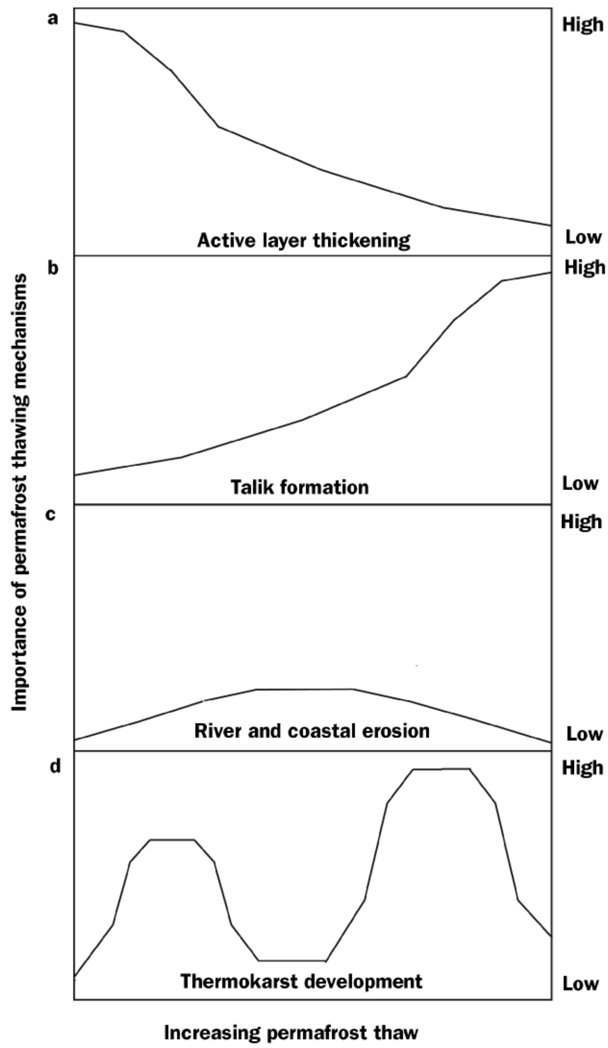

Figure 4. Four different mechanisms that can thaw permafrost. Each panel represents a hypothesis of the relative importance of that mechanism through time as permafrost thawing progresses. (a) Active layer thickening is the most important mechanism early in permafrost thawing as air warming affects the surface permafrost, but then decreases in importance as taliks begin to form. (b) Talik formation occurs only when active-layer thickening has become deep enough so that the entire summer-thawed layer does not refreeze in the winter. Once this has occurred, by definition, deeper permafrost thawing occurs through talik expansion, and thus active-layer thickening does not contribute directly to permafrost thawing at that time. (c) River and coastal erosion increases through time, but after some maximum effect, this mechanism decreases to zero because the influence of the river and coastal processes is limited in spatial extent. (d) Thermokarst development is represented as a threshold process; the first peak is conceptualized as the loss of Little Ice Age ice. Thermokarst subsequently declines in importance until enough thawing has occurred to affect Pleistocene-age ice, typically somewhat deeper in the soil profile, causing the second peak in thermokarst development. This time course is conceptualized as the course of a single latitudinal band through time; if multiple latitudes are considered simultaneously, then more southerly and northerly regions would be on different points on the axis of permafrost thaw at the same time. The actual number of years these time courses take is not yet known and depends on the progression of climate change, but the range is on the order of multiple decades to centuries. Lastly, the importance of the different mechanisms relative to one another is poorly known. It is clear that river and coastal erosion are the most spatially limited. Here, active-layer thickening and talik formation together are shown as roughly equal, or somewhat greater, in importance to thermokarst formation, which is more restricted to areas with higher ice content.

the connection between air and ground temperatures is modulated by snow depth and density. In general, snowfall in autumn and early winter insulates permafrost from cold winter air, causing permafrost to remain warmer in winter than it would otherwise be if exposed directly to the air (Zhang 2005). This effect can then carry over to deeper thaw depths in summer. The effect of snow accumulation—keeping permafrost warmer—attenuates with increasing snow depth, whereby the incremental insulating effect of additional snow on an exisiting snowpack will be less than the insulating effect of that same amount of snow on bare ground; the parameters of this relationship will vary for different climates or soil types (Zhang 2005). Models predict increased wintertime snowfall at high latitudes (IPCC 2007), suggesting that permafrost thawing will be greater if the snow-insulating effect increases; this will be regionally variable, depending on the timing of increased snowfall, the current average snowpack depth, and the redistribution of snow on the landscape. Because surface moss and organic soil also insulate underlying permafrost, changes in thickness or properties of this layer can also affect the ground heat flux. Fires, which may increase in frequency in a warmer and drier climate, can remove the surface organic layer or decrease albedo (surface reflectivity), both of which increase ground heat flux and permafrost thawing (Mazhitova 2000). In fact, natural fires are known to have resulted in repeated permafrost collapse in boreal peatlands during the Holocene, leading to significant changes in vegetation and surface hydrology (Zoltai 1993).

Eventually, active-layer thickening can be of a magnitude such that the soil does not refreeze completely in the winter, creating a talik, a residual unfrozen soil layer with above-freezing conditions favorable for decomposition. Once formed, a talik can withstand interannual heat deficits that could otherwise lead to refreezing because it generally has high moisture content and heat capacity. Increased active-layer thickness and talik formation, which may be caused by both the indirect and the direct effects of climate warming, act on a widespread basis to thaw permafrost C, both regionally and globally.

Although active-layer thickening and talik formation generally proceed incrementally, permafrost thawing can also occur rapidly or even catastrophically. Thermokarst terrain develops when ground ice melts and the remaining soil collapses into the space previously occupied by ice volume (figure 5). The degree of thermokarst subsidence is dependent on ground ice distribution and content and thaw magnitude, which in turn are determined locally by soil characteristics, topography, and geomorphology (Shur and Jorgenson 2007). While thermokarst can occur in areas with stable permafrost in response to localized hydrologic changes and near-surface ice melt, thermokarst terrain is widespread in lower latitudes that have been warming since the end of the Little Ice Age (Vitt et al. 2000). In sloped upland areas, thermokarst initiation creates topographic low points that attract water flow toward subsiding areas, feeding back to further thawing through thermal erosion from moving water, and sometimes to active-layer detachment slides—catastrophic erosion of bulk soil material. Indeed, thawing permafrost and channeling water can thaw and move tons of previously frozen ground within one to several years (figure 5a–5c). In lowlands or flat uplands, thermokarst initiation can lead to the formation of lakes, which thaws permafrost under and at the edges of the lake (figure 5d). Increased lake area has been documented in some areas of the Arctic, presumably as a result of permafrost thaw (Smith et al. 2005). Complicating the situation, increased permafrost thawing can also cause lakes to drain if the thawing exposes the lake bottom to deep gravel layers (Smith et al. 2005). Thermokarst interacts strongly with local hydrology and can lead to either well-drained or saturated conditions that, in turn, have a strong impact on the rate and form of C that will be lost from thawed permafrost. Thermokarst is a unique result of permafrost thawing, as it occurs in discrete locations on the landscape, often unpredictably, and can have large consequences for permafrost C storage and ecosystem C cycling at those locations.

In a geographically more limited fraction of the landscape, erosion at river edges and coastal margins can be a significant transfer mechanism of permafrost C (Mars and Houseknecht 2007) (figure 5e, 5f). As with all mechanisms for C loss, river and coastal permafrost erosion that is occurring now is likely to increase with rising sea level, larger storms, and greater river discharge, as has been observed in Russian Arctic rivers (Peterson et al. 2002). Although modest erosion of permafrost occurs each summer, episodic events can be responsible for a significant proportion of river and ocean erosion. These events include the rapid spring breakup of river ice, storm events that produce large waves, and unusual summer precipitation events that increase river flow when permafrost temperatures are at their warmest. Organic C removed from permafrost by river and coastal erosion may undergo the largest change in decompositional environment of all C from thawed permafrost, moving directly from permafrost on land into a riverine or oceanic environment (Berhe et al. 2007).

The fate of carbon from thawed permafrost

After organic C has thawed from permafrost, the key question from the perspective of feedbacks to climate change concerns the amount and rate of C transfer to the atmosphere as opposed to other terrestrial or marine C storage pools. Implicit in the following discussion is that transfer rates to the atmosphere are always higher after thawing than they were when the organic C was stored in permafrost. Emissions to the atmosphere are controlled by the size of the C pool emerging from permafrost, and by continuous and episodic processes that control the rate of release to the atmosphere after thaw (figure 6). The dominant continuous process is decomposition by soil microbes that derive energy from previously frozen organic C compounds. Disturbance by fire is the dominant episodic process converting soil organic C to inorganic forms. Although the relative importance of continuous and episodic transfer of thawed permafrost C to

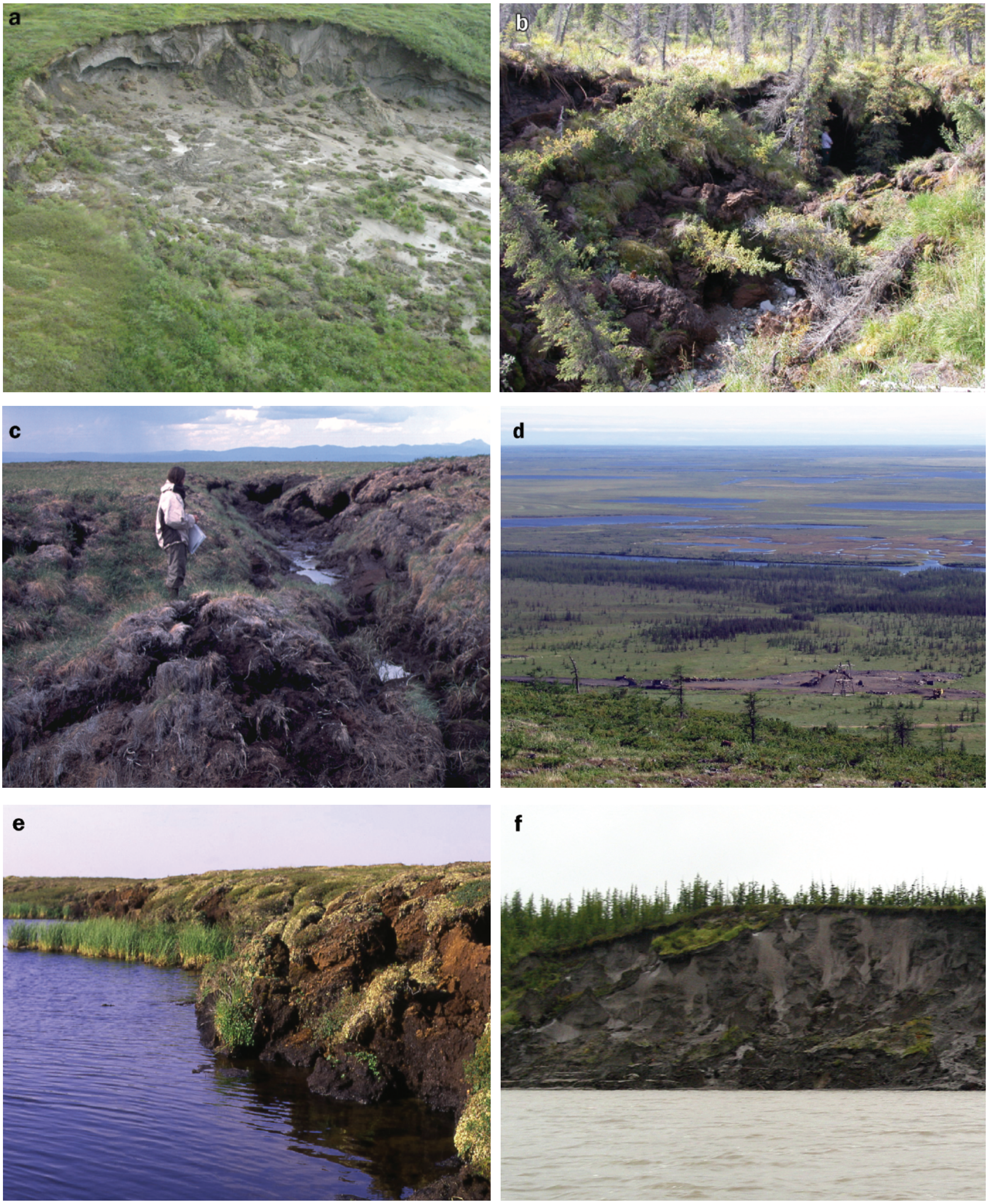

Figure 5. Photographs of typical thermokarst features: (a) in the Noatak River Valley, Alaska, and in forest (b) and tundra (c) on the north slope of the Alaska Range, Denali National Park. Permafrost thawing also results in (d) lowland lakes in northeastern Siberia, (e) lakeside erosion in Russian peatlands, and (f) riverbank sediment deposits in Siberia. Photographs: a, Andrew Balser; b and c, Larissa Yocum; d and f, Edward A. G. Schuur; e, Peter Kuhry.

the atmosphere in any given location depends strongly on the ecosystem type and the timescale under consideration, rates of both microbial decomposition and fire frequency are likely to increase in a warmer climate (Flannigan et al. 2005, Davidson and Janssens 2006).

On a global basis, microbial decomposition of organic matter is the dominant pathway of C return from terrestrial ecosystems to the atmosphere, which is likely to be the case with C from thawed permafrost. Soil organisms oxidize organic C to inorganic forms primarily to extract energy for growth from these reduced compounds. Because C was incorporated into permafrost by different mechanisms, the quality (decomposability) of the organic C varies according to its genesis. Peat, for example, is likely to have been subject to microbial decomposition for significant time periods before its incorporation into permafrost, although this may not be the case for some cryoturbated or sediment-buried organic C. Peat generated in anoxic conditions is likely to decompose at different rates compared with organic C mixed with or adsorbed to soil mineral surfaces. But in general, permafrost C from both peat and mineral soil has a relatively slow decomposition rate after thaw compared with the original C inputs to the soil, because past decomposition left poor-quality C at depth in the soil profile that was then incorporated into permafrost. There are, however, exceptions to this generality in places where sediment deposition rates were high in the past (Dutta et al. 2006, Zimov et al. 2006a).

In addition to the quality of the organic substrate, microbial decomposition rates depend strongly on environmental conditions, which exert strong control over C emissions from thawing permafrost. Standard environmental controls over decomposition are temperature, moisture availability, nutrient availability, and electron acceptor availability. This last factor, which is primarily a measure of oxygen availability, can be particularly important, depending on whether the C emerging from thawing permafrost ends up in an aerobic or an anaerobic environment (Turetsky et al. 2007). Active-layer thickening and talik formation in upland environments typically exposes thawed permafrost C to aerobic conditions, although partially or seasonally waterlogged soils are common even in upland high-latitude ecosystems (Hobbie et al. 2000). In lowland regions, however, development of thermokarst lakes, export of dissolved organic carbon (DOC), and erosion of thawed soil often results in deposition of C in aquatic environments, where oxygen is limited (Walter et al. 2006). The DOC concentrations of cold, permafrost-affected watersheds in western Siberia, for example, are only one-third those of warm, permafrost-free watersheds. Warming could, therefore, increase DOC export from that region by 29% to 46% (Frey and Smith 2005). This tendency is not necessarily universal, however—patterns of decreased summer DOC export have been observed in the Yukon River in Alaska (Striegl et al. 2005).

Microbial decomposition in anaerobic environments, where oxygen resupply is restricted by slow diffusion rates in water, relies on other elements to serve as electron acceptors (such as nitrate, sulfate, iron, and CO_2) for respiration. Decomposition rates using alternate electron acceptors are 5 to 10 times slower because of lower energy yield, and, along with CO_2, can also release methane (CH_4) to the atmosphere with 25 times the greenhouse warming potential on a century timescale (Bridgham et al. 1998, IPCC 2007). The release of methane and CO_2 from wetlands, lakes, streams, and rivers will be an important consequence of thawing permafrost, while transport to the ocean, with its high sulfate concen-

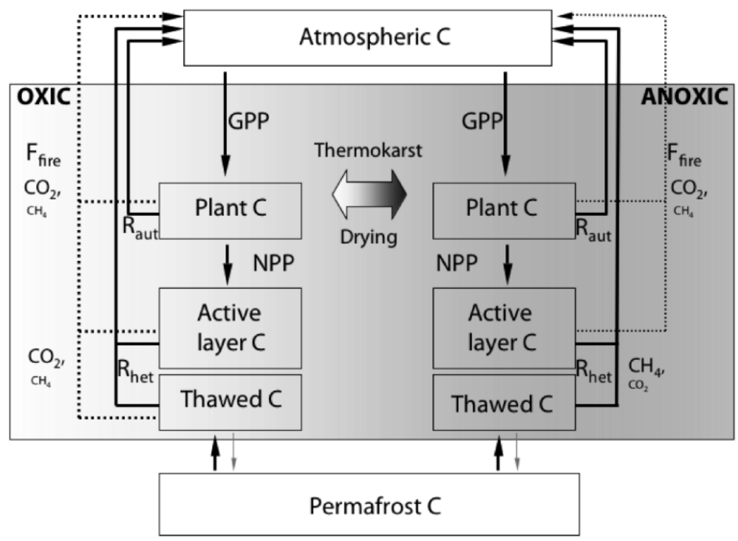

Figure 6. Conceptual diagram of the effect of permafrost thawing on climate. Permafrost C, once thawed, can enter ecosystems that have either predominantly oxic (oxygen present) or predominantly anoxic (oxygen limited) soil conditions. There is a gradient of water saturation on the landscape that ranges from fully oxic to fully anoxic, and ecosystems can become drier as permafrost thaws (shrinking lake area, drying wetland/peatlands), or wetter (thermokarst lakes). The soil oxygen status is a key determinant of the rate and form of C loss to the atmosphere. Decomposition in oxic soils releases primarily CO_2, whereas anoxic decomposition produces both CH_4 and CO_2, but at a lower total emission rate. Fire releases mostly CO_2, but also some CH_4, and can burn upland and wetland ecosystems, although burning of organic soils at depth is restricted in wetter environments unless there is severe drought. These emissions of C through decomposition are offset by gross and net primary productivity (photosynthesis and net plant growth). Under some local conditions, it is possible that C will enter the permafrost pool (grey arrow), although this total amount is small relative to C that is expected to thaw from permafrost as a result of climate change. Abbreviations: C, carbon; CH_4, methane; CO_2, carbon dioxide; F_{fire}, carbon flux from fire; GPP, gross primary productivity; NPP, net primary productivity; R_{aut}, autotrophic respiration; R_{het}, heterotrophic respiration.

tration, may suppress methane release from DOC deposited there. Despite potential electron acceptor limitation, a large portion of the DOC reaching the Arctic Ocean is still quickly mineralized and returned to the atmosphere (Hansell et al. 2004).

Another important environmental difference between decomposition in aquatic and terrestrial environments is the seasonal temperature regime. Active-layer thickening in uplands will expose more thawed permafrost C for decomposition during the warm summer months, but this thawed C will refreeze during the winter until a talik is formed. Thawed permafrost C deposited in an aquatic environment can remain unfrozen during the long winter months but may remain at more consistently low temperatures throughout the year. Decreased microbial decomposition rates attributable to oxygen limitation in aquatic environments are, therefore, offset in part by the greater length of time spent in a thawed state, and by release of CH_4 in addition to CO_2. Based on (a) net C emissions from long-term laboratory anaerobic and aerobic incubations of various wetland soils (Bridgham et al. 1998) and (b) the global warming potential of CO_2 and CH_4 (IPCC 2007), a simple calculation suggests that aerobic decomposition has a greater feedback to warming on a century timescale, ranging from 1.3 to 6.9 times greater than the effect from the same soil decomposed in an anaerobic environment (table 1). This is largely due to differences in C emission rates: aerobic CO_2 release is about an order of magnitude higher than anaerobic CO_2 release, and about two orders of magnitude more C loss than anaerobic CH_4 release (table 1). The strength of this feedback could be reduced by a factor of two if anaerobic decomposition proceeds during the winter, while aerobic decomposition is halted for half the year when frozen conditions prevail. Considering the offsetting factors shown by this calculation, C emissions from decomposing organic matter in both anaerobic or aerobic environments are likely to have important climate feedbacks.

In addition to biological decomposition, disturbance by fire could be an important abiotic mechanism for transferring C thawed from permafrost to the atmosphere. Fire oxidizes organic C primarily to CO_2, but also releases smaller quantities of CH_4, carbon monoxide, and other volatile C compounds. Because organic C emerging from permafrost is typically located deeper in the soil profile when the active layer thickens, it is less vulnerable than surface organic C to burning. However, extremely warm years, when large amounts of permafrost C thaw, are also more likely to have more extensive or severe fires than average. Model scenarios of fire in Siberia show that extreme fire years can result in approximately 40% greater C emissions because of increased soil organic C consumption (Soja et al. 2004). In combination with dry conditions or increased water infiltration, thawing and fires could, given the right set of circumstances, act together to expose and transfer permafrost C to the atmosphere very rapidly. Lastly, fire can interact with decomposition by creating warmer soil conditions and deeper permafrost thaw, which in turn promote the loss of C from increased microbial activity.

Ecosystem responses to thawing permafrost

Until now we have focused on processes that remove C from the permafrost pool and transfer it to the atmosphere, which has the potential to increase climate warming. As high-latitude ecosystems cross the freezing-point threshold, there are a number of other ecosystem factors—ecosystem energy balance and element cycling, for example—that are inextricably linked to permafrost thawing. Changes in some of these factors may serve to accelerate climate change, while others may slow this process and thus offset the effects of C released from permafrost thawing.

Table 1. Relative climate forcing of predominantly aerobic versus predominantly anaerobic decomposition calculated from soil incubations of six contrasting wetland ecosystem types.

		Relative emission rate (grams C emission per gram soil C)					
	Global warming potential	Bog	Acidic fen	Intermediate fen	Cedar swamp	Tamarack swamp	Meadow
Aerobic incubation							
CO_2	1	1535	316	48	114	90	42
Anaerobic incubation							
CO_2	1	199	49	9	19	19	7
CH_4	25	1	1	1	1	1	1
Relative climate forcing[a]	—	6.9	4.3	1.4	2.6	2.0	1.3

C, carbon; CO_2, carbon dioxide; CH_4, methane.

Note: Carbon dioxide emissions from each ecosystem type are relative to the anaerobic methane emission value normalized to a value of 1. Global warming potential values for CO_2 and CH_4 are from IPCC (2007) for a century timescale. Total C emission rates were derived from 59-week paired aerobic and anaerobic soil incubations published by Bridgham and colleagues (1998), presented per unit soil C to compare the effect of different C quality across sites.

a. Relative climate forcing is a ratio of the climate forcing effect of the aerobic incubation to the anaerobic incubation. The climate forcing effect for each incubation was calculated as the relative emission rate of C multiplied by the global warming potential. For the aerobic incubation it is calculated for CO_2 alone, and for the anaerobic incubation it is calculated as the sum of CO_2 plus CH_4. Numbers larger than one indicate the aerobic incubation has a greater total climate forcing effect, all else being equal.

One important offset to permafrost C losses is an increase in C uptake from the atmosphere by photosynthesis and plant growth (figure 6). Higher temperatures can stimulate photosynthetic rates directly, and can also lengthen the growing season (Myneni et al. 1997). This can increase C storage in plant biomass and in new soil organic matter. Field and modeling studies estimate that for each day the growing season increases in length, net ecosystem C uptake will increase from 1 to 6 grams C per square meter (m^2) (Aurela et al. 2004, Euskirchen et al. 2006). Over longer timescales, new plant functional groups with larger biomass and C storage potential may become dominant, as has been observed in Alaska with the expansion of shrubs (Sturm et al. 2005) and some tree species (Wilmking et al. 2004). Higher temperature and decomposition rates can also increase nutrient availability, which often has a greater effect on plant growth than temperature (Chapin and Shaver 1996). Decomposition of soil C (including thawed permafrost C) with concomitant nutrient release could actually increase total ecosystem C storage if low C:N soil organic matter is replaced by higher C:N plant biomass (Shaver et al. 2000). Increased N availability may, however, also stimulate more decomposition from soil where microbes are N limited, furthering loss of C from the ecosystem (Mack et al. 2004). Also, nutrients may not be transferred efficiently from soil to plants because of spatial (e.g., depth in the soil profile) or temporal (e.g., winter versus summer) offsets between the decomposition of soil C and plant nutrient uptake. Nutrients lost from terrestrial ecosystems when permafrost thaws may instead stimulate aquatic productivity, depending on bioavailability and demand for those nutrients.

Apart from changes in the C cycle, changes in ecosystem energy balance can directly affect regional climate, and in the case of permafrost thaw may be inextricably linked with the C cycle changes already discussed. Changes in albedo brought about by changes in plant species composition, length of the snow season, lake area, or fire frequency can have positive or negative effects on climate warming. Increases in shrub cover in graminoid-dominated tundra ecosystems result in greater absorption of solar radiation in summer and winter, leading to local warming in the summertime (Chapin et al. 2005). Similar patterns can be expected as the treeline moves north. Changes in ecosystem albedo can also have a cooling effect. Increased fire frequency in boreal forests alters the proportion of forest dominated by broadleaf deciduous trees. These early-successional species reflect more solar radiation in summer than do the needle-leaved evergreen species they replace, and expose high-albedo snow on the ground in winter. These long-term albedo effects can offset increased warming from both the transfer of C to the atmosphere from fire and the short-term decrease in albedo immediately following fire, and may actually cool the climate (Randerson et al. 2006). Lake or wetland expansion may serve to regionally warm or cool the climate, depending on the type of vegetation replaced.

Other climate and ecosystem changes that could decrease permafrost thawing include (a) decreased summer soil moisture, which limits heat conduction into the soil; (b) decreased snowpack in the winter, which can expose permafrost to extremely cold air temperatures (Stieglitz et al. 2003); and (c) redistribution of sediment on the landscape (Berhe et al. 2007) that can bury soil C, which can then refreeze into permafrost.

Thawing permafrost feedback to climate change

Although the extent or thickness of permafrost may sometimes increase locally through the mechanisms mentioned above, climate warming is likely to lead to net permafrost loss on regional and global scales. Quantifying C release from permafrost to the atmosphere has been the focus of intensive research using a variety of techniques. Risk assessments, based on expert opinion, estimated that up to 100 Pg C could be released from thawing permafrost by 2100 (Gruber et al. 2004). On the basis of laboratory incubation experiments and estimated C stocks, Dutta and colleagues (2006) calculated a potential release of about 40 Pg C over four decades if 10% of the C stock frozen in deep soils in Siberia thawed to 5°C. Tarnocai (2006) estimated that 48 Pg C could be released from Canadian permafrost over this century if the mean annual air temperature increased by 4°C. Model predictions incorporate changes in vegetation and other disturbances, as well as C release from permafrost, to determine the net effect of climate warming. Results for Alaska and for the circumpolar region predict the addition of up to 50 to 100 Pg C to the atmosphere by the end of the century, depending on the particular model scenario (Stieglitz et al. 2003, Zhuang et al. 2006). These models, however, typically do not include the complex interactions that cause thermokarst and more rapid permafrost thaw.

Despite mechanisms that can partially offset some of the effects of thawing permafrost on climate, the loss of C to the atmosphere is likely to represent a substantial C source over the next century. For comparison with other global fluxes, the magnitude of these loss projections of 0.5 to 1 Pg C per year from permafrost zone ecosystems are somewhat similar in size with the much better documented C emissions from land-use change (mostly tropical), estimated to be 1.5 ± 0.5 Pg C per year (Canadell et al. 2007). Increased C uptake by plant growth and an extended growing season are likely to be relatively small, while cooling albedo effects from fires will mostly offset only C emissions from those fires or from other warming albedo effects. None of these ecosystem mechanisms appears likely to offset C loss from permafrost thaw and thermokarst, which could release a large amount of C on a decadal to century timescale. Steady-state C pools from permafrost and nonpermafrost ecosystems can provide some basis for comparing vegetation uptake offsets with permafrost C losses over the long term, even though the transient dynamics of vegetation and soil C may deviate in the short term. Aboveground tundra vegetation contains roughly 0.4 kilograms (kg) C per m^2 (Shaver et al. 1992), whereas boreal forest can average approximately 5 kg C per m^2 (Gower et al. 2001), suggesting that a gain on the order of 4.5 kg C per m^2 is possible as treeline advances into tundra. In contrast, a typical tundra permafrost soil can contain up to 10 times that amount (e.g., approximately 44 kg C per m^2 in the top meter; Michaelson et al. 1996), compared with approximately 9 kg C per m^2 in the top meter of nonpermafrost boreal forest soil (Jobbágy and Jackson 2000), for a potential loss of up to approximately 35 kg C per m^2. This potential loss can become greater (on the order of 100 kg C per m^2) if soil to the depth of 3 m is considered.

Accurate prediction of the magnitude and effect of thawing permafrost on global climate remains difficult, however, for several reasons. The core conceptual issue is that the change from ice to liquid water represents a nonlinear threshold whose effects on ecosystem dynamics are difficult to capture with current modeling approaches. Terrestrial ecosystem model simulations that examine the effects of climate change and biogeochemical feedbacks to the climate system in northern high-latitude ecosystems are few, and do not represent most of the permafrost thawing dynamics or deep soil C stocks described in this review. At broader scales, global circulation models are just beginning to include simple permafrost dynamics (Lawrence and Slater 2005, Delisle 2007), but they are still far from coupling physical permafrost dynamics to hydrology and biogeochemistry to properly represent the C cycle in thawing permafrost, and can yield highly inaccurate results (Burn and Nelson 2006).

Despite such limitations, efforts should be made to assess the overall impact and related feedbacks of thawing permafrost on climate change. Urgent research questions and topics include the following: (a) Does widespread active-layer thickening and talik formation result in greater cumulative permafrost thaw than development of intensive but localized thermokarst? (b) Does the thawing and decomposition of permafrost C in anaerobic environments have a greater impact on climate change than thawing and decomposition in aerobic environments? (c) Is it possible to predict the vulnerability of landscapes to thermokarst development on the basis of information about topography, underlying geology, and ground-ice content? (d) How do changes in temperature and precipitation interact to control permafrost temperature through their control over the timing of snowpack formation and loss? Addressing such questions will help inform the development of models by identifying key processes controlling landscape responses to permafrost thawing.

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