Microbial respiration and DOC composition in leachates from modern, Holocene and Pleistocene soils from the Kolyma River basin in Eastern Siberia

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Abstract:

Permafrost is generally considered a long-term sink for carbon that remains locked away from the global carbon cycle. Climate change is likely to lead to thawing of permafrost and a deepening of the soil active layer. Consequently, this carbon sink may become unlocked and available for bacterial decomposition, returning stored carbon to the active carbon cycle, with potentially severe consequences for atmospheric CO_2 concentrations. The Kolyma watershed, in the Eastern Siberian Arctic, is underlain by continuous permafrost, locally referred to as yedoma, which provides a unique environment to study potential consequences of permafrost thaw for carbon release into the global carbon cycle. In order to predict the effect of carbon release from thawing permafrost, I assessed the relative bioavailabilty of soil carbon by measuring rates of microbial consumption and changes in DOC composition in soil leachates. At two spatially distinct sample sites, soil was collected throughout the profile from the active layer and from permafrost, including soils from both Holocene and Pleistocene-era permafrost. To evaluate the rates of carbon processing and potential linkages to nitrogen and phosphorus cycles, I conducted a series of bottle experiments in which I measured biological oxygen demand as a proxy for carbon processing and assessed changes in the composition of dissolved organic carbon using spectral analyses. Experiments were conducted on soil slurry mixtures collected from each soil type. Each experiment included treatments in which leachates were enriched with nitrogen and phosphorus to determine whether carbon processing in soils was nutrient limited. I found substantial variation in rates of carbon consumption, with yedoma soils generally exhibiting higher rates than modern active layer soils, suggesting higher concentrations of labile carbon. I found no evidence of nutrient limitation of carbon processing in any soil leachates. Spectral slope analysis suggests that a unique carbon composition in yedoma soils is cause for the high initial rates of microbial decomposition observed. Tyrosine and tryptophan-like proteins may be an effective proxy for estimating the amount of initial carbon consumption in yedoma soils.

Introduction:

Arctic ecosystems are experiencing the fastest rates of surface air temperature warming and some of the most dramatic effects from global climate change, including reduction of sea ice and glaciers, thawing permafrost and deepening of active layer soil, change in vegetation composition, lengthening of growing season, and an overall decrease in albedo (Anisimov et al. 2007).

Permafrost is soil that remains frozen for at least two consecutive years. Soil carbon in permafrost remains locked away from biological processing due to the physical constraints of permanently frozen soil and short summer seasons (Pautler et al. 2010). The predicted thaw of circumpolar permafrost would mobilize a huge source of carbon that has historically been considered a permanent and stable carbon reservoir (Dutta et al. 2006, Waldrop et al 2010). As air temperatures warm, more permafrost soil is incorporated into the annual freeze-thaw cycle, allowing microbes to process the carbon in the soil during the summer months (Vorobyova et al. 1997, Uhlirova et al. 2007). Permafrost contains dense communities of microbes that have existed in the soil for geologic time scales in a hypometabolic resting state (Uhlirova et al. 2007, Boddy et al 2008). Under suitable environmental conditions and thaw of permafrost, these microbe communities can exhibit explosive growth and decompose organic matter quickly (Vorobyova et al 1997, Uhlirova et al. 2007).

Preliminary estimates suggest that permafrost soils contain 500 Gt carbon which is twice the size of the carbon stock in the atmosphere (Zimov et al. 2006). Permafrost soils are an accumulation of poorly decomposed plant and animal remains that provide a rich source of carbon (White et al 2004). The carbon content in permafrost ranges between 10 and 30 times more than the carbon content in non-permafrost soils (White et al 2004, Zimov et al. 2006). Siberian permafrost, referred to as yedoma, is formed by carbon-rich loess deposits from the Pleistocene era (Zimov et al 2006).

Because of its large soil carbon stock, arctic tundra is becoming recognized as a potentially important player in the global carbon cycle as permafrost soils transition from a carbon sink to a potential carbon source in the atmosphere (Uhlirova et al. 2007, Schuur et al. 2009). Exposing permafrost soil to microbial decomposition will cause a significant global redistribution of carbon (Uhlirova et al. 2007). Permafrost thaw and the resulting microbial processing of permafrost carbon releases greenhouse gases (CO_2 and CH_4) which amplify arctic warming (White et al. 2004, Dutta et al. 2006, Schuur et al. 2009).

A collection of recent studies attempts to estimate how much and at what rate carbon will be released from arctic permafrost soils if the current rates of arctic warming continue. Estimates for complete yedoma permafrost degradation range from four decades to a century (Dutta et al. 2006, Zimov et al. 2006). Most of the uncertainty in predicting the nature of permafrost degradation from climate change results from an uncertainty in understanding the controls of carbon storage and the mechanism of carbon release through microbial decomposition. Decomposition rates vary among ecosystems. Variables include air and soil temperatures, soil moisture, soil carbon content, nutrient availability, soil pH, and the chemical composition of soils (White et al. 2004). In favorable environmental conditions, the carbon consumption rate by microbes is controlled by the bioavailability of recalcitrant and labile components of soil (Pautler et al. 2010).

This paper describes a study conducted in the Kolyma River watershed in northeast Siberia. The study addresses the effects of three variables on the potential carbon

consumption by microbes in Siberian permafrost soils. These three variables include soil nutrient availability and limitation; the amount of carbon present in yedoma soils, and the chemical characteristics of the carbon present. I asked the following questions: Do yedoma soils respire more carbon than active layer soils? Is the process nutrient limited? Does the microbial respiration of yedoma differ from active layer soils because of chemical composition? I hypothesized that yedoma soils would yield the highest carbon respiration rates because of a unique chemical composition and that they would be significantly nutrient limited.

Methods:

Site Description — The sampling sites are located within the Kolyma River basin in northeast Siberia (Figure 1). Research was based out of the Northeast Science Station in Cherskiy in the northeast part of the Republic of Sakha, Russia (68°47' N, 161° 20'E). This area has a dry continental climate with a mean annual air temperature of -12.5 °C (Corradi et al. 2005, Uhlirova et al. 2007). There is extreme seasonality in air temperatures. The daily mean temperatures in January reach -40°C and there is a short four-month summer season where daily mean temperatures can reach 13°C in July (Corradi et al. 2005, Uhlirova et al. 2007). The annual precipitation ranges from 200-215 mm, with approximately 130 mm as snow and 85 mm as rain (Corradi et al. 2005, Dutta et al. 2006).

The Kolyma River is the largest watershed that exists completely upon continuous permafrost (Corradi et al. 2005). Carbon rich loess permafrost in the Kolyma lowlands is

some of the oldest and most preserved permafrost deposits in the Northern Hemisphere (Shi et al.1997, Sazonova et al. 2004, Zimov et al. 2006). Yedoma permafrost soils are loess deposits formed during the Pleistocene glacial period and are relict soils of mammoth steppe-tundra ecosystems (Zimov et al 2006). Yedoma covers more than one million km^2 in Siberia and averages approximately 25 m deep (Romanovsky 2001, Zimov et al. 2006).

Frozen yedoma is estimated to have carbon content that ranges from 2 to 20% with an average carbon content of 2.6%, which is about 10 to 30 times the carbon content found in non-permafrost Siberian soils (Dutta et al. 2006, Zimov et al. 2006). Permafrost soils can also contain up to 70% ice in the form of ice wedges (Dutta et al. 2006).

Above the permafrost soil, there is a layer of soil that undergoes an annual freeze-thaw cycle called the active layer. The thickness of the active layer ranges from 20 to180 cm (Dutta et al. 2006). The upper organic layer of soil is 10 cm deep on average and is made up primarily of dead leaf material, roots, and rhizomes (Uhlirova et al. 2007). Permafrost is composed primarily of silty loam soil deposited through river transport (Uhlirova et al. 2007). Deposition from regular flooding causes the ground surface to rise 1 mm a year (Uhlirova et al. 2007). The upper layers of the permafrost rise at the same rate during the freeze-thaw cycle and in doing so incorporate organic material from the active layer (Uhlirova et al. 2007). Vegetation types in the watershed are typical of a tussock tundra ecosystem. The area is populated mostly by larch forest, primarily of Dahurian larch (*Larix gmelinii*), with extensive understory vegetation that includes Labrador tea (*Ledum*

palustre), willows, birch, moss, lichens and evergreen deciduous shrubs (Uhlirova et al. 2007, Henson 2010).

Soil Sample Collection — The soil samples collected represent both a temporal and spatial range of carbon content. Two spatially distinct sampling sites were chosen based on accessibility. Because frozen soil is difficult to collect, sites that had natural permafrost exposures, such as landslide exposure and river bank erosion, were preferentially chosen. Soils were collected from two sampling sites: Tube Dispenser Lake and Duvannyi Yar (Table 1, Figure 2, Figure 3).

Tube Dispenser Lake (TDL) is located close to the Northeast Science Station (68° 45' N, 161° 24'E) (Figure 2). Permafrost was exposed at this site because of a naturally caused land slump (Figure 2). Duvannyi Yar (DVY) is located approximately 250 km from the Northeast Science Station (68° 37' N, 159° 02' E) (Figure 3). Duvannyi Yar is a site along the bank of the Kolyma that has an extensive area of permafrost exposed because of natural river erosion. Large yedoma deposits remain in conical deposits after ice wedges melted, yielding unique access to permafrost soils (Figure 3).

Soil samples were collected at different depths within a continuous soil profile to represent distinct soil eras: active layer, Holocene permafrost (transition layer), and Pleistocene permafrost (yedoma). Transition layer permafrost was only present at the TDL site. Transition layer soil was unfrozen during the Holocene era but refroze as permafrost (Spektor 2010). Soils were taken from the interior of the natural exposures to

ensure that no microbial processing had already occurred. Depth of soil collection along with qualitative notes about the soil profile was recorded. Samples were transported on ice back to the lab.

Soil Characterization — Upon arrival in the lab, soils were measured for moisture content and organic matter. Dry mass was determined by completely drying the samples using the drying furnace set at 100 °C. Organic matter was calculated by burning the sample at 500 °C in the muffle furnace for four hours which left the organic matter as ash.

Biological Oxygen Demand — Samples were analyzed to determine the relative bioavailability of carbon in each soil source. Soil organic matter that is degraded preferentially first is considered to be labile, high quality organic matter (White et al. 2004). Contrastingly, soil components that are digested less easily are considered to be lower quality, refractory sources of carbon.

To assess the relative quality of permafrost soils from different ages and locations, I measured microbial carbon consumption using a proxy measurement called biological oxygen demand (BOD). BOD is measured by the decrease in dissolved oxygen in soil slurry mixtures during a controlled incubation period. Decrease in oxygen is related to carbon consumption used for microbial metabolism.

Soil slurries are made by adding 50 g of soil to approximately 500 ml of water. Because no deionized water was available, water from a natural spring was used as the dilutant.

The spring water yielded the lowest levels of DOC content so there would be the least risk of DOC contamination. Experimental replication was ensured by making two duplicate slurry mixtures for each soil sample collected. Slurry mixtures were aerated consistently before the incubation to ensure there was an unlimited source of O_2. Bottles were kept in room temperature conditions and were not exposed to sunlight to limit photodegredation and photosynthesis. The incubation environment provided conducive pH and temperatures to create an organic matter limiting environment.

To assess potential nutrient limitation in soils, slurry mixtures were spiked with excess nutrients. In addition to the control soil sample, slurries were made with three nutrient treatments to observe the potential limitations of nitrogen and phosphorus. Slurries were spiked with 3 ml of highly concentrated ammonia (N), 3 ml of highly concentrated phosphoric acid (P), and a combinatino of 3 ml of both (N/P). For the five soil sources (Table 2), the control and the three nutrient treatments were made in duplicates resulting in a total of 40 BOD bottles. BOD in each sample was monitored over a five-day incubation period.

Oxygen consumption was converted to carbon consumption by multiplying mg O_2 by 0.375 to account for the microbial efficiency of oxygen use in carbon consumption (Sobsczak 2010). Carbon consumption rates in each soil sample were normalized using organic matter content to carbon used per gram of organic matter.

Absorbance — Spectroscopic absorbance was measured to characterize the carbon present in the dissolved portion of each soil slurry leachate. Absorbance was measured for each sample before and after the five-day incubation period. Absorbance spectra from 275 to 400 nm were measured using the Shimadzu UV-1800 Spectrophotometer. The change in absorbance values at 350 nm wavelength indicates how much dissolved carbon is present in the sample (Figure 5). Spectral slope refers to the slope of absorbance within a range wavelengths. Spectral slopes were determined for three absorbance ranges: a(290-350), a(275-295), a(350-400) (Figure 6). The change in spectral slope indicates the change in dissolved organic matter (DOM) composition over the five-day incubation period (Figure 6).

Results:

Soil Characterization —The mean organic matter measured for each soil location ranged from 3.2% to 4.3% (Table 2). No significant difference in organic matter was detected between ages or locations of soil samples (Table 3).

Biological Oxygen Demand — Decrease in dissolved oxygen over the incubation period is related to carbon consumption per gram organic matter used in soil mixtures (mg/L/g) (Figure 4). Active layer soil samples show the least carbon consumption over the five-day incubation period (Figure 4). All samples from the permafrost soils show greater carbon consumption than active layer, but there is variation between locations of permafrost soil (Figure 4, Table 4). Duvannyi Yar soil exhibited the greatest carbon

consumption during the BOD incubation (Figure 4). There is no discernible difference in carbon consumption for any nutrient treatment in any soil sample (Figure 1).

Absorbance — Absorbance measurements indicate the amount and type of dissolved organic carbon (DOC) present in a sample. Measuring the difference in absorbance at wavelength 350, a(350), is a good proxy to estimate the change in the amount of DOC present due to carbon processing over the five-day incubation period (Helms et al. 2008). Because the slurries were created using particulate organic matter, there are at least two simultaneous processes occurring during the incubation period: carbon is being consumed by microbes (DOC is lost) and particulate matter is leaching DOC through mechanical breakdown (DOC is gained) (Sobsczak 2010). Measuring change in a(350) indicates the net loss or gain of DOC as a result of these two processes (Helms et al. 2008). All samples, except for DVY yedoma, exhibit a positive change in DOC which indicates an overall gain of DOC in four of the five soil slurries (Figure 5). DVY yedoma is the only sample that has a negative change in a(350), indicating an overall loss in DOC (Figure 5). The overall loss of DOC in the DVY yedoma sample suggests that there is the greatest dissolved carbon consumption at this location, which supports the BOD results (Figure 5).

Changes in spectral slope indicate the change in the chemical composition of DOC after microbial consumption during the BOD incubation. The change in slope for three absorbance ranges is plotted in Figure 6. A negative change in absorbance slope, as seen in four of the five samples, indicates that carbon processing has increased the proportion of heavy, aromatic carbon compounds (Figure 6, Helms et al. 2008, Mann 2010). A

negative slope suggests that small, low molecular weight carbon compounds were consumed first and most easily (Helms et al. 2008, Mann 2010). A positive change in absorbance slope, which is observed only in the DVY yedoma, indicates that the DOC composition became lighter in molecular weight and contained less aromatic carbon compounds after the microbial respiration during the incubation period (Figure 6, Helms et al. 2008, Mann 2010).

Discussion:

The projected permafrost thaw due to arctic warming threatens to perturb the global carbon cycle by mobilizing an historically permanent carbon stock that is estimated to contain 500 Gt of carbon (Dutta et al. 2006, Zimov et al. 2006, Waldrop et al 2010). Exposure of permafrost soils will contribute to a positive feedback loop in global climate change. Warming air temperatures in the arctic thaw permafrost which allow microbes access to digest permafrost carbon and in doing so release greenhouse gases into the atmosphere which in term amplify global climate warming (White et al. 2004, Dutta et al. 2006, Uhlirova et al. 2007, Schuur et al. 2009). Therefore, understanding the mechanisms of permafrost carbon mobilization through microbial degradation is critical to better estimate the rates of carbon release to the atmosphere through microbial processes. Estimating carbon degradation by microbial consumption in response to warming temperatures is complicated by various environmental factors that are specific to individual arctic ecosystems (White et al, 2004).

Siberian yedoma soils are estimated to have 10 to 30 times more carbon content than non-permafrost soils (Zimov et al. 2006). The organic content of yedoma soils range from 2 to 20% with the average carbon content in soils of 2.6% carbon (Zimov et al. 2006, Dutta et al. 2006). The carbon content of my permafrost soil samples ranged from 3.23 to 4.26%, which is within this (Table 2). My results differ from the Zimov et al. 2006 assertion that carbon content is 10 to 30 times greater in permafrost soils than in active layer soils because I observed no significant difference in the organic carbon content between active layer samples and permafrost samples (Table 2). The lack of variation in carbon content within the soil profile may be unique to the Kolyma River watershed. Carbon content in the active layer may also vary seasonally or topographically. The active layer soil carbon content may be more variable throughout the landscape and the samples may not represent the general trend of active layer soil composition.

Carbon consumption varies according to the age and spatial range of carbon in the soil. Spatial variation in carbon consumption can be attributed to differences in age, origin, composition and stabilization mechanisms in accumulated permafrost carbon (Uhlirova et al. 2007). These differences affect the quality of the soil carbon bioavailability and may cause the variations across permafrost locations as I observed in the results. Although Arctic ecosystems are generally considered to be nutrient limited for tundra primary production, I found that this was not the case for the Kolyma River watershed soils (Uhlirova et al. 2007). Permafrost soils tend to be rich in easily available phosphorus and ammonium that originated from organic matter mineralization in the soil (Uhlirova et al.

2007). The microbial respiration in the yedoma soils are not nutrient suggesting that there is enough nutrients present for unlimited microbial activity.

Previous long-term studies suggest that the amount of bulk carbon present, regardless of its chemical composition, is the main factor affecting how much carbon will be respired (Dutta et al. 2006, Pautler et al. 2010). While certain DOC pools may be initially preferred, long term observations suggest that other DOC pools become increasingly important carbon sources after the most labile carbon has been initially depleted (Dutta et al. 2010). My experiment represents an initial snapshot of microbial respiration as permafrost thaws. Because there is no significant pattern in the amount of carbon in soils, the variation of carbon consumption observed in my experiment suggests that initial consumption is driven by preferential selection of labile carbon components, rather than being determined by the bulk amount of carbon.

The high initial rates of microbial digestion observed can be attributed to the unique chemical composition of DVY yedoma carbon. DVY yedoma is the only soil source to exhibit this shift in chemical composition which suggests that there is a source of heavy aromatic carbon, unique to yedoma soils, that is consumed preferentially over light carbon in other soil sources. Balcarcyzk et al (2009) found that tyrosine and tryptophan-like proteins can be used as a reliable predictor of DOC loss in a similar permafrost watershed. They also found that DOC bioavailability was not significantly related to bulk DOC concentration but rather to relative amounts of tyrosine and tryptophan in the sample (Balcarcyzk et al. 2009). Another study examining carbon consumption in a

marine environment suggests that the bioreactive DOC was correlated to glutamic acid, arginine, glycine, and serine amino acids (Amon & Fitznar 2001). Both studies conclude that in soil respiration certain amino acids are typically more reactive than neutral sugars. The presence of a unique set of amino acids in yedoma soils may be the cause of the elevated levels of initial carbon consumption observed in yedoma soils. This chemical composition may be unique to yedoma because of the undecomposed components of mineral, humus and loess that formed yedoma soils (Zimov et al. 2006).

All other soil samples exhibited a shift in composition indicating more heavy, aromatic compounds at the end of the incubation. This suggests that a lighter source of carbon was initially consumed. This light, non-aromatic carbon source is likely primary polysaccharides, such as glucose (Amon & Fitznar 2001). White et al. 2004 found that compared to a suite of other soil compounds, relative abundance of primary polysaccharides was positively correlated with CO_2 flux and thus microbial consumption (White et al .2004).

Both neutral sugars and amino acids have been found to be excellent indicators of bioavailability of carbon (Amon & Fitznar 2001). The absorbance of the DOC portion of my samples suggests that amino acids, if present, are the most labile, preferred source of carbon that yield the highest immediate respiration. Polysaccharides also seem to be a highly bioavailable and widespread source of carbon that facilitate high rates of initial microbial consumption. This indicates that protein content, most likely of tryptophan and tyrosine, can be used as an indicator of labile carbon in soils in permafrost watersheds,

such as the Kolyma (Balcarcyzk et al. 2009). This is important because protein content may be able to be used as a proxy to estimate initial respiration of organic carbon in soil.

When certain protein signatures are available, possibly with tryptophan and tyrosine-like components, they are preferentially consumed and yield high rates of respiration. Simple polysaccharides are another labile source of carbon that was most likely present and digested in all soil samples. This study demonstrates the potential vulnerability and labile nature of the yedoma carbon stock that has remained frozen since the Pleistocene. However, this study only quantifies the preliminary dynamics of microbial consumption upon initial permafrost thaw. To better understand the long term dynamics of permafrost degradation by microbes, a longer incubation period should be used. For a more detailed understanding of the chemical characteristics of yedoma, the next step would be to do a more sophisticated assessment of the chemical components using techniques such as fluorescence and NMR analysis.

Table 1. Site descriptions of sample locations.

	Tube Dispenser Lake	**Duvannyi Yar**
GPS	68°45’ N, 161°24’ E	68°37’ N, 159°02’ E
Code	TDL	DVY
Site Notes	side of thermokarst lake bank, southern slope site ~10m above lake level	yedoma deposits exposed along river bank, samples taken from within deposit
Sample Soil Depth	active layer: 10 cm transition layer: 90 cm yedoma: 130 cm	active layer: 20 cm transition layer: absent yedoma: 230 cm

Table 2. Mean organic carbon content is estimated for each soil stratum. For each soil sample, two samples were burned in the muffle furnace at 500 °C for four hours to determine organic matter. Mean values for organic matter in each soil location are listed below.

Location	**% Carbon**
DVY Yedoma	4.1
TDL Yedoma	3.2
TDL Transition	4.3
DVY Active	3.4
TDL Active	3.3

Table 3. P-values from t-tests to test whether the mean carbon content differs between soil sources. All p-values are less than 0.05. None of the soils differ significantly in mean carbon content measured.

	TDL ACTIVE	TDL TRANS	TDL PERM	DVY ACTIVE	DVY PERM
TDL ACTIVE	—				
TDL TRANS	0.13	—			
TDL PERM	0.5	0.06	—		
DVY ACTIVE	0.7	0.27	0.63	—	
DVY PERM	0.08	0.3	0.4	0.26	—

Table 4. P-values from t-texts to test whether the mean carbon consumption differs between soil sources. P-values less than 0.05 are bolded and indicate a statistically significant difference in mean carbon consumption between soils collected at these sites.

	TDL ACT	DVY ACT	TDL TRANS	TDL PLEIO	DVY YED
TDL ACT	—				
DVY ACT	0.068506	—			
TDL TRANS	**0.000213**	**0.001325**	—		
TDL PLEIO	**0.000919**	**0.000958**	0.058559	—	
DVY YED	**8.51E-05**	**2.4E-05**	**0.000134**	**0.001678**	—

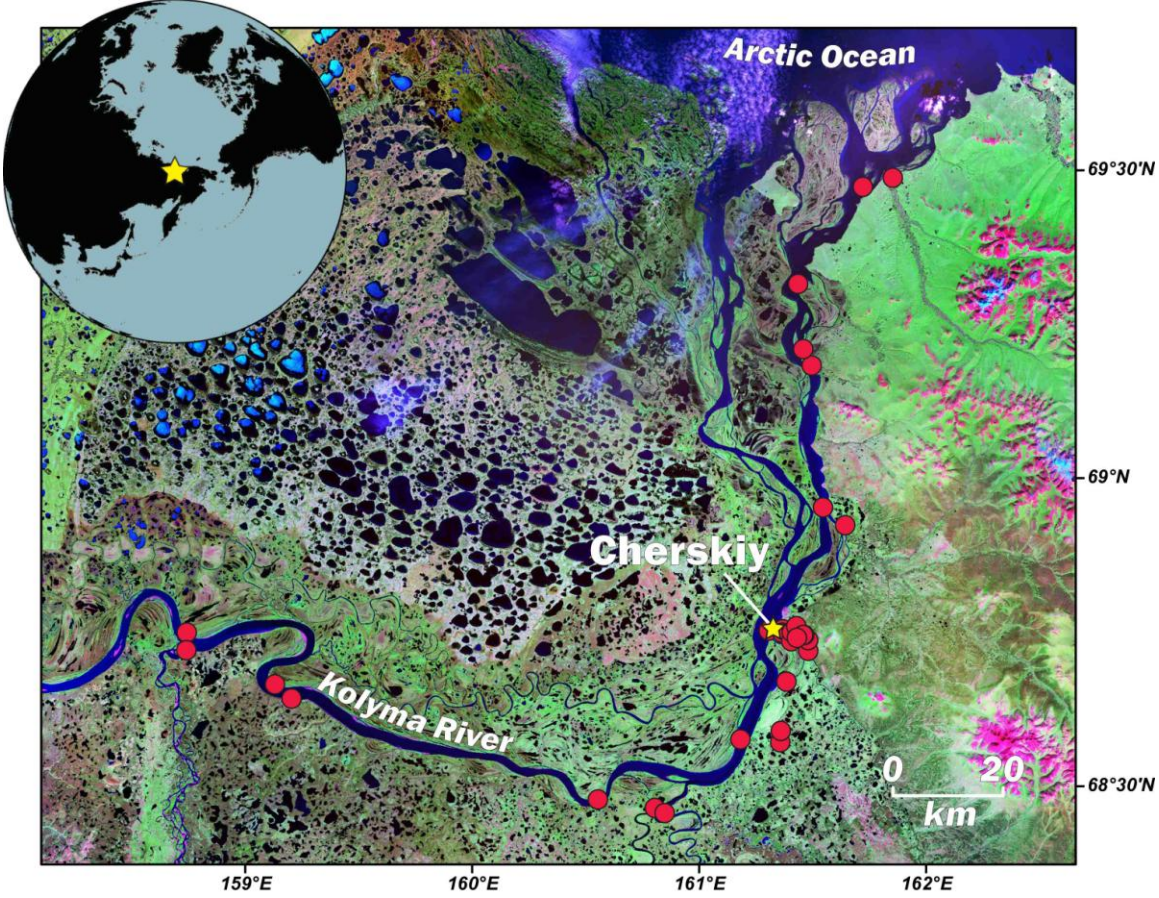

Figure 1. Mosaic Landsat image of Kolyma River watershed. Tube Dispense Lake and Duvanyi Yar sampling sites are indicated by yellow stars.

Figure 2. Tube Dispense Lake (TDL) sample sites (68°45’ N, 161°24’E)

Figure 3. Duvannyi Yar (DVY) sample sites (68°37’ N, 159°02’E)

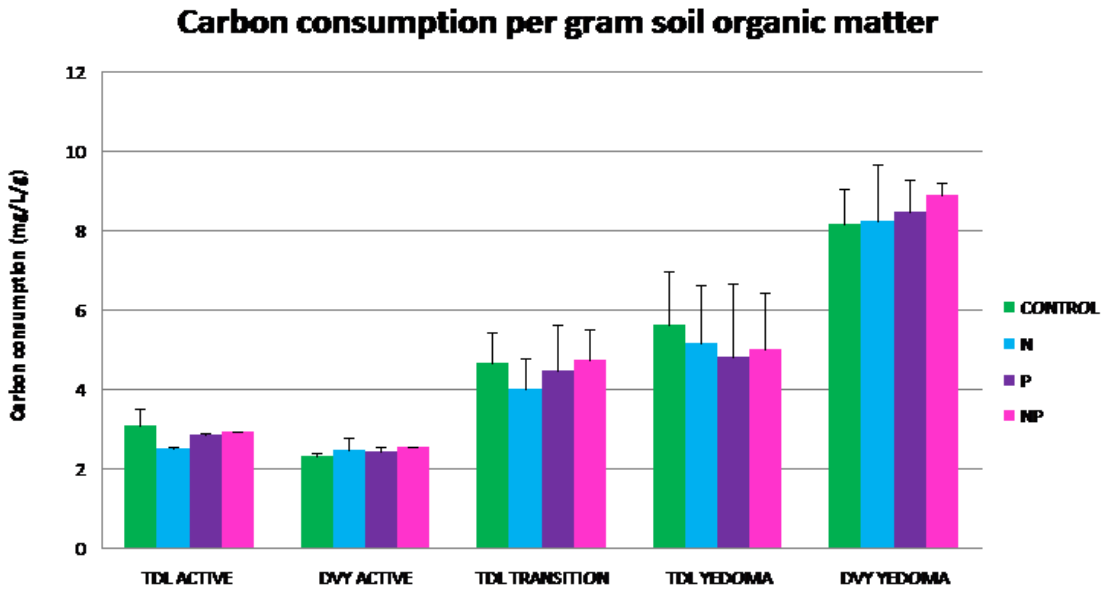

Figure 4. Decrease in dissolved oxygen in five-day BOD incubation period is converted to carbon consumption (mg/L) using the conversion factor of 0.375 (Sobsczak 2010). Carbon consumption (mg/L) is related to gram of organic matter present in each sample for each soil site (Figure 2). Mean carbon consumption (mg C / L slurry / g organic matter) is plotted for each soil location with nutrient treatments plotted according to color key. "Control" refers to the slurry that has no nutrient amendment. Slurries were spiked with 3 ml ammonia (N), 3 ml phosphoric acid (P), and both (N/P). For the five soil sources (Table 2), the control and the three nutrient treatments were made in duplicates resulting in a total of 40 BOD bottles. Mean values are plotted with one standard deviation is used to create error bars.

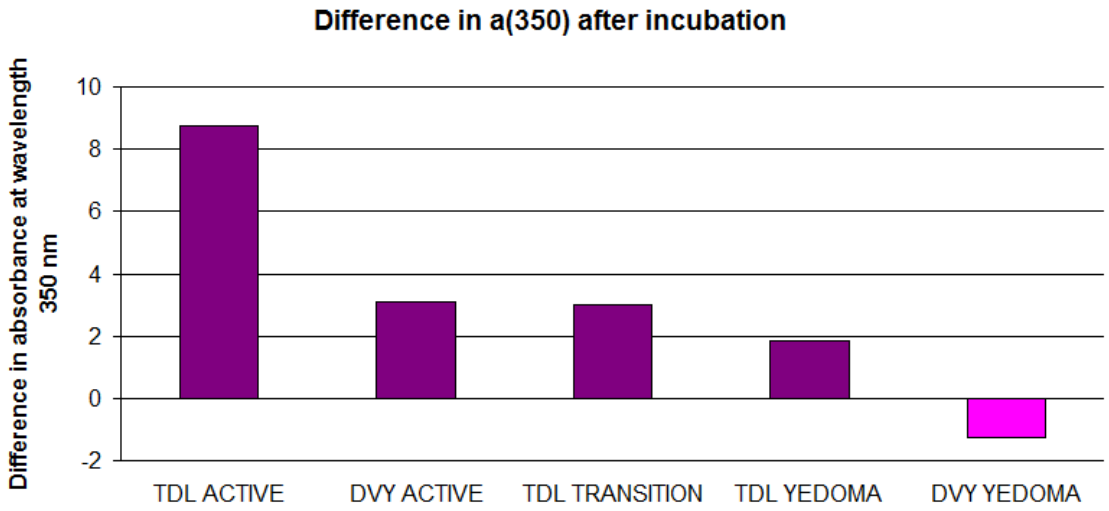

Figure 5. Differences in absorbance at wavelength 350 nm, a(350), after the BOD incubation indicates a change in the amount of dissolved organic carbon (DOC) in the sample. a(350) measurements were taken for each control slurry sample before and after the five-day incubation. Absorbance measurements for duplicates were averaged and plotted for each site. A positive change in a(350) indicate a net gain in DOC and a negative change in a(350) indicates a net loss in DOC. DVY yedoma was the only sample to exhibit a net loss of DOC after the five-day incubation.

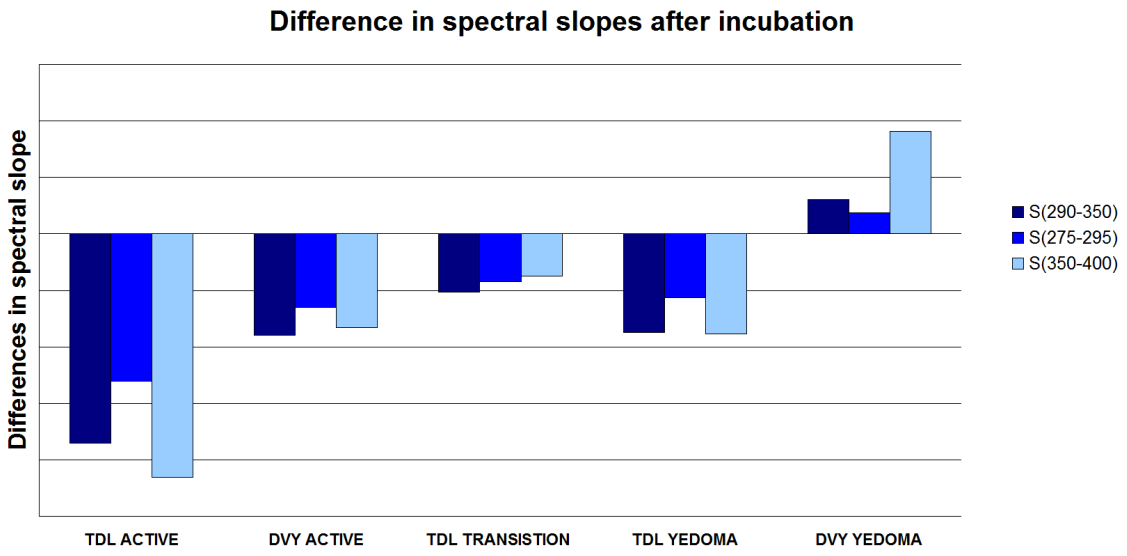

Figure 6. Change in absorbance slope indicates the change in the chemical composition of DOC. A negative slope indicates that the proportion of DOC shifts to contain more heavy, aromatic carbon compounds. A positive slope, exhibited only by Duvannyi Yar yedoma, suggests a shift in DOC makeup to contain more light, non-aromatic carbon compounds. Observing the shift in DOC chemical composition after the incubation allows inference as to what types of carbon compounds are preferentially degraded first by microbes.

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