Methane emission and transport by arctic sedges in Alaska: Results of a vegetation removal experiment

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Abstract. Methane flux and below-ground methane profile studies were conducted in a wet meadow vegetation manipulation site at the Toolik Lake Long-Term Ecological Research (LTER) site during the summers of 1995 and 1996. Control plots, moss-removal plots, and sedge-removal plots were studied to determine the role of these vegetation types in wetland methane emission and to study the gas transport mechanism. Methane emission was greatest from plots with intact sedges. Depth distributions of root density collected in 1995 showed a strong inverse relationship to pore water methane concentration. Results on insertion of arrays of gas-permeable silicone rubber tubing into the soil indicate that they are reasonable analogs for the physical process of gaseous diffusion through plants. The observed differences in flux between plots with and without sedges cannot be fully explained by differences in methane production or dissolved organic carbon concentrations in our measurements.

1. Introduction

Methane (CH$_4$) is well recognized as an atmospheric trace gas with important radiation-absorbing properties that influence the greenhouse effect on Earth. While the increase in atmospheric CH$_4$ concentration has varied around 1% per year [Dlugokencky et al., 1995], research has focused on monitoring and defining sources and sinks of CH$_4$ and the factors that influence them. Process-based model results match observations of CH$_4$ emission only under certain conditions [Cao et al., 1995, 1996; Walter et al., 1996]. Therefore we must improve our understanding of the processes and mechanisms to improve our ability to predict CH$_4$ emission.

Arctic wet meadow tundra represents an important source of CH$_4$ to the atmosphere. Approximately 30% of CH$_4$ emitted from natural wetlands is emitted from high-latitude wetlands such as wet meadow tundra [Reeburgh and Whalen, 1992; Reeburgh et al., 1993; Whalen and Reeburgh, 1988]. These ecosystems are especially important to study because they are predicted to experience greater change in response to changes in climate than temperate or tropical regions [Intergovernmental Panel on Climate Change (IPCC), 1992; Mitchell, 1989; Routel et al., 1992].

It is well recognized that plants greatly influence the processes which determine net CH$_4$ emission. Plants may influence CH$_4$ emission by (1) transporting CH$_4$ from below ground to the atmosphere through lacunae, (2) transporting oxygen from the atmosphere to the roots for root respiration and CH$_4$ oxidation, and (3) providing carbon substrates for CH$_4$ production through root respiration and exudation.

Previous studies of trace gas transport by plants, including several studies of northern wetlands, have demonstrated that plants play an important role in determining net emission through transport [Bubier et al., 1995; Chanton et al., 1992, 1993; Conrad, 1993; Dacey and Klug, 1979; Happell et al., 1993; Knapp and Yavitt, 1992; Mikkeldi et al., 1995; Miura et al., 1992; Nouchi et al., 1994; Saarnio et al., 1997; Schimel, 1995; Schütz et al., 1991; Sebacher et al., 1985, 1986; Shannon et al., 1996; Torn and Chapin, 1993; Whiting et al., 1992; Yavitt and Knapp, 1995]. The possible pathways of CH$_4$ emission are reviewed by Schütz et al. [1991] and Sharkey [1991]. Ongoing debate in the literature shows that the exact mechanism of CH$_4$ emission through plant transport is uncertain [e.g., Chanton et al., 1992; Kelker and Chanton, 1997; Morrissey et al., 1993; Schimel, 1995]. Regardless of whether the mechanism of CH$_4$ emission is stomatically controlled or pressure-controlled, net emissions measured above ground are insufficient to distinguish the relative importance of the plant influences listed above. Relatively few studies have made extensive measurements of below-ground CH$_4$ concentrations, and simultaneous aboveground and below-ground measurements should give better insight into the role of plants.

A study conducted at the Long-Term Ecological Research (LTER) site at Toolik Lake, Alaska, during 1993 and 1994 explored the effects of temperature and vegetation type on CH$_4$ and carbon dioxide (CO$_2$) fluxes in wet meadow and tussock tundra communities. The composition of plant growth forms appeared to be the most important factor controlling CH$_4$ emission in the wet meadow sites [Verville et al., 1998]. To understand the CH$_4$ production and emission processes as well as the relationship between aboveground and below-ground processes in these sites, we conducted more extensive measurements of CH$_4$ flux, below-ground CH$_4$ concentrations, root distribution, CH$_4$ production rates, and dissolved organic carbon, in a subset of the original treatment plots during the 1995 and 1996 growing seasons. Details about the study site are given by Verville et al. [1998], and essential background information is given below.
2. Methods

2.1. Study Site

The established experimental site at the Toolik Lake LTER (68°38' N, 149°36' W, elevation 720 m) [O'Brien, 1992] was chosen for this study for its advantageous location and well-maintained vegetation manipulations. The experimental site is a wet meadow tundra area on the margin of Toolik Lake. The area is saturated with water during the entire growing season and experiences only small changes in water table. Carex aquatilis and Eriophorum angustifolium are the dominant plant species. The moss Drepanocladus spp. forms a mat on the surface of the soil. The average depth to permafrost in this area was 55 cm.

The experimental plots were established in 1993, and the vegetation manipulation has been maintained by "weeding out" new shoots at the beginning of every field season since the plots were established. At the time of our study, the treatments had been maintained for 2 years. For this reason we believe that observed differences between treatments are likely to be real, rather than disturbance induced.

The removal treatments were established by removing all aboveground and much of the below-ground parts of the sedges in the sedge-removal plots and by removing the Drepanocladus mat in the moss-removal plots. The control plots were disturbed by hand to mimic the disturbance from vegetation removal [Verville et al., 1998]. Maintenance of the treatments from year to year involves removal of a relatively small number of sedges and mosses. To avoid disturbance effects, we did not make measurements on these plots immediately following vegetation removal.

2.2. Methane Fluxes

Two chamber sizes were used in this study: 1 m² (large) chambers described by Verville et al. [1998] and 0.076 m² (small) chambers described by Whalen and Reeburgh [1988]. Methane fluxes were measured on six plots using 1 m² chambers in 1995: two plots from which the moss layer had been removed (moss removal), two plots from which the sedges had been removed (sedge removal), and two plots from which no vegetation was removed (control). In 1996, two sedge-removal plots implanted with lengths of silicone rubber tubing (tubing implant, described below) were measured using 1 m² chambers in addition to the original six plots. Methane fluxes were also measured on 12 plots using 0.076 m² chambers, including three replicates of each plot type. The plots were surrounded by a boardwalk to prevent disturbance during sampling.

Gas-permeable silicone rubber tubing (Dow Corning, Silastic®) in 50 cm lengths was sealed on one end and inserted into the soil 15 cm. The open, aboveground end was attached to an aboveground wooden framework. The mixture of tubing sizes included 2.4 mm OD, 0.8 mm wall; 2 mm OD, 0.5 mm wall; and 1.7 mm OD, 0.9 mm wall. Results of laboratory experiments demonstrated that the gas inside the tubing immersed in water equilibrates with dissolved gases in the water within approximately 8 hours (S. K. Regli, unpublished data, 1996).

Compared to previous studies which used stainless steel tubes to study gas transport [Torn and Chapin, 1993], this method of physically mimicking plant transport more closely imitates diffusional transport through plants. The tubing is sealed at the bottom, does not fill with water, and allows gases to diffusionaly exchange across the tubing at any point.

Plant density was estimated by counting shoots of Carex aquatilis, Eriophorum angustifolium, and Eriophorum scheuchzeri in 1 m² quadrats. Tubes were inserted into the large (1 m²) plots to represent 7% of the average sedge density and into the small (0.076 m²) plots to represent 87% of the average sedge density. The tubing insertion tool used in these plots was also used in the other six plots in order to cause the same disturbance in all plots.

Methane fluxes were measured using static chamber procedures similar to Whalen and Reeburgh [1988]. The chamber bases remained on the plots throughout the season. Chamber tops were placed on the plots temporarily for each flux measurement. Duplicate air samples were taken every 10 min for 30 min from the large chambers and every 15 min for 45 min from the small chambers. Fans inside the large chambers insured adequate mixing of the headspace. Air temperature and soil temperatures to a depth of 11 cm were taken at every flux measurement using thermistor probes. The air samples were analyzed within 12 hours using a gas chromatograph (Shimadzu 8A and Mini-2) equipped with a flame ionization detector and a 1 m molecular sieve 5A column. The National Institute of Standards and Technology (NIST) and NIST-related standards were used to calibrate the gas chromatographs.

The estimates for annual emission are based on a growing season determined by soil temperature. The beginning of the growing season was defined as the first day the soil temperature at 10 cm rose above 0°C. The end of the growing season was defined as the first day the soil temperature at 10 cm was less than 0°C. Winter fluxes are assumed to be negligible for the annual estimate. Observed fluxes were linearly extrapolated to zero CH4 flux on these dates and integrated for a calculation of annual emission. Emissions during the measurement period were integrated using the trapezoidal rule. Soil temperature records from the LTER database (J. Laundre, Marine Biological Laboratory, Woods Hole, Massachusetts) were used to determine the length of the growing season.

2.3. Pore Water Methane

Pore water CH4 concentrations were sampled using a pore water equilibration sampler [Hesslein, 1976] made of 1/2 inch acrylic with ports of approximately 2 mL volume. The ports were filled with deionized water and sealed with a gas-permeable Teflon membrane. The samplers were placed in degassed deionized water to remove most of the dissolved gases in the sampler. The samplers were inserted and allowed to equilibrate in the ground for 6-8 days. The water samples were extracted from each port by syringe and injected into 20 mL serum vials filled with nitrogen gas (N2). The serum vials were shaken to extract the dissolved gases and allowed to equilibrate to room temperature. The headspace of the serum vial was sampled by syringe and analyzed by gas chromatography. Solubility coefficients for CH4 from Yamamoto et al. [1976] were used to convert measured headspace concentrations to the micromolar (µM) concentrations reported.

2.4. Root Density Depth Distribution

Two soil cores approximately 8 cm diameter and 30 cm long were collected for root density distribution measurements from an area adjacent to the study site. The cores were frozen and transported to the laboratory in Irvine, California, where each
core was divided into 3 cm depth sections, and live and dead roots were separated from other dead organic matter. Live and dead roots were distinguished on the basis of their color and texture. Live roots were white in color and demonstrated structural resistance to pinching; dead roots were dark in color and limp. The roots were dried at 60°C to constant weight following separation from the soil matrix.

2.5. CH₄ and CO₂ Production

Three soil cores (6.5 cm diameter, 18 cm long) were collected from each of three types of plots (control, moss removal, and sedge removal). The cores were cut into 6 cm depth sections, placed in 27 individual 1 L Mason jars, and flushed with pure N₂. The sealed jars were placed in an incubator at 7°C, and 10 mL of headspace gas were sampled from each jar every day for up to 7 days. The air samples were analyzed for CH₄ and CO₂ concentrations by gas chromatography (Hach Carle Series 100 AGC with FID and TCD). Following the incubation, the soil cores were dried at 60°C to constant weight.

Two separate sets of cores were collected for two incubation experiments during the 1996 field season. The second incubation experiment was done approximately 1 week after the first incubation experiment. The soil cores were collected just before the start of each experiment, and both incubation experiments were performed under the same conditions. The accumulation rate of CH₄ and CO₂ was expressed as production rate of CH₄ or CO₂ per gram dry weight of soil. Data were analyzed for depth as the controlling variable and for treatment as the controlling variable.

2.6. DOC Concentrations

Pore water samples for dissolved organic carbon (DOC) analysis were collected using 1/8 inch diameter stainless steel tubing probes. The perforated end of each probe was inserted into the ground to a known depth, and pore water samples were withdrawn using a 60 mL syringe. Samples were immediately filtered in the field (Whatman GF/F, precombusted) and then acidified with HCl and stored in the dark at 4°C. The samples were analyzed by a Shimadzu TOC-5000 analyzer in the laboratory of George Kling at the University of Michigan.

3. Results and Discussion

3.1. Methane Flux Measurements

Seasonal CH₄ flux measurements are plotted in Figure 1. During the 1996 season fluxes were measured on large (1 m²) plots (Figure 1b) and also on small (0.076 m²) plots (Figure 1c) for a shorter period of time. Data points have been connected sequentially with straight lines to show the curves which were integrated as part of the calculation of annual emission.

Methane emission from plots having intact sedges was significantly higher than emission from plots without intact sedges in both 1995 and 1996 (Table 1). The effect of sedges on CH₄ emission has been observed in many other studies [Mikkela et al., 1995; Schimel, 1995; Thomas et al., 1996; Torn and Chapin, 1993; Verville et al., 1998; Waddington et al., 1996; Whiting and Chanton, 1992]. Increased emission from vegetated areas is primarily attributed to plant-mediated transport.

Emission of CH₄ from moss-removal plots tended to be higher than emission from control plots, as observed previously [Verville et al., 1998]. Methane oxidation is highly dependent on water table level and floristic association. Vecherskaya et al. [1993] found high CH₄-oxidizing activity associated with moss layers. Also, removal of the moss layer removes any physical impediment to CH₄ diffusion through the soil surface. Less CH₄ is oxidized on its way out; therefore emission of CH₄ is higher.

Soil temperatures were measured along with each flux measurement and varied at the soil surface depending on the time of day and the amount of incident light. Average soil temperatures measured in treatment plots did not significantly

![Figure 1](image-url)
Figure 1. (continued)

differ from the control plots (averages of 4.5°, 4.7°, 5.8°, 5.6°C at 1 cm depth, from control, moss-removal, tubing-implant, and sedge-removal plots, respectively). Sedge-removal plots tended to have higher soil surface temperatures due to the greater absorption of radiation by the dark-colored moss layer. However, there were no statistically significant differences in soil temperature between plots. Since the water table in all of these plots was at or above the soil surface, the soil pore water acted as a buffer against large soil temperature variations.

Silicone rubber tubing inserted into sedge-removal plots in 1996 created tubing-implant plots. The tubing mimics diffusive gas transport by sedges but does not add organic matter to the soil. Silicone rubber tubing has been used in the past to make artificial roots for oxygen diffusion studies [Armstrong, 1967, 1972] and to introduce propane into peat for tracer studies [Fechner and Hernond, 1992]. Addition of the silicone rubber tubing to imitate plant transport of CH₄ tended to increase emission over the CH₄ emission observed from sedge-removal plots (Figure 1b). The effect of the silicone rubber tubing insertion is more obvious in the smaller plots where tubing was inserted to a density more closely approximating true plant density (Figure 1c). The relatively high initial emissions in the small plots may be due to the release of high below-ground concentrations of CH₄. These emissions reflect a transition between two steady state conditions. Fluxes from tubing-implant plots did not fall below the fluxes from sedge-removal plots, indicating that the increased emission from tubing-implant plots was not a temporary effect of the addition of tubing.

3.2. Pore Water Methane Concentration

Three below-ground CH₄ concentration profiles were obtained from each experimental plot during the 1996 growing season (Figure 2). Such detailed concentration profiles have not previously been measured in tundra. Comparison of CH₄ concentrations at the same depths across treatments shows that plots with intact sedges (Figures 2a-2d) had lower below-ground CH₄ concentrations below 10 cm than plots without sedges (Figures 2e-2f). Also, the total below-ground CH₄ concentration was lower in plots with intact sedges. This observation agrees with the observations of aboveground emission and can also be attributed to plant-mediated transport of CH₄ out of the soil.

The below-ground profiles suggest that plant transport of gases is the first limiting factor for emission because the pore water CH₄ concentrations in the sedge-removal plots are high, but the emissions are low. Although we expect to find higher below-ground CH₄ concentrations in plots with plants because the plants contribute organic matter (i.e., methanogenic substrate) to the soil [Whiting and Chanton, 1992], we found lower concentrations in plots with sedges than in plots without sedges. This result must be due to the increased transport of CH₄ out of the soil facilitated by the sedges and/or the increased amount of CH₄ oxidized in the rhizosphere due to transport of oxygen to the roots of the sedges. In unvegetated areas, CH₄ appears to be oxidized before it reaches the atmosphere.

Plots with silicone rubber tubing inserted into the soil had lower CH₄ concentrations than sedge-removal plots. This effect may be due to a combination of processes. The silicone rubber tubing facilitates transport of CH₄ from the soil to the atmosphere and does not add organic matter to the soil. At the same time, the tubing allows transport of oxygen into the soil, which may increase CH₄ oxidation.

Solid and dashed lines in Figure 2 indicate the soil surface and approximate water table level, respectively. Water table level has an obvious effect on diffusion of CH₄ through the soil and degree to which CH₄ is oxidized as it diffuses through the soil surface (Figure 2). Our study site, located on the margin of Toolik Lake, did not experience dramatic fluctuations in water table level, and the water table remained at or above the soil surface during the entire growing season. We did not observe any treatment effects on water table.

The oxic zone near the water table surface is indicated in the below-ground profiles by a dramatic decrease in the CH₄ concentration. The CH₄ concentration approached atmospheric below the

![Table 1. Average Annual Methane Emission (mg CH₄ m⁻² y⁻¹)](attachment)

<table>
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<th>Plot Type</th>
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<th>1996</th>
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<td>4300 (2240-6434)</td>
<td>6800 (3962-9834)</td>
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<td>5300 (5262-5273)</td>
<td>7300 (4973-8787)</td>
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<tr>
<td>Sedge Removal</td>
<td>700 (309-1103)</td>
<td>500 (122-884)</td>
<td>730 (71-1832)</td>
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<tr>
<td>Tubing Implant</td>
<td>700 (687-712)</td>
<td>700 (687-712)</td>
<td>3500 (1128-6820)</td>
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</table>

*Results from small plots, n=3.

Values are means and ranges (in parentheses); n=2.
Figure 2. Below-ground pore water CH$_4$ and dissolved organic carbon (DOC) concentration profiles collected in 1996 for (a) control plot 1, (b) control plot 2, (c) moss-removal plot 1, (d) moss-removal plot 2, (e) sedge-removal plot 1, (f) sedge-removal plot 2, (g) tubing-implant plot 1, (h) tubing-implant plot 2. Pore water CH$_4$ sampled on July 15, 1996 (squares), July 30, 1996 (circles), and August 12, 1996 (triangles) for Figures 2a, 2c, 2e, and 2h, and on July 23, 1996 (squares), August 6, 1996 (circles), and August 17, 1996 (triangles) for Figures 2b, 2d, 2f, and 2g. DOC (crosses) sampled on July 9, 1996, in all plots. Soil surface (solid lines, defined as 0 cm depth) and average water table level (dashed lines) are shown for each plot.
Figure 2. (continued)
CH₄ concentration at the water table level, except for two plots without sedges (Figures 2e and 2g), in which the CH₄ concentration decreased to a minimum several centimeters below the water table level. Plots without sedges had oxic zones which extended deeper in the soil. Pore water CH₄ concentrations began to decrease as much as 20 cm below the soil surface. The thicker oxic zone may be due either to decreased CH₄ production or to increased oxygen availability through decreased organic matter oxidation in the absence of sedges. We expect that the lower CH₄ concentrations in the top 10 cm of the profile might be due to decreased organic substrate availability [Whiting and Chanton, 1992] but our measurements of dissolved organic carbon (DOC) did not show differences between plots.

Within each treatment, pore water CH₄ concentrations reflected the relative emissions observed aboveground. Below-ground concentrations generally stayed within the same range throughout the measurement period and did not change drastically relative to plant growth stage. The shapes of the profiles also remained relatively constant through the measurement period.

3.3. Correlation of Pore Water CH₄ and Root Density Depth Distribution

We expect that plant-mediated transport would have significant effects on the below-ground concentration of CH₄. Changes in CH₄ concentration profiles corresponding to changes in oxygen profiles have been observed in a subtropical wetland [King et al., 1990]. In the soil, plant-mediated transport is centered at the roots, and greater root density also means greater root surface area for exchange of gases.

The below-ground CH₄ concentrations and the root density distribution profiles sampled in 1995 showed a strong inverse relationship for both cores (see, for example, Figure 3). In zones of high root density the CH₄ concentrations are lowest, and in zones of low root density, the CH₄ concentrations are highest (see Table 2; correlation coefficient $r = -0.9, n = 14, p < 0.05$). This result suggests that roots play an important role in determining CH₄ transport and rhizosphere oxidation.

Our results are in agreement with results of incubation studies by Gerard and Chanton [1993], which show a relationship between CH₄ uptake rates and live root density. We are not, however, able to distinguish the processes of rhizospheric oxidation and lacunar transport with these data alone. Future isotopic analyses of archived headspace and soil pore water CH₄ samples in addition to CH₄ tracer studies are needed to understand the importance of rhizospheric oxidation in this system.

3.4. DOC Concentrations

The DOC values for pore water samples taken from different depths are shown in Figure 2 with the pore water equilibration sampler profiles from those plots. There was no obvious treatment effect on the DOC concentrations. The DOC concentrations may be more closely related to the quality of the soil organic matter (past vegetation growth) rather than the current surface vegetation; if the DOC pool is dominated by relatively older, recalcitrant carbon, the effects of vegetation manipulation would not be apparent (G. W. Kling, personal communication, 1997).

A recent study by Bianchi et al. [1996] investigated the possibility of DOC as a predictor of CH₄ emission from a

<table>
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<th>Core</th>
<th>Category</th>
<th>$R$</th>
<th>$p$</th>
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below-ground CH₄ production has little to do with observed aboveground fluxes. In a study also conducted in a wet meadow community at the Toolik Lake LTER, Schimel [1995] also found that CH₄ production was not a good predictor of CH₄ flux. On the basis of our results, however, we cannot exclude the possibility that differences in CH₄ production may explain differences in CH₄ fluxes between control and moss- and sedge-removal plots.

The differences in the results of these two incubations may be due to several factors. Methane emissions, although clearly different according to treatment in this study, are highly variable in general. We expect that CH₄ production will show the same kind of high spatial variability. Saarnio et al. [1991] also observed differences in CH₄ production in different microsites, but these differences were not sufficient to explain the variation in CH₄ emissions from a mire study site in Finland. There is no direct, noninvasive way of measuring CH₄ production in soil, and removal of soil from its natural environment for laboratory study inevitably disturbs its natural state. Use of tracers to study CH₄ production may provide a more realistic measurement of CH₄ production rates.

Both incubation experiments showed a significant effect of depth on CO₂ production ($p<<0.05$; Figure 5). It appears that the most active zones of respiration are the top layers of the soil and that carbon substrate from recent plant production is not limiting. We did not observe any effects of treatment on CO₂ production. Although respiration derived from plant roots is thought to account for 35-45% of total soil respiration [Silvola et al., 1996], production of CO₂ in our system did not depend on the presence of live roots. Our depth pro-
files of root density do indicate that the greatest density of roots occurs in the top 15 cm of the profile. High dissolved carbon content of the soil pore water and high rates of lateral transport of soil pore water may account for the lack of effect of vegetation removal on CO₂ production.

4. Conclusions

The experimental manipulation of these plots has allowed us to closely study the gas transport processes and their effects on below-ground CH₄ concentration and production. Our simultaneous measurements of aboveground emissions combined with measurements of below-ground profiles of CH₄ concentrations and root density give us insight into the role of plants in controlling net CH₄ emissions. High-resolution measurements of below-ground CH₄ concentrations combined with analyses of root density depth distribution indicate that vegetation strongly affects CH₄ emission by facilitating gas transport between the soil and the atmosphere.

Our emission measurements agree with previous measurements of CH₄ emission in this ecosystem. We confirmed that aboveground observations of CH₄ emission are primarily dependent on the mode of CH₄ transport from the soil to the atmosphere, which depends on the presence of plants. The extent of CH₄ oxidation determines CH₄ emission from unvegetated areas. In addition to using vegetation removal treatments, we used silicone rubber tubing to study passive gas transport unaffected by plant biology. We demonstrated that silicone rubber tubing serves as a reasonable physical analog with analyses of root density depth distribution indicating that vegetation strongly affects CH₄ emission by facilitating gas transport between the soil and the atmosphere.

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