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# Production and export of dissolved C in arctic tundra mesocosms: the roles of vegetation and water flow

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**Abstract.** To better understand carbon (C) cycling in arctic tundra we measured dissolved C production and export rates in mesocosms of three tundra vegetation types: tussock, inter-tussock and wet sedge. Three flushing frequencies were used to simulate storm events and determine potential mass export of dissolved C under increased soil water flow scenarios. Dissolved C production and export rates differed between vegetation types (inter-tussock > tussock > wet sedge). In the absence of flushing, dissolved organic C (DOC) dominated production in tussock and inter-tussock soils but was consumed in wet sedge soils (8.3, 32.7, and –0.4 $\mu$g C g soil$^{-1}$day$^{-1}$). Soil water dissolved C concentrations declined over time when flushed at high and medium frequencies but were variable at low flushing frequency. Total yield of dissolved C and DOC increased with increased flushing frequency. The ratio of DOC to dissolved inorganic C exported dropped with increased flushing under tussock but not inter-tussock or wet sedge vegetation. Mass export per liter of water added declined as flushing frequency increased in tussock and inter-tussock mesocosms. Export and production of dissolved C were strongly correlated with above ground biomass, but not with photosynthetic rates or below ground biomass. DOC quality was examined by measuring production of Toolik Lake bacteria fed mesocosm soil water. When normalized for DOC concentration, wet sedge soil water supported significantly higher bacterial production. Our results indicate that arctic tundra soils have high potentials for dissolved C export, that water flow and vegetation type mainly control dissolved C export, and that responses of aquatic microbes to terrestrial inputs depend on the vegetation type in the watershed.

## Introduction

Water flow provides a major link between land and water by physically transporting dissolved carbon and nutrients from soils to streams and lakes. The export of carbon and other materials from land is controlled strongly by the amount and timing of water flowing through the system. Many studies have demonstrated this relationship in a variety of environments (Likens and Bormann 1975; Fisher and Likens 1973; Lewis and Grant 1979; Peterson et al. 1986; Dillon and Molot 1997a; Hope et al. 1997). Although annual discharge events such as spring run-off often dominate the export of materials, individual storm events may also be important (Hinton et al. 1997). The ultimate potential for export of materials from land resides in the land surface characteristics and in processes that occur during and between water flow events. Important characteristics include soil pH, mineralogy, organic matter (Jardine et al. 1989), C content (Moore 1987), and the overlying vegetation (Cronan and Aiken 1985; Kling 1995; Giblin et al. 1991; Shaver and Chapin 1991). Important soil processes include plant and microbial production, decomposition, and sorption. For example, McDowell and Wood (1984) found that adsorption of dissolved organic carbon (DOC) to spodic horizons was a major control on DOC concentrations in a New Hampshire stream. In addition, experiments on boreal temperate forest soils showed that increased frequency of leaching led to increased DOC export but not $CO_2$ mobilization (Godde et al. 1996). However, there are few published field studies that have analyzed the specific relationship between the net rates of soil production of materials and the frequency of water flow events removing those materials.

It is particularly important to understand the relationship between water flow and material transport in the Arctic because the land-water linkage is very strong (Kling 1995; Kling et al. 1991). The strength of this connection is due in part to the presence of a permafrost boundary in the soil that prevents deep groundwater movement. Additionally, the high ratio of productivity to decomposition in arctic systems results in a great potential for export of materials from land to water. Low rates of decomposition due to reduced drainage and a cooling effect of the underlying permafrost result in a thick organic layer with a high organic matter content. Despite much lower rates of net annual production in the arctic, the magnitude of dissolved C export from arctic systems ( $\sim 3.7$ g C $m^{-2}$ of basin, including gaseous losses (unpublished data)) can lie within the ranges observed in temperate systems (Table 1). Dissolved exports in temperate and boreal systems account for about 2% of net primary production (NPP) on average, and are unlikely to account for more than 20% (based on data from Hope et al. (1994); Goetz and Prince (1998); Waring et al. (1998)). In contrast, dissolved losses from arctic systems can reach 37% of net ecosystem production (NEP) during years of highest production and may be even greater than production when NEP is low or negative. These dissolved losses, and their impacts on C balance in the Arctic, can be especially important in the summer months during rain events; this is because the main drainage even of the year, spring thaw, occurs when arctic soils are still frozen.

In addition to altering terrestrial export, changes in water flow and material transport impact aquatic food webs by affecting the DOC and nutrients available for bacterial and primary production. Because NPP is low in arctic streams (Peterson et al. 1986) and lakes (Miller et al. 1986), terrestrial inputs represent an important source of nutrients and of C to aquatic systems. The bioavailability of terrestrial DOC inputs to aquatic bacteria may play an important role in controlling microbial food web dynamics in downstream receiving waters. DOC bioavailability can be assessed through analysis of the chemical composition (e.g., Peuravuori and Pihlaja (1991); Malcolm (1990)) or by measuring its capacity to support bacterial production (Meyer et al. 1987). As DOC is transported downslope, it generally becomes less available due to uptake of labile forms of DOC (e.g., hydrophyllic neutrals) by soil microbes (Michaelson et al. 1998). Other influences on DOC bioavailability include landscape geomorphology (Munn and Meyer 1990), overly-

*Table 1.* Summary of studies examining the annual export of dissolved organic C from watersheds in various regions

| Ecosystem type | Watershed description | DOC yield (kg C $ha^{-1}$ $y^{-1}$) | Reference |
|---|---|---|---|
| Tropical | Orinoco River drainage basin | 54 | Lewis and Saunders 1989 |
| | Amazon River | 53 | Richey et al. 1994 |
| | Amazon River tributaries | 95–5740 (avg = 916) | Guyot and Wasson 1994 |
| Temperate | Maine, USA catchment – forested | 48 | Cronan et al. 1999 |
| | Maine, USA catchment – farmland | 30 | |
| | 2 NE Scotland rivers | ~20 | Hope et al. 1997 |
| | Great Whale River, Quebec, CA | 21 | Hudon et al. 1996 |
| | St. Lawrence River Drainage Basin | 14 | Pocklington and Tan 1987 |
| Temperate/Boreal | Various temperate & boreal catchments in N. America, Europe & New Zealand | 10 –100 | Hope et al. 1994 |
| Arctic | North Slope of Alaska, USA | 18 –27 | Peterson et al. 1986 |
| Desert | Sycamore Creek, Arizona, USA | 0.2 –15 | Jones et al. 1996 |

ing vegetation (Schimel and Clein 1996), and stream discharge (Leff and Meyer 1991). Labile forms of DOC will be incorporated into food webs more readily and retained by the system, whereas highly refractory DOC is more likely to be exported from the system. Thus understanding patterns of DOC bioavailability is necessary for predicting C balances and responses of microbial communities in streams and lakes.

Arctic ecosystems in general are easily affected by disturbance and slow to recover, and the permafrost boundary is sensitive to changes in water flow patterns (see Reynolds and Tenhunen (1996)). In addition, disturbance caused by climate change is expected to be most dramatic in arctic regions (Schlesinger and Mitchel 1985). Predictions of the effect of climate change on soil moisture and precipitation patterns are mixed; some tundra regions are expected to experience increased precipitation while other regions will become drier (Lachenbruch and Marshal 1986; Maxwell 1992). Although current models disagree over which regions will be wetter and which drier, it is likely that any changes in the permafrost boundary will strongly impact the transport of materials from land to water. Such changes in land-water export may also have implications for regional and perhaps global carbon budgets. The present net exchange of C between land and atmosphere in the arctic is small compared to the net global exchange. However, arctic soils contain considerable C stores, up to 200 Pg C (Oechel and Billings 1992), and store about 13% of the soil C on earth (Post et al. 1982). With the threats of a different moisture balance from climate change and increased disturbances from human development, these large stores now locked up in permafrost could re-enter the active C cycle on earth's surface.

To determine the controls on production and export of dissolved C in arctic soils we used a mesocosm approach similar to that of Johnson et al. (1996). Examining C dynamics in mesocosms presents a powerful tool for obtaining rates of ecosystem processes, (i.e., dissolved C production and export) because the confounding effects of lateral flow of material in to and out of a sampling area can be removed. In this study we used plant-soil mesocosms to address the following questions: (1) what are the production rates of dissolved carbon and nutrients in arctic tundra soils? (2) What is the potential mass export of dissolved carbon from arctic tundra soils during summer rain events? (3) How does the overlying vegetation influence dissolved C production rates and mass export? (4) How does flushing frequency affect the export of carbon? And (5) how is DOC quality related to vegetation cover?

## Study area and materials and methods

### *Tundra mesocosms*

Twelve intact soil-plant cores (28 cm diameter to depth of permafrost boundary (15–36 cm)) from two distinct landscape types (tussock and wet sedge tundra) were collected near Toolik Lake, Alaska (68°38′00″ N, 149°36′15″ W). Cores were transferred to five gallon (20 L) buckets and cooled with circulating lake water; this maintained a range of soil temperatures (8 to 15 °C) in all mesocosms (ambient air temperature ranged from 1 to 21 °C during the study period). We chose landscape types that are important in their extent across arctic regions ( ~ 3/4 of arctic land surface is wet sedge or tussock tundra) and their potential to impact C export under changing climatic conditions. These landscape types also occupy different topographic locations within the catchment. Wet sedge tundra occurs at lake margins in poorly drained lowland sites, and is found extensively throughout the Northern Coastal Plain region. In these communities, water tables are generally above the soil level. Tussock tundra occurs on gentle upland slopes. Tussock tundra water tables fluctuate with precipitation, but soils are better drained than in wet sedge tundra.

Within these two general landscape types we distinguished between three vegetation types (and used four mesocosms of each type). At small scales, (< 1 m) wet sedge tundra is fairly homogeneous and *Carex chordorrhiza, C. rotundata, Eriophorum aquatilis*, and *E. angustifolium* were the most abundant species. Tussock tundra, however, consists of two distinct vegetation and hydrologic types; tussock and inter-tussock vegetation. Tussocks were dominated by sedges (*Eriophorum vaginatum*) although a few dwarf shrub species occurred. Between tussocks (inter-tussocks), ground cover is moss-dominated (*Sphagnum* spp., *Hylocomium* spp., and *Aulacomium* spp.), but also includes dwarf shrubs (*Betula nana, Vaccinium vitus idaea, Ledum palustre*). Hydraulic conductivity is higher in inter-tussock soils and the majority of water flows through inter-tussock areas, around the dense tussocks areas.

Although there are limitations to the use of mesocosms in studying ecosystem-level processes (e.g., lack of horizontal water flow, disturbance induced by coring, potential deviations from natural temperature regimes), arctic tundra soil mesocosms have been shown to provide reliable information on plant physiological processes. Natural photosynthetic rates compare well with photosynthetic rates of mesocosm plants (Johnson et al. 1996), which suggests that any limitations of mesocosms do not in general affect plant physiological processes.

### *Treatments*

Two water flushing treatments were used. After a nine-day acclimation period, one set of six mesocosms (two replicates of the three vegetation types) was flushed once every other day for 16 days. This treatment is referred to as the low flushing frequency. A second set of six mesocosms was flushed 4 times daily for 2.5 days (*high* flushing frequency), allowed to sit for 12 days (*non-flushing* period), and then flushed 2 times daily for 2 days (*medium* flushing frequency). This alternating treatment is referred to as the *high/ medium* flushing frequency. High and medium flushing frequencies were carried out in the same set of mesocosms due to time limitations; thus while these treatments are not statistically independent, they do represent what happens in nature because the same ″plot″ of soil and vegetation

*Table 2.* Average soil mass, above ground biomass, summary of water additions, and comparison to natural rainfall for each set of replicate microcosms. Low frequency flushing lasted 15 days. High frequency flushing lasted three days, followed by no flushing for 12 days and then medium flushing for two days ($n$ = 2. T = tussock, IT = Intertussock, and WS = wet sedge).

| | Low flushing | | | High/med flushing | | |
|---|---|---|---|---|---|---|
| | T | IT | WS | T | IT | WS |
| Soil mass microcosm$^{-1}$ (g) | 3988 | 1286 | 2474 | 3434 | 1692 | 2105 |
| Above ground biomass (g) | 20.05 | 25.6 | 11.35 | 18.5 | 25.6 | 11.6 |
| Total $H_2O$ added (cm) | 33.29 | 28.54 | 39.14 | 71.62 | 65.37 | 47.58 |
| Proportion of 1997 summer rain fall | 1.55 | 1.33 | 1.82 | 3.33 | 3.04 | 2.21 |
| Proportion of rainfall during experiment | 8.62 | 7.39 | 10.14 | 18.55 | 16.94 | 12.33 |

receives varying amounts of rain over time. Additionally, DOC concentrations in the soil waters at the beginning of each flushing treatment were similar.

We chose flushing frequencies that represent rain events in excess of current natural precipitation patterns in order to (1) examine the effect of a brief, intense physical flushing on the soil, (2) reduce soil water C concentrations through dilution in order to measure the production of C over time without flushing, and (3) determine the maximum potential for export in terms of extremes of water flow. Low frequency flushing simulated a rain event of typical intensity ($\sim$5.5 mm d$^{-1}$) but of longer duration than current precipitation patterns. Both medium ($\sim$20 mm d$^{-1}$) and high ($\sim$45 mm d$^{-1}$) intensity flushing simulated precipitation in excess of current natural conditions. Water additions were 1.3 to 1.8 (low) and 2.2 to 3.3 (medium and high) times the average summer rainfall (Table 2), and 7–19 times the natural precipitation that fell during the length of the experiment (to which all mesocosms were exposed). The mass of soil in each mesocosm was determined using measured soil volumes from this experiment and bulk densities (Johnson et al. 1996) of organic layers for each vegetation type. Soil sub-samples were analyzed for C and N content on a Carlo Erba elemental analyzer.

### *Flushing*

Soil water was exchanged by draining soils to field capacity (about 2 L removed). Tussock and inter-tussock soil water was collected in an evacuated flask by sucking soil water through 0.5 cm diameter tygon tubing. This method was not suitable in wet sedge mesocosms, so soil water was collected through a drain hole in the bottom of the mesocosms. Immediately after flushing, mesocosms were refilled with Toolik Lake water that was bubbled with $N_2$ to remove $O_2$ and $CO_2$. A fertilizing effect on plants or soil microbes is unlikely because Toolik Lake water is extremely low in available nutrients (Whalen and Cornwell 1985; Miller et al. 1986). Soil water levels were maintained to simulate field conditions ('just below' the soil surface in tussocks and inter-tussocks and 'just above' the surface in wet sedge).

### *Soil water sampling*

Before each water exchange, soil water was collected for dissolved gas samples ($CO_2$ and $CH_4$) and dissolved inorganic carbon (DIC, includes carbonate, bicarbonate, and $CO_2$). Samples were collected by drawing water through a steel needle using a syringe. Soil water samples were collected from effluent water for chemical analysis. During the non-flushing period a total of 200 mL of soil water was removed by needle and syringe.

### *Soil water analysis*

Soil water and Toolik Lake water samples were analyzed for DOC, DIC, $CO_2$, and $CH_4$. Soil water sample concentrations were corrected for the original concentration of dissolved substances in Toolik Lake water. Gas samples were analyzed on a gas chromatograph after a headspace equilibration following Kling et al. (2000). Concentrations of gases and DIC were estimated by interpolation for every fourth flush during the high frequency flushing regime. Soil water samples were filtered through pre-rinsed, precombusted GF/F filters to remove particulates. DOC concentrations were measured using a Shimadzu TOC 5000 Carbon Analyzer. Total dissolved C was calculated as the sum of DOC, DIC, and $CH_4$. Soil water absorbance at 360 nm was measured on a spectrophotometer to determine general differences in DOC composition.

### *Bacterial production*

To examine the bioavailability of DOC to aquatic microbes, we measured bacterial activity as the incorporation of the radiotracer $^{14}$C-leucine. Soil water DOC was used as the substrate for growth for an inoculum of Toolik Lake water bacteria ($1.55 \times 10^6$ cells mL−1; M. Bahr pers. comm.). Seven mL of a 0.22 $\mu$m membrane filtered soil water and 50 $\mu$L $^{14}$C-leucine were added to 3 mL of the inoculum. $^{14}$C-leucine incorporated into bacterial biomass was measured on a scintillation counter. Bacterial production was calculated following Simon and Azam (1989). Results are reported from soil waters from low flushing frequency treatments. To examine DOC quality, bacterial production was normalized for DOC concentration in soil waters.

## Results

### *Dissolved C production*

Regression analyses were run to determine whether production of dissolved C was significant (slope > 0). Soil water concentrations of DOC and total dissolved C increased significantly ($p < 0.01$) under wet sedge, tussock, and inter-tussock vegetation types (Figure 1 a&b). Dissolved C production was significant ($p < 0.05$) for

DOC in tussock and inter-tussock soils, for DIC in wet sedge soils, for $CO_2$ in inter-tussock and wet sedge soils, and for $CH_4$ in wet sedge soils (Table 3). Significant consumption (slope < 0) of DIC occurred in inter-tussock soil waters. Methane (tussock and inter-tussock) and $CO_2$ (tussock) concentrations increased but not significantly throughout the sampling period (Table 3).

*Dissolved C concentrations*

In general, at the low flushing frequency dissolved C concentrations were variable over time and did not consistently decline (Figure 2a, data not shown for other forms of dissolved C). Medium and high flushing frequencies resulted in a decline and eventual leveling off of soil water dissolved C concentrations with successive flushes (Figure 2b, data not shown for other forms of dissolved C). In wet sedge mesocosms, initial DOC concentrations were low (12.0 mg $L^{-1}$) and remained fairly constant throughout flushing episodes; however, initial DIC concentrations were high (64.3 mg $L^{-1}$) and showed a consistent decline during flushing (to 26.7 mg $L^{-1}$). DIC concentrations in tussock and inter-tussock mesocosms were lower than DOC concentrations and fluctuated throughout flushing events at all flushing frequencies. DOC concentrations in inter-tussock soil waters were dramatically higher than in tussock and wet sedge soils at the onset of the medium frequency flush (Figure 2a) due to high DOC production rates during the non-flushing period. Four flushes over a two-day period were sufficient to reduce DOC concentrations to levels similar to those achieved with the high frequency flushing. $CO_2$ concentrations were not significantly different between the three vegetation types (data not shown). Methane concentrations were about two orders of magnitude greater in wet sedge (0.23–4.41 mg $L^{-1}$) than in either tussock (0.009–0.396 mg $L^{-1}$) or inter-tussock (0.003–0.116 mg $L^{-1}$) vegetation. Under low frequency flushing, wet sedge soils showed the only clear pattern of decreasing concentration with continued flushing was for DIC (57.4 to 49.3 mg $L^{-1}$), and $CH_4$ (3.6–1.4 mg $L^{-1}$).

*Mass export of dissolved C*

Cumulative mass export of total dissolved C at a given flushing frequency fit a linear model well for all vegetation types and flushing frequencies ($R^2 > 0.95$). Inter-tussock soils exported more dissolved C per g of soil than tussock or wet sedge soils for all flushing frequencies. This difference was most dramatic at high flow. The mass of $CH_4$ exported from tussock and inter-tussock soil waters was insignificant compared to DOC and DIC, but accounted for 3–6% of total dissolved C losses from wet sedge soils. Daily export rates of total dissolved C increased with flushing frequency for all vegetation types (Figure 3). The increase was linear and significant (slope of regression analysis, $p < 0.005$) in tussock and wet sedge soils over the range of flushing frequencies used, but leveled off with increased flushing in inter-tussock soils (linear model $p = 0.11$). Export rates per gram of soil were greatest from inter-tussock mesocosms at all flushing frequencies, but because soil volume and bulk densities were greater in tussock and wet sedge mesocosms; tus-

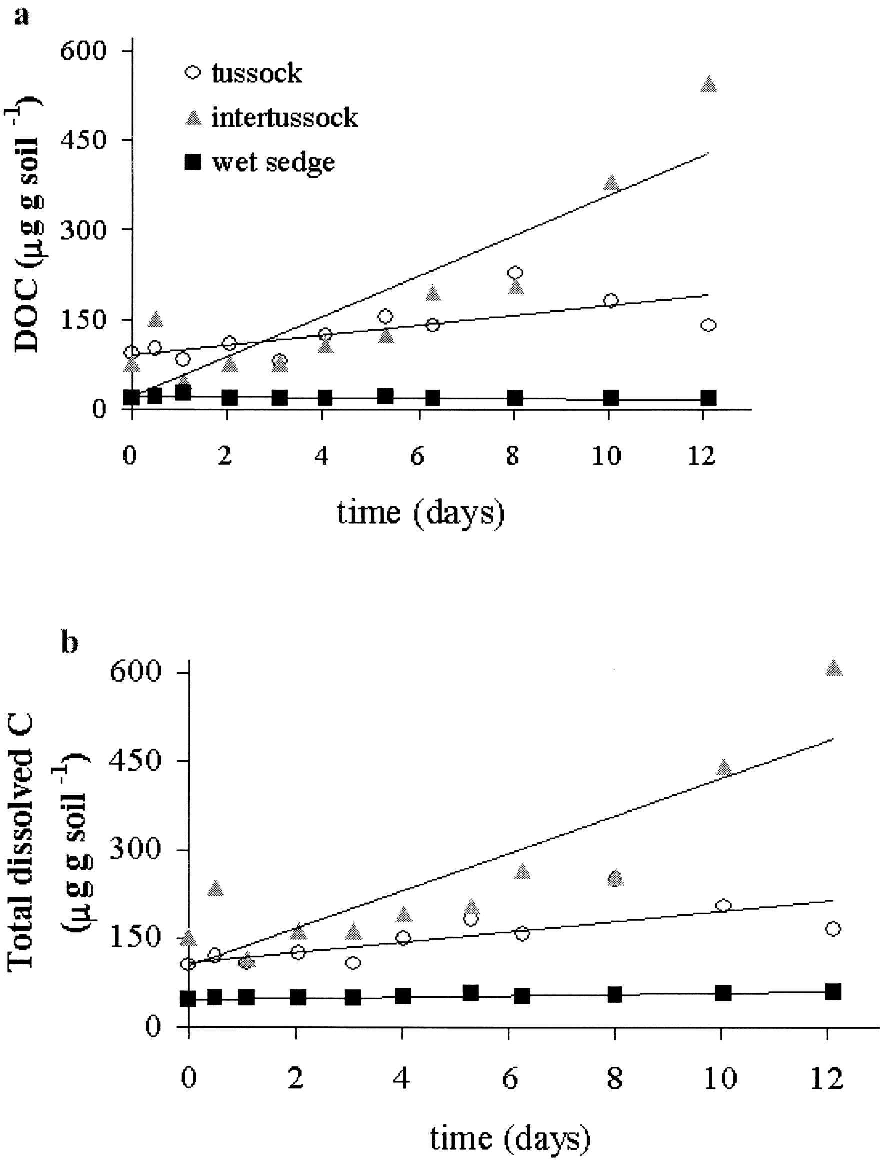

*Figure 1.* Change in concentration of (a) DOC and (b) total dissolved C (DOC + DIC + $CH_4$) per gram of soil in buckets during the non-flushing period (days 2.5–15.5) in tussock (circles), inter –tussock (triangles), and wet sedge (squares) soils. X axis indicates days since flushing has ceased. *n* = 2. Regressions indicate the rate of production.

sock mesocosms had the highest export rates per square meter at low and high frequency flushing (see Table 4 for export rates of dissolved C per $m^2$). Export rates were lowest in wet sedge mesocosms at all flushing frequencies. Export rates of

*Table 3.* Summary of dissolved C production. Production rates of dissolved C during non-flushing period are in $\mu$g C g soil $^{-1}$ day $^{-1}$ ($n$ = 2). Estimates of annual production of total dissolved C (g C m $^{-2}$ yr $^{-1}$) are based on a 90 day growing season. Estimates of annual production as % GEP are calculated from averaged data from Johnson et al. (1996); Vourlitis and Oechel (1993). Production of total dissolved C per gram of above ground biomass (agb) was estimated by harvesting aboveground biomass. Microcosm photosynthetic rates (g C m $^{-2}$ d $^{-1}$, $n$ = 4 tussock and wet sedge, $n$ = 3 intertussock) are from J. King (unpublished data) and were compared to dissolved C production. Standard deviations are in parentheses

| | | Tussock | Intertussock | Wet sedge |
|---|---|---|---|---|
| DOC | production rate | 8.25 (2.5) | 32.7 (19.3) | −0.4* (0.2) |
| | annual production | 41.4 | 81.1 | −1.3 |
| | %GEP | 13.2 | 25.7 | −0.4 |
| DIC | production rate | 0.25* (0.19) | −0.11 (0.07) | 0.64 (0.4) |
| | annual production | 2.6 | −4.9 | 4.1 |
| $CO_2$ | production rate | 0.42* (0.31) | 2.11 (0.66) | 0.52 (0.50) |
| | annual production | 2.1 | 5.2 | 1.6 |
| $CH_4$ | production rate | 0.0003* (0.0006) | 0.0050* (0.0004) | 0.0425 (0.0831) |
| | An. Prod | 0.00 | 0.01 | 0.13 |
| total dissolved C | production rate | 8.8 (2.2) | 34.9 (22.4) | 0.9 (0.2) |
| | annual production | 44.1 | 86.3 | 2.9 |
| | %GEP | 14.0 | 27.4 | 0.9 |
| | production (g g $^{-1}$agb) | 0.47 | 1.36 | 0.08 |
| Photosynthetic rate | | 3.63 (0.64) | 0.67 (0.25) | 2.58 (0.28) |
| Dissolved C Prod: PS | | 0.13 | 1.43 | 0.01 |

* change in concentration over the sampling period was not significant.

dissolved C were up to two orders of magnitude greater than production rates. Total dissolved C and DOC export per liter of water added decreased in tussock and inter-tussock mesocosms, but showed no relationship to flushing intensity in wet sedge mesocosms (data not shown). The total amount of dissolved C export from the mesocosms over the course of the experiment ranged from 3 to 18 % of estimated annual gross ecosystem production (Table 4; GEP from Johnson et al. (1996); Vourlitis and Oechel (1993)). The ratio of organic to inorganic dissolved C decreased with increased water flow in tussock (ANOVA, $p < 0.05$), but did not change significantly ($p > 0.4$) as flushing increased in inter-tussock or wet sedge soils (Figure 4).

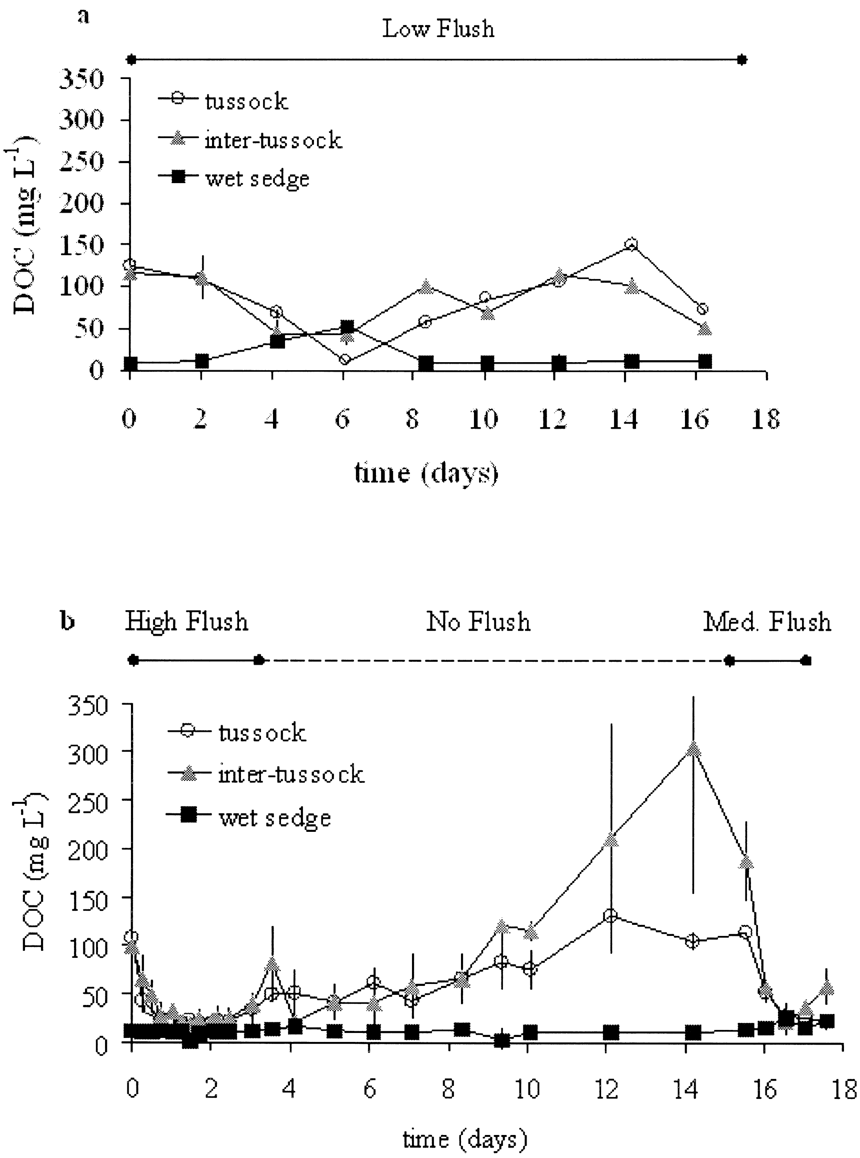

*Figure 2.* Dissolved organic C concentrations in soil water extracts during low (a) and high and medium (b) frequency of flushes in tussock (circles), inter-tussock (triangles), and wet sedge (squares) microcosms. $n = 2$.

### *C dynamics and above ground biomass*

Dissolved C production ($\mu$g C g soil$^{-1}$ d$^{-1}$) per gram of above ground biomass ranged from 1.36 (inter-tussock) to 0.47 (tussock) to 0.08 (wet sedge). A regression

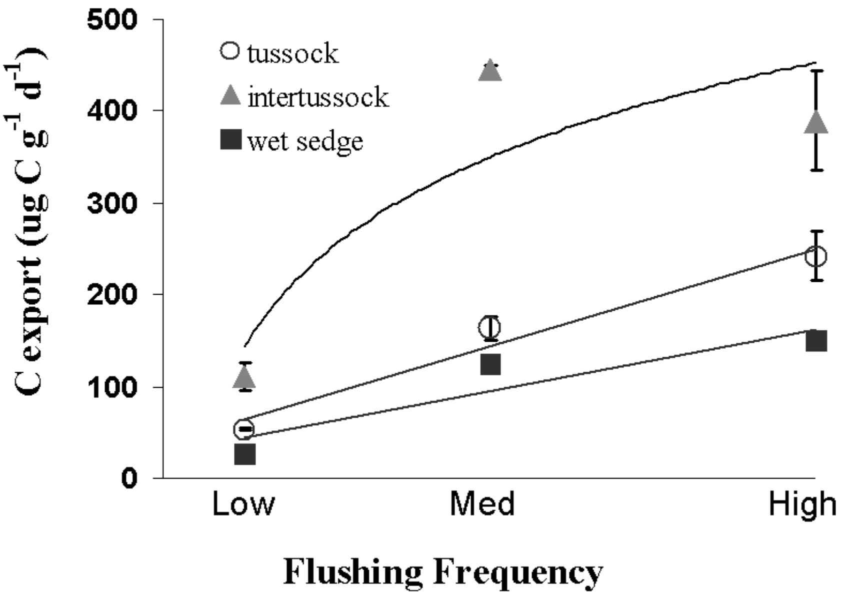

*Figure 3.* Relationship between total dissolved C export per day and flushing frequency in tussock (circles), inter-tussock (triangles), and wet sedge (squares) microcosms with standard errors. $n = 2$.

analysis indicated that a positive correlation existed between above ground biomass and both total dissolved C production ($R^2 = 0.580$, $p = 0.05$) and export (high/ medium treatment $R^2 = 0.722$, $p = 0.02$; low treatment $R^2 = 0.602$, $p = 0.04$) (Figure 5). There was a positive correlation between soil C and dissolved C export in the medium/ high treatment ($R^2 = 0.715$ $p = 0.03$), but not in the low treatment.

### *Soil water absorbance*

The relationship between DOC concentration and absorbance at 360 nm differed between the three vegetation types (Figure 6) and was positive only in tussock soil waters. Absorbance declined throughout flushing events in wet sedge soil water, but DOC concentrations remained stable.

### *Bacterial production*

Bacterial production (BP) was significantly greater (ANOVA, $p < 0.05$) when inter-tussock or wet sedge soil waters were added to lake water than when tussock soil water was added (Figure 7a). Wet sedge soil water supported the greatest bacterial production per amount of soil water DOC, followed by inter-tussock and tussock (Figure 7b). Differences were significant between all three vegetation types (ANOVA, $p < 0.05$).

*Table 4.* Daily mass export of DOC, DIC, $CO_2$, and $CH_4$ and total dissolved C (g C m $^{-2}$ day $^{-1}$) for low, medium and high flushing frequencies. Values are averages from replicate buckets for each vegetation type (*n* = 2). Total C export over the course of each treatment as a % of GEP is estimated from Johnson et al. (1996); Vourlitis and Oechel (1993)

| Veg. Type | Tussock | | | Intertussock | | | Wet sedge | | |
|---|---|---|---|---|---|---|---|---|---|
| Flush rate | Low | Med. | High | Low | Med. | High | Low | Med. | High |
| DOC | 2.56 ± 0.04 | 4.28 ± 0.38 | 7.00 ± 0.25 | 1.52 ± 0.17 | 7.90 ± 1.95 | 5.70 ± 0.47 | 0.17 ± 0.01 | 1.20 ± 0.18 | 1.35 ± 0.18 |
| DIC | 0.72 ± 0.27 | 1.81 ± 0.37 | 1.07 ± 0.28 | 1.57 ± 0.39 | 5.28 ± 1.22 | 2.42 ± 0.18 | 0.68 ± 0.17 | 2.14 ± 0.76 | 1.15 ± 0.05 |
| $CO_2$ | 0.74 ± 0.11 | 0.40 ± 0.09 | 6.27 ± 1.11 | 0.50 ± 0.05 | 2.37 ± 0.39 | 4.82 ± 0.19 | 0.51 ± 0.14 | 1.25 ± 0.38 | 3.49 ± 1.37 |
| $CH_4$ | 0.0012 ± 0.0006 | 0.0195 ± 0.0070 | 0.0138 ± 0.0160 | 0.0050 ± 0.0050 | 0.0065 ± 0.060 | 0.0065 ± 0.0058 | 0.0435 ± 0.0241 | 0.1248 ± 0.0113 | 0.3288 ± 0.1716 |
| Total diss. C | 3.46 ± 0.20 | 7.32 ± 0.31 | 13.29 ± 1.34 | 2.25 ± 0.19 | 12.20 ± 1.62 | 10.53 ± 0.28 | 1.09 ± 0.10 | 4.25 ± 0.30 | 5.18 ± 1.52 |
| % GEP | 99 | 209 | 379 | 64 | 349 | 300 | 31 | 121 | 148 |

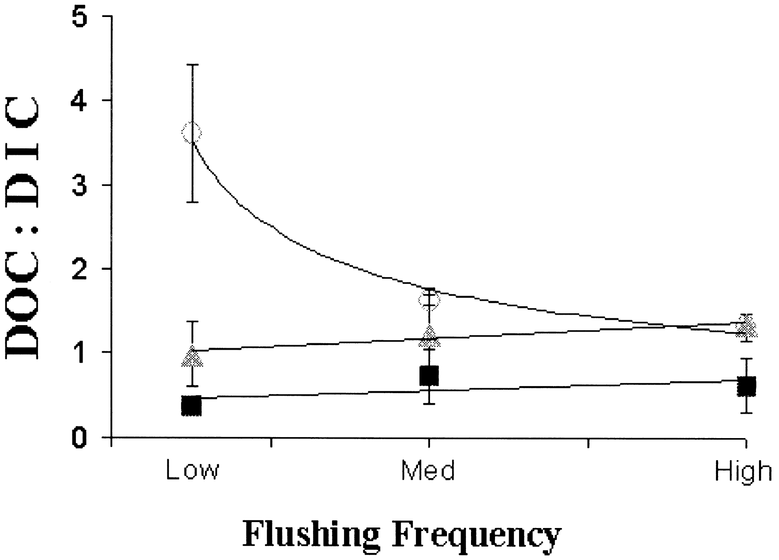

*Figure 4.* Relationship between DOC to DIC ratio ($\mu$g C $^{g\ -1}$ d $^{-1}$) and flushing frequency in tussock (circles), inter-tussock (triangles), and wet sedge (squares) microcosms with standard errors. $n = 2$.

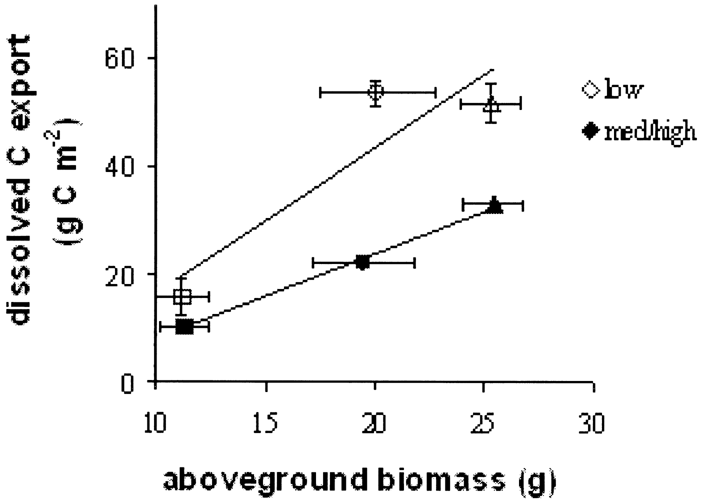

*Figure 5.* Relationship between above ground biomass and dissolved C export. Filled symbols indicate microcosms subjected to high and moderate intensity flushing ($n = 2$). Tussock (circles), inter-tussock, (triangles), and wet sedge (squares) microcosms.

## Discussion

Our results indicate that both the overlying vegetation and the amount of rainfall are important controls on production and movement of dissolved C through arctic

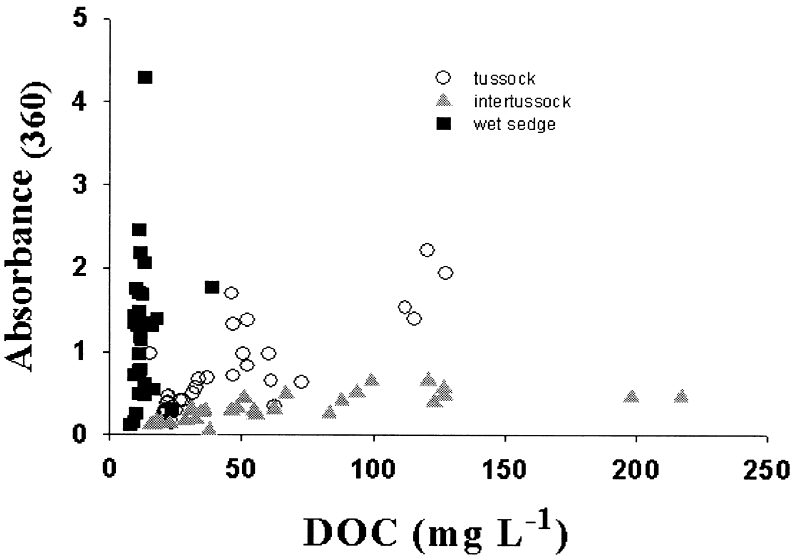

*Figure 6.* Relationship between DOC concentration and absorbance at 360 nm in tussock (circle), intertussock (triangle) and wet sedge (square) soil waters.

catchments. It is clear that changes in precipitation and plant species composition brought about by climate change or human disturbances will impact arctic C cycling by influencing the amount and bioavailability of dissolved C export from land.

At the scale of the catchment, increased rainfall flushes soils and results in increased stream discharge. The link between stream discharge and C export from catchments has been well studied; the majority of studies report a positive relationship between stream discharge and DOC concentrations due to the build up of DOC in soils between flushing events both in the Arctic (Peterson et al. 1986) and in other systems (Hope et al. 1994). However, because soils do not have an infinite capacity to export dissolved C, there must be a transition from positive to negative relationships between stream discharge and DOC concentration as soil C stores are depleted and export overwhelms dissolved C production. This transition state has been observed in several natural systems. Weak (Guyot and Wasson 1994; Jones et al. 1996; Ciaio and McDiffet 1990) or negative relationships between discharge and DOC concentration may result from low inputs of terrestrial C (e.g., Sonoran Desert stream (Jones et al. 1996)) or high water flow depleting soil stores (e.g., Hornberger et al. (1994); Godde et al. (1996)). In the Arctic, snow melt runoff is not sufficient to reverse the relationship between DOC and discharge (Michaelson et al. 1998), indicating that arctic soils have a high capacity for release of dissolved C throughout the summer.

Our results show that flushing frequencies between that of our low and medium frequencies, or slightly greater than a high intensity natural rain event, are likely to result in a transition from a positive to a negative relationship between discharge and dissolved C concentration and discharge (Figure 2). Dissolved C production

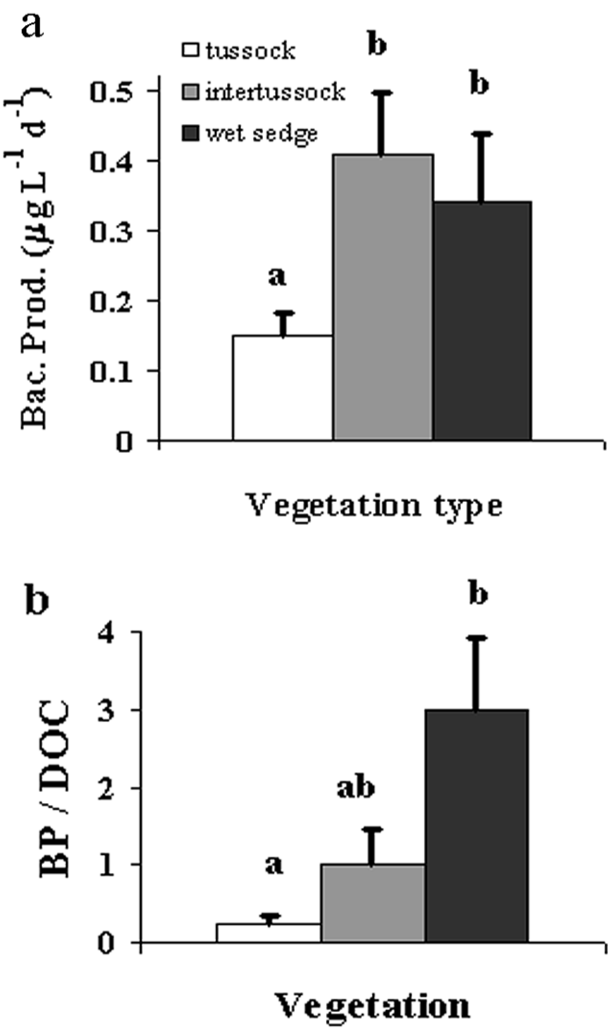

*Figure 7.* Bacterial production (a) and bacterial production normalized for DOC (b) in Toolik Lake water with soil water additions from tussock, inter-tussock and wet sedge vegetation.

and export were positively correlated, but export was up to two orders of magnitude greater than production rates. This indicates that (1) there are large stores of C in soils relative to the production rates, (2) physical flushing of these stores overwhelms soil production, and (3) long term storage of C in soils is a function of short term production of dissolved C integrated over long periods of time. The importance of C storage and dissolved C production in controlling C export differs between vegetation types. In inter-tussock soils, despite high rates of dissolved C production, high water flow depletes soil stores and the increase in export is asymptotic (Figure 3). In tussock and wet sedge soils, soil C stores do not limit export (Figure 3), indicating that flushing, rather than soil C availability, limits dissolved C exports even at very high flushing rates. This difference between vegetation types is likely due to both the soil structure and soil C stores. Inter-tussock soils are less dense, and water flowing through them can more easily reach soil interstices than in the tussock or wet sedge soils.

Patterns of dissolved C production and export of dissolved C indicate that vegetation type is an important control on these processes in arctic soils. While we expected initial concentrations of dissolved C to be lower in wet sedge soils due to high rates of flushing, we found that low production rates of dissolved C (Table 3) also contribute to the low dissolved C concentrations in these soils. The response of wet sedge soils to flushing differed as well. DOC concentrations remained relatively low but constant (Figure 2b). The topographic position within the catchment of the upland tussock and lowland wet sedge vegetation is also an important factor in determining the contribution of dissolved C to aquatic systems. Because wet sedge occupies low positions in the landscape, exchange between wet sedge and streams or lakes is likely to be more important, simply due to spatial proximity, than is the exchange between upland tussock vegetation and surface waters.

The positive relationship between aboveground biomass and dissolved C export suggests that new C from photosynthesis is driving export (Figure 5). However, there was no relationship between whole system photosynthetic rates (g C $m^{-2}$ $d^{-1}$) in the mesocosms (J. King, unpublished data) and dissolved C export. Photosynthate allocated to roots may enter the active dissolved fraction of the soil either through structural or metabolic pathways. We estimated below ground biomass using root to shoot ratios (K. Nadelhoffer, pers. comm.) for tussock and wet sedge plants, but found no relationship between below ground biomass and export. It is difficult to estimate inter-tussock root biomass, as mosses are the dominant vegetation. Thus it is unclear whether differences in root biomass control dissolved C exports. In addition, it is likely that physiological processes such as root production and turnover and root biochemistry are more important than root biomass in controlling dissolved C exports. At the present, however, our understanding of these dynamics in fine roots remains limited (Hendricks et al. 1993). Plant derived C is an important source of energy for microbial communities, and microbial activity may also impact dissolved C export. Therefore, while the relative importance of each of these pathways of dissolved C flux is uncertain, it is clear that dissolved C exports especially over longer time scales are mediated by the composition of the overlying plant community. Different responses of dissolved C export to increased flushing between vegetation type indicates that understanding biogeochemical processes at the community level is important in predicting C fluxes at the ecosystem level.

Comparing dissolved C losses to photosynthetic rates provides a measure for the magnitude of dissolved C production. GEP and NEP in inter-tussocks were about half that of tussock in a similar mesocosm experiment (Johnson et al. 1996). Decreased biomass and lower photosynthetic rates in mosses may account for these differences (L. Johnson, pers. comm.). Comparing dissolved C production and export to annual GEP (estimated using data from (Vourlitis and Oechel 1993; Johnson et al. 1996)) shows that production and export occurring during the experiment accounted for a significant portion of fixed C (Tables 3 and 4). Export of dissolved C exceeded both production rates of dissolved C and daily GEP estimates at medium and high flushing intensities (with the exception of high frequency wet sedge mesocosms). Export of dissolved C from mesocosms was three to fourteen times greater than the average annual C losses from the Kuparuk Basin ( $\sim 3.7$ g C $m^{-2}$); even when scaled back to the level of natural precipitation, dissolved exports from the mesocosms exceeded average annual losses measured for a catchment. While this may suggest that buffering zones at the bottom of catchments are important in modulating C export at large scales, it also indicates that arctic soils have the potential for very high rates of dissolved C losses relative to inputs.

Differences in the ratio of organic to inorganic C lost during increased flushing (Figure 4) have implications for regional C balances. DIC is lost more readily from the system via $CO_2$ evasion from lakes (Kling et al. 1992; Dillon and Molot 1997b) or export to the ocean (Degens et al. 1991). In contrast, dissolved C that is incorporated into living biomass through bacterial production has a longer residence time within the system. Because aquatic primary production is low in the arctic (Miller et al. 1986), the uptake of organic C by microbes is an important route for incorporation of dissolved C into aquatic foodwebs. Therefore, in tussock-dominated catchments, increased water flow will increase export rates and may amplify catchment losses of carbon by decreasing the ratio of organic to inorganic C.

Absorbance, which is often a good estimator of DOC concentration (Lewis and Canfeild 1977), varied in its relationship to DOC concentration according to vegetation type (Figure 6). Only tussock soil waters showed the expected positive relationship between DOC concentration and absorbance. Differences in DOC quality may account for differences in this relationship. Low absorbance is often characteristic of newly produced DOC, while high absorbance is characteristic of older, more recalcitrant forms of DOC (Frimmel and Abbt-Braun 1989). The bacterial production experiments, however, do not support this general characterization. Wet sedge soil water, which had higher absorbances, supported significantly greater bacterial production per amount of soil water DOC compared to inter-tussock soil water which had the lowest absorbances.

While the absolute amount of dissolved C export is of interest for carbon budgets, the bioavailability of DOC exported from land to receiving surface waters may have important biological consequences. Many studies have found no correlation between DOC concentration and bacterial production (e.g., Coffin et al. (1993); Findlay et al. (1996)), indicating that the composition of DOC, and not just its amount, is an important control on bacterial production. In our experiment bacterial production (Figure 7a) was not correlated with soil water DOC concentration (DOC: inter-tussock > tussock > wet sedge; BP: inter-tussock > wet sedge > tussock), suggesting that DOC composition differs under different vegetation types. Indeed, BP normalized for DOC concentration (Figure 7b) reveals that the DOC from different vegetation types differs with respect to its bioavailability to microorganisms, and wet sedge DOC has the highest quality as measured by bacterial activity. Furthermore, if wet sedge soil water exchanges more directly with surface waters as discussed above, its importance to aquatic DOC input is further increased. Thus changes in vegetation within a watershed due to climate change or disturbance may impact the production of aquatic microbial communities.

### *Summary*

Our results indicate that in the Alaskan Arctic dissolved C exports are controlled by the soil-level processes of flushing and dissolved C production. Because dissolved C export greatly exceeded net rates of dissolved C production, potential for export is mainly controlled by soil C stores. However, the positive relationship between dissolved C production and export (Tables 3 and 4) clearly indicates that short-term production processes in soils result in long-term accumulation of soil C stores. Production of dissolved C and soil C stores (and therefore export) are controlled by the composition of the overlying vegetation. The export of this dissolved C from land is mainly controlled by water flow. Water flow in excess of natural rainfall events resulted in declining concentrations but continued increases in export of dissolved C. Factors such as aboveground biomass and soil C content are also strongly correlated to C production and export. Ratios of organic to inorganic dissolved C exported to aquatic systems are influenced by both vegetation type and flushing frequency. Because organic C is more readily retained through microbial uptake, decreasing the ratio of DOC:DIC could lead to increased C losses from the region by increasing losses to the atmosphere and the ocean. These results suggest that changes in hydrology or vegetation species composition due to disturbance or climate change will alter regional C cycling dynamics and responses of aquatic systems.

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