

Impacts of ultraviolet-B radiation and regional warming on antarctic vascular plants

THOMAS A. DAY, CHRISTOPHER T. RUHLAND, and FUSHENG XIONG, *Department of Plant Biology, Arizona State University, Tempe, Arizona 85287-1601*

The Antarctic Peninsula provides a unique opportunity to examine the influence of climate change on plants. Stratospheric ozone depletion events over the continent during spring and early summer lead to well-documented enhanced levels of ultraviolet-B (UV-B) radiation [280–320 nanometers (nm); UV-B] levels (Booth et al. 1994; Madronich et al. 1995). In addition, mean summer air temperatures along the peninsula have risen more than 1°C in the last 45 years (Smith 1994; Smith, Stammerjohn, and Baker 1996).

The 1996–1997 field season (November to March) was the second year of our main field experiment on Stepping Stones Island, near Palmer Station, Antarctic Peninsula. We are using filters to manipulate UV levels and temperatures around naturally growing plants of *Deschampsia antarctica* (antarctic hair grass) and *Colobanthus quitensis* (antarctic pearlwort), the only vascular plant species native to Antarctica. The treatments involve reducing different components of UV radiation [UV-B and/or ultraviolet-A radiation (UV-A; 320–400 nm)] in combination with passively increasing temperatures around plants. Additionally, in some treatments, we supplement soil nutrients or water.

We assessed the performance of *Deschampsia* and *Colobanthus* under each frame by monitoring leaf photosynthetic rates, as well as more integrated measures such as plant growth rates and reproductive success. Reducing ambient UV radiation levels with filters did not appear to have any large effects on field net photosynthetic rates (Pn). Pn of both species, however, was usually higher under warming treatments than under ambient treatments. The notable exception was on warm, sunny days (canopy air temperature >20°), when Pn of plants under all treatments were negligible. Further laboratory experiments at Palmer Station and Arizona State University have confirmed that high temperatures are responsible for the depressions in Pn we observe in the field on warm days. Both species are quite sensitive to higher temperatures, and Pn begin to decline abruptly at temperatures above their photosynthetic temperature optima of 12°. The main reason for this sensitivity to supraoptimal temperatures is that these species have high rates of temperature-enhanced respiration; at higher temperatures, photosynthesis or carbon dioxide (CO₂) assimilation is offset by high rates of respiration or CO₂ evolu-

tion. Additionally, key enzymes in the photosynthetic Calvin Cycle of these species appear sensitive to higher temperatures and further depress photosynthetic rates.

Because of the sensitivity of the photosynthetic apparatus to higher temperatures in these species, continued regional warming might prove detrimental to their performance on the peninsula, but an assessment of their performance under rising temperatures also depends on

- their ability to acclimate photosynthetically to warmer growing temperatures as well as
- how well photosynthetic rates predict plant growth rates and overall performance.

With respect to acclimation, when we grew both species under contrasting temperature regimes (ranging from 7 to 20°) in growth chambers at Arizona State University, their photosynthetic temperature optima changed very little (<2°C), suggesting that these species have a very limited ability to acclimate photosynthetically to warmer temperatures. Although little acclimation of the photosynthetic apparatus to warmer growing temperature regimes was apparent, somewhat surprisingly, plants grown at warmer temperatures (20°) had higher growth rates and produced more biomass than those grown at their photosynthetic temperature optima (12°). Thus, Pn may not be a straightforward predictor of plant growth rate and overall performance.

We did not detect any large changes in growth rates under our field warming treatments, although the slow growth rates exhibited by these species under field conditions may make such changes difficult to detect in only two seasons of field manipulations. In contrast, we found that leaf elongation rates of both species during the second field season were improved when we reduced ambient UV-B levels with filters. This finding suggests that enhanced levels of UV-B could be stunting leaf elongation and the growth of these species. Although the mechanism for this stunting is not clear, it does not appear to involve UV-induced reductions in Pn.

Our warming treatments had very strong effects on sexual reproduction of both species. Under warming, the reproductive structures of both species were more developed or mature throughout both of the first two growing seasons. In addition, under warming, *Colobanthus* produced more seeds per repro-

ductive structure or capsule. However, these seeds were not heavier than seeds from ambient-temperature treatments, and they were no more viable than their ambient-temperature counterparts, based on seed germination studies.

Taken collectively, our preliminary results suggest that with continued regional warming and a greater prevalence of warm days during the growing season, Pn and carbon uptake of these species may be reduced, but growth may improve with these warmer temperatures. Indeed, increases in the number of individuals and populations of *Colobanthus* and *Deschampsia* have been documented over the past 5 years along the peninsula, and these increases have been attributed to rising temperatures (Fowbert and Smith 1994; Smith 1994; Grobe, Ruhland, and Day 1997). Results from this past field season also suggest that enhanced UV-B levels may stunt leaf elongation and growth in these species. Thus, enhanced UV-B associated with ozone depletion events could potentially offset some of the improvements in plant growth brought about by rising air temperatures.

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Photosynthetic rhythmicity in an antarctic microbial mat and some considerations on polar circadian rhythms

CHARLES S. COCKELL, *Carnegie Institute of Washington, Stanford, California 94305-1297*

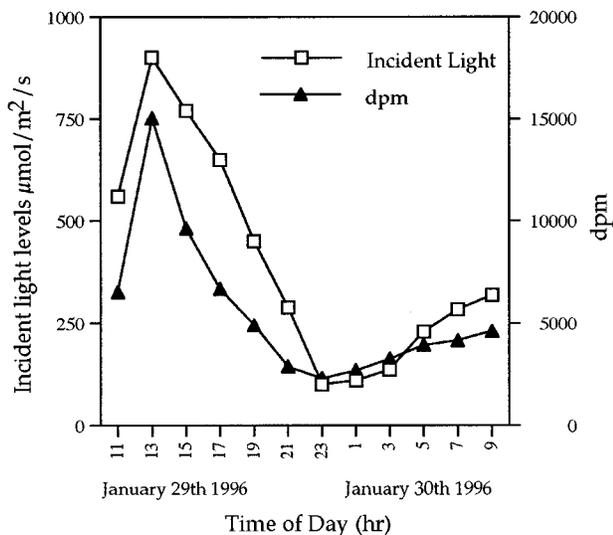
LYNN J. ROTHSCHILD, *Ecosystem Science and Technology Branch, National Aeronautics and Space Administration, Ames Research Center, Moffett Field, California 94035-1000*

Many physiological processes in organisms, particularly photosynthesis, exhibit diurnal patterns (e.g., Hoffman and Dawes 1980; Rothschild 1991; Stock and Ward 1991). The light/dark cycle that all organisms above the Antarctic Circle (66°S) experience allows related physiological processes to become entrained in a circadian fashion, for example, amino-acid uptake, enzyme levels, and the onset of mitosis. Continuous light is often found to result in a disruption of entrainment (e.g., Chen et al. 1991; Makarov, Schoschina, and Luning 1995). At the poles, photosynthetic organisms are subjected to a 24-hour light cycle during the summer, without a dark period. Diurnal light intensity approaches near continuous at 90°S. Here, data from a simple study of the diurnal photosynthetic pattern in an *Oscillatoria* mat from Bratina Island are shown. Associated thoughts on possible research directions on natural photosynthetically driven polar cycles are made.

Experimental procedures and results

The mat studied was collected from Skua Pond, Bratina Island, part of the McMurdo shelf ablation zone (78°S 166°E). Mats from this pond have been described previously (Vincent et al. 1993) and are composed primarily of the filamentous cyanobacteria *Oscillatoria*. Cores of mat of size 1.9 square centimeters were collected in water from Skua Pond and returned to McMurdo Station (78°15'S 166°30'E), which had the same light cycle as Bratina. Mats were maintained in trays at a water depth similar to that found in the field (5 centimeters). The following day, carbon fixation was studied using carbon-14-bicarbonate using a modification of Goldman (1963) and as described in Rothschild (1991). Three cores were placed in separate whirlpak bags, and 10 microcuries per milliliter of carbon-14-bicarbonate (New England Nuclear, Wilmington, Delaware, catalog number NEC 086H) were added to 3

milliliters of Skua Pond water in the bags with a final concentration of 10^2 microcuries per milliliter. The mats were incubated for 2 hours under natural light and frozen on dry ice. Five milliliters of 0.5 molar Tris pH 7.5 were added to each bag and cores were sonicated until a homogenate had been formed. Two-hundred microliters of homogenate was removed and added to 100 microliters of acetic acid in a scintillation vial. Samples were air dried and counted. Results are plotted as the mean of the triplicates against time of day (figure). Results are plotted as disintegrations per minute per hour of incubation since the dissolved inorganic carbon concentration of the Skua Pond water is not known. Standard deviations were no more than 5 percent of each point. At each time point, a dark control was run (a sample covered in silver foil). The temperature of the mats remained at 5°C , ambient air temperature, throughout the experiment. Light measurements were taken every 2 hours using a LiCor Model L-189 light meter (LiCor, Lincoln, Nebraska). Chlorophyll was extracted with methanol and concentrations calculated using the equations of Lorenzen (1967). Chlorophyll-*a* concentrations were an average of 13.4 micrograms of chlorophyll-*a* per square centimeter, similar to previous observations on antarctic freshwater Oscillatoracean mats (Vincent et al. 1993).



Diurnal pattern of photosynthesis in an Oscillatoracean mat from Bratina Island, 78°S on the McMurdo Shelf Ablation Zone. Corresponding levels of photosynthetically available radiation are shown. ($\mu\text{mol}/\text{m}^2/\text{s}$ denotes micromoles per square meter per second. dpm denotes disintegrations per minute.)

Discussion

Organisms below the Antarctic Circle (66°S) and in the corresponding Arctic regions, experience a 24-hour light cycle during the photosynthetically active summer period, but one that has varying intensity and magnitude of variation depending on latitude. In this study, a simple examination of the summer photosynthetic pattern in a natural *Oscillatoria*

microbial mat from Skua Pond, Bratina Island, Antarctica, was made.

At McMurdo Station, an order of magnitude difference in photosynthetically available radiation between midnight and midday occurs during January. This difference was found to be tracked by the diurnal photosynthetic response. Photosynthesis was not completely shutdown at midnight but instead continued to occur above background similarly for other antarctic microbial communities that have been studied (e.g., Goldman 1972). A midday drop in photosynthesis was not observed in the microbial mat as is observed in temperate mats (Rothschild 1991). This absence of a drop may be due to better photoprotection and probably differing light inhibition levels of antarctic organisms.

Other ecological factors such as temperature may determine diurnal response of mats in different areas of Antarctica, and so response to irradiance may not necessarily be a simple correlation. Diurnal photosynthetic changes in such communities, however, raise interesting questions on polar circadian rhythms.

Photosynthetic organisms that approach 90°S , such as the lichens in the Horlick Mountains (86°S) (Wise and Gressitt 1965), will experience less diurnal rhythmicity in light intensity since light approaches continuous nearer 90°S . Such organisms would be an interesting target of study for research on polar circadian cycles since continuous nonvarying light cycles result in the disruption or change of rhythms in many organisms (e.g., Chen et al. 1991; Makarov et al. 1995). Future research might also concentrate on studying the continuity of physiological rhythms after light has been shut off. Such a study would allow for the examination of entrainment and how rhythms are regulated in natural photosynthetic communities exposed to near continuous light.

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Characteristics of streams in the Garwood Valley, McMurdo Dry Valleys

NATHANIEL BOOTH, DAVID KASMER, and DIANE MCKNIGHT, *Institute for Arctic and Alpine Research, University of Colorado, Boulder, Colorado 80302*

Glacial meltwater streams are common features of the McMurdo Dry Valleys (Vincent, Howard-Williams, and Broady 1993). Stream research has focused primarily on the Taylor and Wright Valleys with occasional studies in Miers Valley and the Alph River. The record of lake-level rise and the long-term record for the Onyx River in Wright Valley indicate that a warming trend has occurred over the last several decades in the McMurdo Dry Valleys (Chinn 1993). To understand the effects of climate and landscape position on dry valley streams, it is useful to know more about the other streams in other valleys. Several descriptors, such as flow, chemical, physical, and biological characteristics, are helpful in compar-

ing stream systems. Garwood Valley is located approximately 56 kilometers south-southeast of Taylor Valley and provides a stream system containing a relatively long second-order stream.

Two site visits to the Garwood Valley occurred on 24 January 1995 and 18 January 1997 as part of the McMurdo Dry Valleys Long-Term Ecological Research project. Both visits included flow- and field-meter measurements and sample collection at various locations along the four main reaches of the river. Measurements were made following methods described by Alger et al. (1997) and Von Guerard et al. (1994). The results are presented in tables 1–3.

Table 1. Field-meter and discharge results

Location	Date	Flow ^a	Conductivity ^b	Water temperature ^c	pH
Garwood River south fork below glacier	1/24/95	5.7	203	1.7	7.7
Garwood River below confluence	1/24/95	8.5	175	1.0	7.8
Garwood River between confluence and flats	1/24/95	8.5	165	0.9	7.7
Garwood River at flats	1/24/95	8.5	166	2.6	7.6
Garwood River south fork below glacier	1/18/97	6.3	115	3.0	7.6
Garwood River south fork above confluence	1/18/97	6.3	114	4.1	7.8
Garwood River north fork above confluence	1/18/97	4.9	66	6.0	7.8
Garwood River below confluence	1/18/97	11.2	93	5.1	7.8
Garwood River at flats	1/18/97	11.2	110	6.8	7.8

^aIn cubic feet per second. Flow measurements made at flats and assumed constant upstream. Values from 24 January 1995 are estimated. Values from 18 January 1997 were determined by pygmy meter measurement at flats and estimated above confluence by mass balance calculations using conductivity data.

^bµmhos

^cIn degrees Celsius.

The Garwood River is approximately 8 kilometers long, starting at the Garwood Glacier and discharging into McMurdo Sound. The Garwood Valley is a wide, steep valley composed mainly of sand and gravel-sized till. It is open to maritime air masses. The river has relatively high flow and can be characterized into four main reaches: the headwater tributaries, the confluence to the flats, the flats, and the ponds. All reaches are relatively straight, except for a meander before the flats. Two tributaries, the north and the south forks, join approximately 1.6 kilometers below the glacier. The reaches of the tributaries between the glacier and the confluence are steep-sloped narrow channels of cobble and gravel substrates, and flow is turbulent with high velocities. The green alga *Prasiola* sp. was found growing as mats attached to the underside of the rocks in the south fork of the Garwood River. These *Prasiola* streamers are common in steep rocky reaches of Bohner Stream and several other streams in Taylor Valley (Alger et al. 1997).

From the confluence to the flats, the river continues down a steep, narrow channel with very high set-in banks of fine gravel. This loose material is at its angle of repose on both sides of the stream. Two small streams drain high snow fields through the steep southern valley wall into this reach. These extremely low-flow streams have stable cobble substrates with diverse algae including *Prasiola* streamers, orange-colored mats of filamentous cyanobacteria, and dark red-colored algal mats on the rocks. These orange- and red-colored mats appear to be similar to orange mats found in Taylor Valley streams in that they occur in flowing-water habitat (Alger et al. 1997).

The steep, narrow channel opens up on to a flats area of sand and gravel. The gradient is low and evidence of stream meandering within this area is apparent. Some orange-colored algal mats are found in bands on the sides of the widened channel. The final reach of the river is characterized by several ice-covered ponds terraced along the last 100 meters of flow to the ocean. Diverse types of algal mats occur in the ponds.

Table 2. Anion and cation concentrations

Location	Date	Chloride ^a	Sulfate ^a	Lithium ^a	Sodium ^a	Potassium ^a	Magnesium ^a	Calcium ^a	Ammonia ^b	Nitrate ^b	Nitrite ^b	Phosphate ^b
Garwood River south fork below glacier	1/24/95	14.0	18.8	0.0027	13.3	3.1	2.7	24.0				
Garwood River below confluence	1/24/95	8.9	14.3	0.0023	8.3	2.4	2.2	23.3				
Garwood River between confluence and flats	1/24/95	8.2	13.0	0.0023	8.1	2.4	2.1	22.0				
Garwood River at flats	1/24/95	8.3	13.4	0.0025	8.6	2.7	2.2	22.3				
Garwood River south fork below glacier	1/18/97	7.0	7.6	0.0010	7.0	1.9	1.2	15.2	Not detected	1.852	Not detected	0.212
Garwood River south fork above confluence	1/18/97	6.4	7.0	0.0009	5.2	1.7	1.0	14.5	0.121	1.674	Not detected	0.263
Garwood River south fork above confluence	1/18/97	4.9	5.5	0.0009	6.5	1.8	1.1	15.1				
Garwood River at flats	1/18/97	5.0	5.8	0.0008	5.1	1.5	0.9	13.4	0.191	1.288	Not detected	0.336

^aIn milligrams per liter.
^bMicromolar.

Table 3. Ion ratios by weight

Location	Date	Sodium-to-chloride ratio ^a	Calcium-to-chloride ratio
Garwood River south fork below glacier	1/24/95	0.95	1.72
Garwood River below confluence	1/24/95	0.93	2.61
Garwood River between confluence and flats	1/24/95	0.99	2.66
Garwood River at flats	1/24/95	1.04	2.70
Garwood River south fork below glacier	1/18/97	1.00	2.17
Garwood River south fork above confluence	1/18/97	0.81	2.26
Garwood River north fork above confluence	1/18/97	Not measured	Not Measured
Garwood River below confluence	1/18/97	1.33	3.08
Garwood River at flats	1/18/97	1.02	2.65

^aThe sodium-to-chloride ratio by weight of sea water is 0.56.

The flow in the Garwood River system was several times greater than streams in Taylor Valley at the same time. The climate may be more moderate and sunnier in Garwood Valley. Comparison of the south fork and confluence reaches in tables 1 and 2 shows that the north and the south forks contribute similar flow.

The south fork has higher ionic concentrations, in particular sulfate and chlorine. The sodium-to-chloride ratios given in table 3 are higher than those of sea water, which indicates that, in addition to dissolution of marine aerosols, mineral weathering may be a source for sodium in this stream system. Comparison of the results from the two field trips shows that chloride, sulfate, sodium, and calcium concentrations are higher at low flow in January 1995, whereas the ratios of major ions were similar. These results indicate that dilution by the glacial meltwater is one factor, in addition to mineral weathering, that controls the streamwater chemistry. Regarding ion concentration changes downstream, on both dates the values of the major ions were very similar at the flats site and the site immediately below the confluence of the north and south forks. This result suggests that exchange of water between the stream and the adjacent hyporheic zone does not result in a downstream increase in solute concentrations as has been observed in Von Guerard Stream in Taylor Valley.

In summary, the geomorphological features of the Garwood River are similar to those of streams throughout the

McMurdo Dry Valleys. The same types of algal mats appear to be common in Garwood Valley. The main differences of this system, compared to those in the Taylor and Wright Valley, may be a warmer, sunnier climate and a longer period of streamflow during some colder summers.

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A comparison of two separate visits to the Alph River system with the Onyx River system

DAVID KASMER, NATHANIEL BOOTH, and DIANE MCKNIGHT, *Institute for Arctic and Alpine Research, University of Colorado, Boulder, Colorado 80302*

Two major river systems receive inflow from numerous tributaries in the McMurdo Dry Valleys: the Alph River system and the Onyx River system located in Wright Valley. The Onyx River has been studied extensively since first being gauged in 1969; the Alph River was studied during the 1985-1986 season. We report here results obtained in January of 1996 and 1997 on the Alph River, including the flow and water chemistry. Also, a comparison of the distribution/location of algal mats in the Alph River to other streams in the McMurdo Dry Valleys is presented.

The Alph River runs roughly 15 kilometers along the side of the Koettlitz Glacier. Trough Lake and its inflow tributaries are the source. We studied the Alph River below Howchin Lake, an ice-covered lake receiving flow from tributaries originating at the Walcott Glacier and Howchin Glacier. From Howchin Lake, the Alph flows through a channel away from the Koettlitz

Glacier to the sampling site at 78°12'57.7"S 163°33'95.8"E. The river at the sampling site has riffles and runs. Orange algal mats occur in the riffles and sides of runs as in the Commonwealth Stream (in Taylor Valley) but at a larger scale (Alger et al. 1997). Within the stream bed, ripples in the sand occur in the runs.

The Alph River and the Onyx River are similar in that both flow from a headwater lake (Trough Lake and Brownsworth Lake, respectively), but Brownsworth Lake abuts a piedmont glacier whereas Trough Lake is more inland. Because of its proximity to the Ross Sea, the Onyx River system is affected by a maritime climate. Further, the Alph River runs at the base of a glacier through other lakes whereas the Onyx River runs down valley through dry land. The Alph River below Howchin Lake was visited on 18 January 1997. During this visit, pH, specific conductivity, and temperature were recorded with field

Table 1. Alph field-meter data collected during 1996 and 1997 field seasons

Sample location	Date	Water temperature ^a	Specific conductivity ^b	pH ^c	Discharge ^d
Alph River at Trough Lake	1/25/96	6	52.3	8.8	
Alph River below Walcott Lake	1/25/96	3	74.1	8.3	
Alph River below Howchin Lake	1/25/96	1	72.4	8.7	
Alph River below Alph Lake	1/25/96	3	94.3	7.7	
Alph River below Howchin Lake	1/18/97	1.5	74.9	7.4	0.86

^aIn degrees Celsius.
^bIn microsiemens per centimeter.
^cIn standard units.
^dIn cubic meters per second.

Table 2. Amounts of major cations and anions (milligrams/liter) found in samples taken during the 1996 and 1997 seasons at the Alph River

Sample location	Date	Lithium	Sodium	Potas- sium	Magne- sium	Calcium	Fluorine	Chloride	Nitrate	Sulfate
Alph River at Trough Lake	1/25/96	0.001	5.66	1.094	0.892	4.19	0.23	3.67	0.015	2.52
Alph River below Howchin Lake	1/25/96	0.002	8.85	1.363	1.199	5.73	0.249	5.44	0.021	4.17
Alph River below Howchin Lake	1/25/96	0.001	7.91	1.266	1.104	6.64	0.154	5.34	0.024	3.92
Alph River below Alph Lake	1/25/96	0.002	12.38	1.621	1.39	6.97	0.162	9.35	0.02	6.05
Alph River below Howchin Lake	1/18/97	0.001	7.005	1.098	1.014	6.384	0.13	4.3	0.013	3.89

meters following methods described by Alger et al. (1997). A discharge measurement was performed to U.S. Geological Survey standards using a pygmy meter and wading rod over a measured cross section. Table 1 contains the results, along with data collected in a similar manner during the 1996 field season. A stream sample was collected and filtered for major cations and anions, dissolved organic carbon, and alkalinity. The concentrations of major cations and anions found during the analysis of the sample can be found in table 2.

Howard-Williams and Vincent (1986) showed that the flow remained constant over several days of measurements. We gauged the river at the same site. The constant flow was attributed to the dampening effects of the lakes (Trough, Walcott, and Howchin) on the typical diurnal cycle seen in other dry valley streams (Howard-Williams and Vincent 1986). Measurements made on 18 January 1997 show a discharge of 0.86 cubic meters per second (m³/sec); Howard-Williams and Vincent report a discharge of 1.17 m³/sec on 18 January 1986. Discharge measurements made in January 1997 at the Onyx at the Vanda weir ranged from 0.67 m³/sec on 7 January 1997 to 0.12 m³/sec on 20 January 1997. The water temperature of the Alph on 18 January 1997 was 1.5°C whereas on 18 January 1986 Howard-Williams and Vincent (1986) report water tempera-

ture ranging from 0.5°C to 0.8°C. Water temperatures of the Onyx at the Vanda weir were 3.2°C on 7 January 1997 and 2.4°C on 20 January 1997.

Table 1 reports the field meter data for pH and conductivity obtained by two separate trips to the Alph River. It can be seen that the levels of major cations and anions found in water samples taken at the same site both years remained somewhat constant. This finding holds with the fact that the pH and specific conductivity are fairly constant. Table 3 contains field-meter data obtained at the Onyx during the 1997 season. By comparing the field-meter data contained in table 1 of the Alph River and the field-meter data contained in table 3 of the Onyx River, it can be seen that the pH and specific conductivity of the Onyx River are lower than the sample site on the Alph River below Howchin Lake.

Although the Alph River and Onyx River share the similarity of being the largest flowing freshwaters in Antarctica, the pattern of flow and chemical makeup of each differs due to geographical location and type of terrain. The Onyx experiences a maritime climatic influence due to its proximity to the Ross Sea.

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Table 3. Onyx River field-meter data

Sample location	Date	Water temperature ^a	Specific conductivity ^b	pH ^c	Discharge ^d
Onyx River at Lake Vanda Weir	1/7/97	3.2	58.8	6.8	0.67
Onyx River at Lake Vanda Weir	1/20/97	2.4	60.5	6.8	0.12

^aIn degrees Celsius.
^bIn microsiemens per centimeter.
^cIn standard units.
^dIn cubic meters per second.

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