



Factors affecting the distribution and abundance of aquatic macrophytes in parts of the Madison,
Firehole and Gibbon rivers
by Abraham Andrew Horpestad

A thesis submitted to the Graduate Faculty in partial fulfillment of the requirements for the degree of
MASTER OF SCIENCE in Botany
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Abstract:

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Five transects were run across each of eleven stations, two on the Firehole, one on the Gibbon, and eight on the Madison River. Physical factors and taxa present at one meter intervals were determined. Some chemical factors were determined at three hour intervals for a 24 hour period on each of the 10 weeks of the study period.

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OF AQUATIC MACROPHYTES IN PARTS OF THE
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ABRAHAM ANDREW HORPESTAD

A thesis submitted to the Graduate Faculty in partial
fulfillment of the requirements for the degree

of

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Botany

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ABSTRACT

A study was made during the summer of 1966 of the floral distribution and of some physical and chemical factors which may have been responsible for this distribution in parts of the Madison River and its tributary streams, the Firehole and Gibbon Rivers, Yellowstone National Park, Wyoming.

Five transects were run across each of eleven stations, two on the Firehole, one on the Gibbon, and eight on the Madison River. Physical factors and taxa present at one meter intervals were determined. Some chemical factors were determined at three hour intervals for a 24 hour period on each of the 10 weeks of the study period.

The diversity indices of the single community present was correlated with total soluble inorganic carbon, free carbon dioxide, and total alkalinity. The total per cent canopy cover of the community present in the Madison River was significantly correlated with current speed, temperature, substrate texture, and the amount of total soluble inorganic carbon. When all rivers were considered the total per cent canopy cover of the single community present was significantly correlated with substrate texture and the amount of total soluble inorganic carbon. Most of the taxa present appeared to be responding primarily to the current speed or substrate texture. However, some appeared to be also responding to one or more of the following factors: the amount of total soluble inorganic carbon, the amount of free carbon dioxide, depth, temperature, competition with other taxa, and other undetermined factor(s).

INTRODUCTION

The growing scarcity of water has in recent years caused an increased interest in the productivity of streams, the organisms involved, and the factors affecting these organisms. The macrophytic communities of streams have been largely overlooked in spite of this increased interest.

The effects of the substrate on the growth of aquatic plants has been pointed out by several workers including Pond (1903), Pearsall (1920), Misra (1938), and Curtis (1959). Current speed has been mentioned as the most important factor affecting the distribution of aquatic macrophytes in the English rivers by Butcher (1933). The effects of interspecific competition on the aquatic community has been discussed by Misra (1938) and Bourn (1937) among others. The study of Wright and Mills (1967) indicated the possibility that the downstream decrease in macrophyte standing crop in the Madison River was related to the downstream decrease in the concentration of free carbon dioxide as they could detect no appreciable changes in the other chemical parameters.

This study is an attempt to determine how various physical and chemical factors and interspecific competition affected the distribution of aquatic macrophytes in part of the Madison River system.

Description of the Study Area

Eleven sampling stations were established on the Madison River and its headwater streams, the Firehole and Gibbon Rivers. These streams are located in the west-central part of Yellowstone National Park in north-

western Wyoming and adjacent areas of Montana and Idaho (Figure 1).

The Firehole River originates from Madison Lake at an elevation of 2,500 m (8,209 ft) MSL and flows 34.6 km (21.5 miles) before joining with the Gibbon River to form the Madison River. The bedrock throughout these 34.6 km is composed of a Pleistocene plateau flow of rhyolite (Boyd 1961). The Firehole receives the discharge of many geysers and hot springs. The total amount of thermal water entering the river has been estimated at $1.55 \text{ m}^3/\text{sec}$ ($54.92 \text{ ft}^3/\text{sec}$) by Allen and Day (1935).

Two sampling stations were established on the Firehole River: the upper station (1) was located 3.22 km (2 miles) above the confluence of the Firehole and Gibbon Rivers. This is below all discernible thermal discharges and just above the Firehole Canyon. The other sampling station (2) was located 0.8 km (0.5 miles) above the confluence of the Firehole and Gibbon Rivers.

The Gibbon River originates from Grebe Lake at an elevation of 2,338.6 m (8,028 ft) MSL in an area of Pliocene rhyolite tuff and Quaternary alluvial deposits. It flows approximately 45 km (27.9 miles) before joining the Firehole River. In the lower reaches of the river the parent materials are rhyolite on the south and welded rhyolite tuff on the north (Boyd 1961). The total discharge of thermal water flowing into the Gibbon River has been estimated at $0.19 \text{ m}^3/\text{sec}$ ($6.85 \text{ ft}^3/\text{sec}$) by Allen and Day (1935).

The sampling station (3) on the Gibbon River was located 91 m (300 ft) above the confluence of the Gibbon and Firehole Rivers.

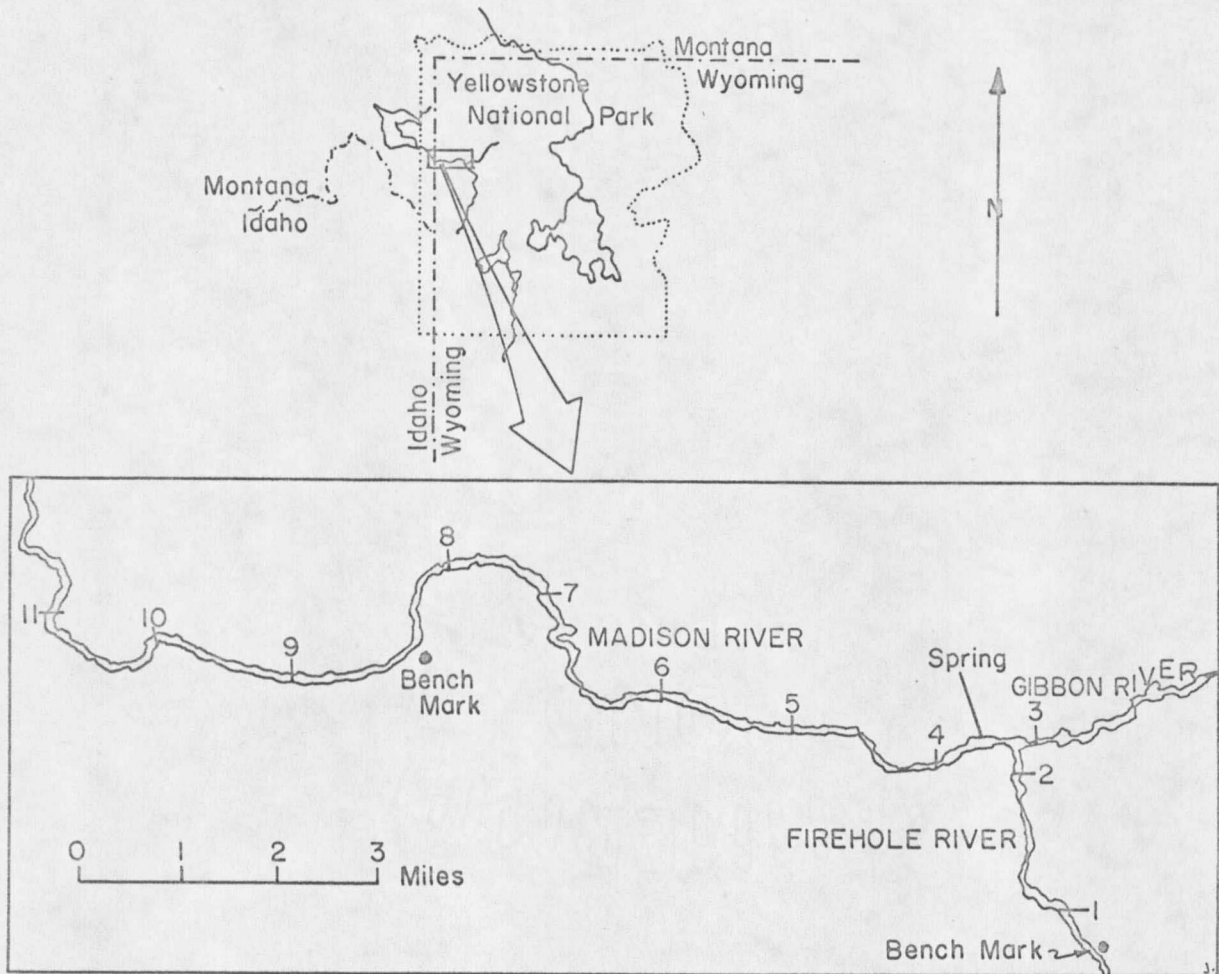


Figure 1: Map of study area

The upper 10 km (6.2 miles) of the Madison River are in a canyon formed of cliffs and hills of welded tuff on the north and more rugged cliffs of rhyolite on the south. Below the canyon the river flows through an area of decomposed rhyolite and tuff (Boyd 1961).

Eight stations (4-11) were established on the Madison River. Station 4 was located 1.89 km (1.18 miles) below the confluence of the Firehole and Gibbon Rivers. About 0.8 km (0.5 miles) above this station is an area where thermal discharges occur both on shore and in the stream channel (Figure 1).

Station 5 was located 5.18 km (3.22 miles) below the river's source and about 0.8 km (0.5 miles) below a small unnamed creek which flows into the river from the south.

Station 6 was located 7.76 km (4.82 miles) below the river's source.

Station 7 was located 11.02 km (6.85 miles) below the river's source.

Station 8 was located 12.95 km (8.05 miles) below the river's source near the lower end of a large, deep pool.

Station 9 was located 16.15 km (10.04 miles) below the river's source.

Station 10 was located 18.89 km (11.74 miles) below the river's source.

Station 11 was located 21.24 km (13.20 miles) below the river's source. This sampling area is near the lower end of a long riffle which extends nearly to station 8.

The chemical composition of the water in these rivers is directly related to the sodium and potassium aluminosilicates which comprise the rhyolite bedrock of this region. The decomposition of this type of rock is intensi-

fied by the thermal waters present which tend to leach out the sodium and potassium. The rate of solubilization of the potassium is lower than for sodium, and other processes tend to return it to the solid phase (Boyd 1961). These thermal waters are also enriched in chloride, fluoride, carbon dioxide, bicarbonate and boron by magmatic gases (Allen and Day 1935).

Due to the composition of the bedrock and the thermal enrichment, these rivers can be classified as sodium-bicarbonate-chloride waters (Wright and Mills 1967).

The discharge rate of the Madison River measured between stations 10 and 11 has averaged $13.35 \text{ m}^3/\text{sec}$ ($477 \text{ ft}^3/\text{sec}$) for the fifty-one years of record (1915-1966). The average yearly fluctuation in rate is from $8.5 \text{ m}^3/\text{sec}$ ($300 \text{ ft}^3/\text{sec}$) in the winter to $43.9 \text{ m}^3/\text{sec}$ ($1550 \text{ ft}^3/\text{sec}$) in the spring. Throughout the study (6 June - 8 September, 1966) the rate of discharge averaged $13.58 \text{ m}^3/\text{sec}$ ($485.3 \text{ ft}^3/\text{sec}$) and ranged from $14.98 \text{ m}^3/\text{sec}$ ($535 \text{ ft}^3/\text{sec}$) to $10.1 \text{ m}^3/\text{sec}$ ($360 \text{ ft}^3/\text{sec}$) (U. S. Geological Survey 1966).

Methods

Water Chemistry

Water samples were collected at weekly intervals from July 6, through September 7, 1966. Surface samples were taken near the center of the river at each of the eleven stations. On each sampling date collections were made at 1500 hours. All samples were collected in one liter polypropylene plastic screw cap bottles which were rinsed with water from the sampling point before being filled.

Immediately after returning to the field laboratory, samples were analyzed for pH, total alkalinity and electrical conductivity. A Beckman Model 76 Expanded Scale pH meter was used to determine pH. Total alkalinity of each sample was determined titrimetrically according to the procedures given in Standard Methods for the Examination of Water and Waste Water, 11th Edition (1960). The electrical resistance of each water sample was determined using a Yellow Springs Instrument Co. Model 31 conductivity bridge and an Industrial Instruments Model CEL 4 dipping cell. The specific conductance at 25°C of all water samples collected on all sampling dates was computed from the observed resistance, temperature and cell constant.

Concentration of free carbon dioxide was calculated for all samples by converting the milliequivalents per liter total alkalinity to parts per million alkalinity as HCO_3^- and using the formula derived by Rainwater and Thatcher (1960):

$$\text{ppm CO}_2 = 1.589 \times 10^6 \text{ H}^+ \times \text{ppm alkalinity as HCO}_3^-$$

Concentrations of total carbon were calculated for all samples using the method of Saunders, Trama and Bachman (1962).

Temperature

The temperature of the river water at each station was measured with a standard laboratory thermometer at 0600 hours on all sampling dates.

Elevations and Gradients

The elevation at each station and at two points on the river above the uppermost stations (Figure 1) were determined using a Short and Mason Sur-

veying Aneroid Compensated Barometer (No. A 19360). Two local bench marks were used as controls (Figure 1).

The gradient at each station was computed as follows:

$$G = \frac{Eu - Ed}{D}$$

Where G = gradient,

Eu = the elevation at the nearest upstream station,

Ed = the elevation at the station for which the gradient is being determined,

D = the river distance between two stations.

Plant Canopy Cover and Substrate Texture

A water telescope was constructed by replacing the bottom of a plastic water pitcher with transparent plastic and installing two sets of cross hairs. This device was used to determine the presence or absence of plants contacting a vertical line from the water's surface to the bottom of the river. (Hereafter these line intercepts shall be referred to as points).

Five transects were established within 100 meters of each station. An attempt was made to have these transects include both fast and slow water. At each transect a line marked at one meter intervals was strung across the river. No attempt was made to place the first mark on the line in any particular relationship to the bank.

The water telescope was placed under a mark on the line. The point under the cross hairs, when they first lined up, was used in an attempt to avoid bias in the selection of the point. After the species present were recorded the texture of the substrate adjacent to the point was also record-

ed. The substrate texture was coded from 1 to 4, with 1 being rocky (over 2 centimeters in diameter), 2 being gravel (0.2 to 2 centimeters in diameter), 3 being sand (0.0625 to 2 millimeters in diameter), and 4 being silt (less than 0.0625 millimeters in diameter).

Depth and Current Speed

The current speed was determined at each point 15 cm (0.5 feet) above the bottom (or above any plants present) using a rod supported Gurley Current Meter (No. 622) and its rating table. The depth at each point was then determined and recorded using graduated marks 3.1 cm (0.1 feet) apart on the rod supporting the velocity meter.

These methods made possible the computation of mean depth, current speed, substrate texture, and the per cent of the ground covered by each taxon under each of 55 transects.

Mean free carbon dioxide, total carbon dioxide, total alkalinity, conductivity, and the pH range at 1500 hours and the mean river temperature at 0600 hours were determined for each station. It was assumed that these chemical values did not change appreciably within 100 meters of each station. Therefore, the chemical data for each station was applied to 5 transects. Although the gradient was calculated for each station, it must be applied to the five transects occurring at each station with caution because the gradient may change appreciably in 100 meters.

Results and Discussion

Chemical Data

The mean specific conductance, total alkalinity, free carbon dioxide, and total soluble inorganic carbon present at each station at 1500 hours are given in Table I. The mean temperature at 0600 hours at each station are also given in Table I.

Because the Firehole River (stations 1 and 2) had a larger fraction of chemically enriched thermal water than did the Gibbon River, the mean specific conductance, total alkalinity, and river temperature were higher at stations 1 and 2 than at station 3. The mean total alkalinity, specific conductance, and temperature of the Madison River were more closely related to the Firehole than the Gibbon since the Firehole contributed a larger discharge to the Madison than did the Gibbon River. These values were higher at station 5 than at station 4. This indicates that the discharge of the thermal spring (see Wright and Mills (1967) for a partial listing of chemical values) above station 4 did not mix completely with the river water until it was below station 4. From station 5 downstream there was a progressive decline in mean total alkalinity, specific conductance, and temperature (Table I).

The Gibbon River (station 3) had a much higher mean concentration of free carbon dioxide at 1500 hours than did the Firehole River (stations 1 and 2). Thus, the free carbon dioxide concentration of the first station on the Madison River was intermediate between the values for the Firehole and Gibbon Rivers. The Madison River is enriched in free carbon dioxide

TABLE I. CHEMICAL AND PHYSICAL PARAMETERS AT EACH STATION

	SC	TA	T ^o	CO ₂	TC	Gradient	pH	V	D	ST
Station	Micro/Mhos	Meq/l	°C	ppm	ppm	ft/mile (m/km)	Range	ft/sec (m/sec)	meters	
1	501	2.22	19.6	.34	25.6	3.3 (.62)	8.80-9.01	1.05 (.32)	1.09	2.60
2	495	2.24	18.8	.39	26.3	228.7 (43.32)	8.65-8.81	2.69 (.82)	.33	1.00
3	423	2.04	14.5	10.72	28.6	36.3 (6.87)	7.20-7.31	1.28 (.39)	.46	2.74
4	493	2.31	17.9	3.62	28.6	11.7 (2.22)	7.69-7.90	1.56 (.48)	.97	2.94
5	497	2.41	17.9	5.77	30.1	16.3 (3.09)	7.40-7.69	2.33 (.71)	.55	1.92
6	478	2.37	17.7	3.05	29.4	3.8 (.72)	7.79-7.96	1.31 (.40)	.70	2.62
7	481	2.36	17.7	1.98	28.4	4.9 (.93)	7.98-8.15	1.49 (.46)	.60	2.16
8	480	2.34	17.7	1.36	28.1	8.3 (1.57)	8.12-8.27	1.13 (.35)	.65	2.50

9	478	2.36	17.6	.93	28.4	16.1 (3.05)	8.33-8.45	1.79 (.55)	.33	1.26
10	481	2.35	16.8	.73	28.2	40.0 (7.58)	8.43-8.54	2.22 (.68)	.38	1.15
11	480	2.36	16.9	.76	28.4	11.6 (2.20)	8.80-8.91	2.34 (.72)	.29	1.13

Key to Abbreviations

SC = specific conductance

TA = total alkalinity

T° = degrees centigrade

CO₂ = free carbon dioxide

TC = total soluble inorganic carbon

G = gradient

V = current speed

D = depth

ST = substrate texture

by the thermal spring discharge mentioned previously, with the same delayed mixing. From station 5 through station 11 there is a progressive decline in mean free carbon dioxide (Table I).

The pH changes vary inversely with the free carbon dioxide changes, with the highest pH occurring at the station with the lowest amount of free carbon dioxide (Table I).

The mean concentration of total soluble inorganic carbon at 1500 hours was higher in the Gibbon (station 3) than in the Firehole River (stations 1 and 2). The concentration of total soluble inorganic carbon in the Madison River was enriched in the same manner as the other parameters by the previously mentioned thermal spring. Thus station 5 had the highest value; there was then a progressive decline from station 5 to station 7 with no significant change from station 7 through station 11 (Table I).

Gradients

The elevation and gradient of each station are presented in Table II.

Current Speed, Depth and Substrate Texture

The mean current speed, mean depth, and mean substrate texture of each station are given in Table I.

According to Leet and Judson (1965), the speed of a stream should increase and the depth of a stream should decrease with increasing gradient (especially if the discharge is constant). These relationships should be apparent, if Table I is examined. Thus if station 1 is compared to station 2, the gradient increases, the speed increases, and the depth decreases. In all possible comparisons of all stations, this relationship holds in about two-thirds of the comparisons. Some possible reasons for the non-correspondences are: (1) the speed and depth measurements are not necessarily representative of the entire reaches between stations while the gradients were calculated over the entire reaches, (2) current speed measurements were not made so as to be representative of the actual mean speed

TABLE II. ELEVATIONS, DISTANCES AND GRADIENTS AT EACH STATION

Station No. (Location)	Distance Between km (miles)	Elevation above MSL m (ft)	Gradient m/km (ft/mile)
Pt. above No. 1		2170 (7120)	
No. 1	.97 (.60)	2169 (7118)	.62 (3.3)
No. 2	2.41 (1.50)	2065 (6775)	43.32 (228.7)
Pt. above No. 3		2097 (6880)	
No. 3	4.83 (3.00)	2064 (6771)	6.87 (36.3)
No. 4	1.93 (1.2)	2059 (6757)	2.22 (11.7)
No. 5	1.67 (1.04)	2054 (6740)	3.09 (16.3)
No. 6	2.57 (1.60)	2052 (6734)	.72 (3.8)
No. 7	3.27 (2.03)	2049 (6724)	.93 (4.9)
No. 8	1.93 (1.20)	2046 (6714)	1.57 (8.3)
No. 9	3.2 (1.99)	2037 (6682)	3.05 (16.1)
No. 10	2.74 (1.70)	2016 (6614)	7.58 (40.0)
No. 11	2.35 (1.46)	2011 (6597)	2.20 (11.6)

of the streams, and (3) the gradient-speed-depth relationship may be influenced by the width of a stream.

There should be a direct relationship between substrate texture and the speed of a stream because as the speed of a stream increases, its ability to transport sediment also increases as does the size of the particles which may be transported. Therefore, the finer textured substrates should be coincident with lower speeds. Due to the method of coding substrate texture (high number equals fine substrate texture), this is seen as an inverse relationship when mean speed is compared to mean substrate texture (Table I). This relationship does not hold for some comparisons of stations. For example, in comparing station 1 to station 3, the velocity is higher at 3 and the substrate is finer textured at 3. The probable reason for this anomaly was that most of the scouring and deposition in a stream takes place in a short period of time during and after peak discharge (Leet and Judson 1965) and that the velocities reported here were obtained after peak discharge for the season had occurred. The anomalies in the other comparisons may also have been due to the deposition occurring at a time other than when the velocities were measured. However, these other anomalies may also be due to the method of measuring the velocities, i.e., it was measured 15 cm above the bottom or above any plants present and the plants present at a station may slow the current and thus promote a deposition of fine textured materials (Butcher 1933).

Plant Data

Within the study area 16 angiosperms, 2 mosses, 1 liverwort, and 1 alga were encountered. Because of difficulty in identifying genera and species of the family Characeae in the field, all members of this family were treated as a single taxon.

In order to determine the effects of changes in abundance and/or size of the plants during the course of this study (28 June - 25 August), one transect was sampled three times, once on 28 June and twice on 25 August. These observations (Table III) indicate there was as much variation due to sampling methods as there was due to more than two months time. It was concluded that seasonal changes had little effect on the validity of the sampling methods used, within the time interval during which the data was collected.

TABLE III. PER CENT OF COVER

TAXA	Dates		
	June 28	August 25	August 25
Characeae		1.75	3.84
<u>Myriophyllum exalbescens</u> Fern.	16.00	17.54	17.30
<u>Fissidens grandifrons</u> Brid.		1.75	1.92
<u>O. virens</u>	6.00	10.52	7.69
<u>Berula erecta</u> (Huds.) Cov.	18.00	24.56	17.30
<u>Glyceria borealis</u> (Nash) Batchelder	2.00	1.75	
TOTAL COVER	52	57.87	48.05

The per cent of a substrate that is covered by plants should be a reflection of that substrate's suitability for habitation. The mean per cent canopy cover of each taxon for each station is given in Table IV.

The mean total per cent canopy cover for all taxa was much lower at station 2 than at station 1 (Table IV). This decrease was due to the large decrease in the per cent canopy cover of Characeae and an absence of Potamogeton filiformis, P. strictifolius, and Ranunculus aquatilis at station 2. The per cent canopy cover of Myriophyllum exalbescens was very similar at the two stations (Table IV).

Three taxa, Characeae, Potamogeton strictifolius, and Ranunculus aquatilis had their highest per cent canopy cover at station 1 but also occurred in the Madison River.

Eight taxa, Eleocharis acicularis, Glyceria borealis, Jungermannia, Mimulus guttatus, Oncophorus virens, Potamogeton gramineus, Sparganium angustifolium, and Utricularia vulgaris, were found only in the Madison River.

TABLE IV. PER CENT CANOPY COVER OF EACH TAXA AT EACH STATION AND TOTAL PER CENT CANOPY COVER AT EACH STATION

TAXA	STATION NO.										
	1	2	3	4	5	6	7	8	9	10	11
<u>Berula erecta</u> (Huds.) Cov.			6.0	34.7	35.6	43.6	25.3	15.9	28.7	9.8	17.7
<u>Carex rostrata</u> Stokes			4.4		0.5						
Characeae	56.7	4.7	9.6	14.7	5.7	51.6	31.5	40.7	6.1	3.1	1.1
<u>Deschampsia caespitosa</u> (L.) Beauv.			29.9	3.7	5.2	7.1		0.4			
<u>Eleocharis acicularis</u> (L.) R. & S.				0.8			4.1	0.8			
<u>Fissidens grandifrons</u> Bird.		0.8			5.0				6.1	4.8	0.7
<u>Glyceria borealis</u> (Nash) Batchelder				4.2	17.5	25.6	15.8	4.7	15.4	0.9	0.8
<u>Juncus ensifolius</u> Wiks.			4.9	2.3	0.7	1.8	0.4				
Jungermannia					2.8						
<u>Myriophyllum exalbescens</u> Fern.	8.3	6.1		61.7	33.7	17.6	9.1	10.1	13.4	13.1	15.4
<u>Mimulus guttatus</u> Fischer					0.5	1.3					
<u>Oncophorus virens</u>					4.2		1.3		6.3	4.3	7.4

<u>Potamogeton filiformis</u> Pers.	21.6			9.5	1.1	26.4	17.9	18.6			
<u>P. gramineus</u> L.						0.8	0.5	2.0		0.5	
<u>P. natans</u> L.			1.3	2.9		11.5	1.9	5.9			
<u>P. nodosus</u> L.			1.3	59.2	8.6	24.5	4.8	6.1			
<u>P. strictifolius</u> Benn.	37.0			3.1		0.9	1.9	0.4			
<u>Ranunculus aquatilis</u> L.	10.5						0.5				
<u>Sparganium angustifolium</u> Michx.				2.2		2.3	2.1	3.1			
<u>Utricularia vulgaris</u> L.				2.0	2.3	5.6	2.3	5.5		0.5	
<u>TOTAL</u>	134.1	11.6	57.4	201.0	122.9	221.1	119.4	114.2	76.0	37.0	43.1

PHYTOSOCIOLOGICAL CONSIDERATIONS

Index of Similarity

Indices of similarity were computed for all pairs of species using the formula described by Curtis (1959) which he states was first proposed by Czenkanowski in 1913:

$$I = \frac{2c}{a+b} \times 100$$

Where:

I = index of similarity

a = number of transects in which the first taxon was found

b = number of transects in which the second taxon was found

c = number of transects in which both taxa were found

Attempts were made to arrange these indices as described by MacFadyen (1957) in order to determine if separate floristic groups could be delimited. However, no arrangement of the indices was found that would justify designating separate floristic groups (Table V). Accordingly this assemblage of taxa should be considered as one community (MacFadyen, 1957). The studies of Rasmussen (1968) and Roeder (1966) which dealt with the macrophytes of the Firehole and the diatoms of the upper Madison River system respectively, also indicated that in parts of their study area which were coincident with the area of the present study, there was only one community.

TABLE V. INDEX OF SIMILARITY

	C	ME	FG	OV	J	DC	CR	BE	PNA	PNO	UV	JE	GB	PS	PF	EA	SA	MG	PG	RA
C																				
ME	46																			
FG	42	48																		
OV	35	48	69																	
J	4	4	22	22																
DC	34	24	71	0	14															
CR	4	4	0	0	0	26														
BE	82	86	50	50	9	36	9													
PNA	43	43	0	7	0	39	24	48												
PNO	55	53	0	6	0	44	17	50	77											
UV	48	50	12	6	0	29	0	53	53	61										
JE	25	27	6	15	17	55	0	37	58	47	46									
GB	73	72	47	47	6	28	6	83	53	51	55	29								
PS	44	43	0	7	0	8	13	28	37	30	35	26	33							
PF	74	73	47	9	7	37	7	62	68	77	60	43	66	65						
EA	16	15	0	10	0	11	0	17	42	40	19	27	22	33	31					
SA	36	35	0	8	0	36	15	37	67	60	38	30	44	26	54	40				
MG	12	12	0	0	0	27	33	13	24	26	21	15	18	25	20	0	15			
PG	26	26	9	9	0	21	0	27	38	30	43	12	32	10	35	17	59	0		
RA	23	19	0	0	0	0	0	4	10	7	0	0	5	63	36	18	13	0	0	

Index of Diversity

An index of community diversity was calculated for each station by using the formula suggested by Gleason (1922) and cited by Margalef (1958):

$$d = \frac{m-1}{\log_e n}$$

Where:

d = index of diversity

m = number of taxa present at the station

n = number of occupied points at the station

These indices (Table VI) give a comparative measure of the floral variety at each station. In general the stations with high diversity indices have more taxa present and a higher per cent canopy cover than the stations with low diversity indices. (If m=1 and n=100 then d=0. If m=100 and n=100 then d=4.6.)

TABLE VI. DIVERSITY INDICES FOR STATIONS 1-11

Station	Diversity Index
1	0.84
2	0.74
3	1.37
4	1.93
5	2.40
6	2.25
7	2.70
8	2.20
9	0.92
10	1.60
11	1.05

Relationships Between Diversity Indices and Environmental Factors

Simple correlation coefficients were calculated between the diversity indices and the considered environmental factors. The significant correlation coefficients were as follows: total soluble inorganic carbon and diversity index (all stations); $r = 0.81^{**}$, free carbon dioxide and diversity index (without the Gibbon station): $r = 0.79^{*}$, total alkalinity and diversity index (without the Gibbon station): $r = 0.88^{**}$. None of the other possible combinations of the considered environmental factors with the diversity index had significant correlation coefficients.

Statistical Analyses

A disk loaded "library" program was used with an IBM 1620 Model 2 computer. This program computes the mean, standard deviation, variance, and the sum of the squares of each variable. It also computes the simple linear regression coefficients for all pairs of variables and multiple linear regression coefficients, coefficients of determination, standard error of the estimates, t values, partial correlation coefficients, and F ratios once using the total per cent canopy cover and once using the per cent canopy cover of each taxon as the dependent variable and all of the measured environmental factors as independent variables.

The independent variables in this study were mean depth, current speed, and substrate texture measured at each transect; and the mean concentration (as ppm) of free carbon dioxide, total soluble inorganic carbon, the mean

*significant to 5% level

**significant to 1% level

total alkalinity, specific conductance, and hydrogen ion concentration.

In order to make possible comparisons with the data of Todd (1967) and Wright and Mills (1967), the various statistical parameters were computed twice, once using only the data from the stations on the Madison River (4-11) and once using the data from all stations.

When considering the various statistical parameters obtained when the data from all stations are used it should be kept in mind that these parameters will be greatly affected by the extremes found in the Gibbon and Firehole Rivers. The Gibbon is characterized by low temperatures, low concentrations of dissolved materials and pH, high concentration of free carbon dioxide and a relatively low plant cover. The Firehole in contrast has higher temperatures, higher concentrations of dissolved materials and pH values and lower concentrations of free carbon dioxide.

On the other hand when just the data from the Madison River are used in computing the statistical parameters, these parameters reflect the effects of concurrent but not necessarily connected downstream changes in pH, the concentration of free carbon dioxide, temperature, velocity, depth, and substrate texture.

Simple Correlations of Environmental Factors and Total Per Cent Canopy Cover

Table VII contains the simple correlation coefficients obtained by using the various environmental variables and the total per cent canopy cover of all plants. The upper of each pair of correlation coefficients are those obtained when all data were used, and the lower of each pair are those obtained when only the data from the Madison River were used.

At this point, the correlation coefficients in Table VII which were significant at the 1% level of probability will be briefly discussed by columns, except that all correlations with per cent canopy cover will be discussed together at the end of this section.

Correlations with Free Carbon Dioxide

The positive correlations with total soluble inorganic carbon could be expected in view of the action of the carbon dioxide-bicarbonate-carbonate equilibrium.

Positive correlations of free carbon dioxide with total alkalinity would be expected in one water mass because the total alkalinity in these rivers is essentially a measure of bicarbonate ion concentration (Rainwater and Thatcher 1960) and the bicarbonate ion concentration is related to the concentration of free carbon dioxide concentration through the equilibrium mentioned above. However, if all data are considered the correlation is negative. This is probably due to the different levels of free carbon dioxide and total alkalinity in the Firehole, Gibbon and Madison Rivers which have been mentioned previously.

The negative correlation with specific conductance when all rivers were considered was probably due to the extreme values of free carbon dioxide and specific conductance in the Firehole and Gibbon Rivers. The positive correlation with specific conductance when just the Madison River was considered may be due to the effects of bicarbonate diminution downstream or to a downstream decrease in other ions.

TABLE VII. SIMPLE CORRELATION COEFFICIENTS BETWEEN PHYSICAL AND CHEMICAL FACTORS AND TOTAL PER CENT CANOPY COVER (ALL COMBINATIONS)

	CO ₂	TC	TA	SC	pH	T ^o	D	V	ST
CO ₂									
CO ₂ #									
TC	.50 **								
TC #	.91 **								
TA	-.59 **	.34 **							
TA #	.50 **	.74 **							
SC	-.72 **	-.19 *	.74 **						
SC #	.95 **	.83 **	.304 *						
pH	-.89 **	-.80 **	.22 *	.53 **					
pH #	-.96 **	-.85 **	-.36 *	-.91 **					
T ^o	-.67 **	-.44 **	.50 **	.92 **	.60 **				
T #	.81 **	.67 **	.25 *	.69 **	-.91 **				
D	.007	-.15	.04	.34 **	-.05	.44 **			
D #	.525 **	.28 *	-.30 *	.58 **	-.67 **	.65 **			
V	-.22 *	.03	.21 *	.24 *	.24 *	.09	-.65 **		
V #	.047	.14	.36 *	.11	.18	-.37 **	-.59 **		
ST	.41 **	.15	-.21 *	-.14	-.45 **	-.05	.63 **	-.65 *	
ST #	.43 **	.27 *	-.16	.42 *	-.58 **	.60 **	.72 **	-.54 *	
Cover	.11	.37 **	-.32 **	.30	-.37 **	.262	.68 **	.54 **	.67 **
Cover #	.57 **	.496 **	-.055	.58	-.73 **	.72 **	.76 **	-.54 **	.799 **

indicates Madison River stations only

*-significant to 10% level

**-significant to 1% level

The negative correlations with pH could be expected in view of the carbon dioxide-bicarbonate-carbonate equilibrium and the consequent effects on the hydrogen and hydroxide ion concentrations.

The negative correlation with temperature when all rivers were considered is due to the high carbon dioxide concentration of the Gibbon River which also has a low temperature. The positive correlation when only the Madison River was considered was undoubtedly due to the concurrent but unrelated cooling and loss of free carbon dioxide downstream from station 4.

The positive correlation with depth when just the Madison River was considered was also probably due to concurrent but unrelated changes downstream from station 4.

The positive correlations with substrate texture are probably coincidental although it is possible that there may have been some trapping of fine textured material by plants and that the amount of plants present may be related to the concentration of free carbon dioxide available.

Correlations with Total Soluble Inorganic Carbon

The positive correlations with total alkalinity could be expected because at the pH's encountered in this study most of the inorganic carbon will be present as bicarbonate (Hutchinson 1957) and as previously mentioned total alkalinity in these rivers is essentially a measure of bicarbonate ion concentration.

The positive correlation with specific conductance in the Madison River may have been due to the effects of bicarbonate ion diminution downstream or to the downstream decrease in other ions.

The negative correlations with pH are expected for the same reasons as for the correlations between free carbon dioxide and pH.

The correlations with temperature are expected for the same reasons as those discussed for free carbon dioxide with temperature.

Correlations with Total Alkalinity

The positive correlation with specific conductance could have been expected because bicarbonate ion concentration is one of the major ions contributing to specific conductance and is essentially the only factor determining the total alkalinity.

The positive correlation with temperature when all rivers were considered was probably the result of the extreme values of total alkalinity and temperature in the Gibbon and Firehole Rivers.

Correlations with Specific Conductance

The positive correlation with pH when all rivers were considered was probably due to the extreme values in the Firehole (high pH, and high specific conductance) and Gibbon (low pH, and low specific conductance) Rivers. The negative correlation with specific conductance in the Madison River may have been due to the downstream diminution in bicarbonate ion or the correlation may have been the result of a downstream decrease in the concentration of other ions and a coincidental increase in pH.

The positive correlations with temperature could have been expected because the various thermal discharges these streams receive are also chemically enriched.

The positive correlations with depth were undoubtedly coincidental.

The positive correlations with substrate texture in the Madison River was probably also coincidental.

Correlations with pH

The positive correlation with temperature when all rivers were considered was probably due to the great contrast between the Firehole (high temperature, high pH) and the Gibbon (low temperature and low pH). The negative correlation with temperature in the Madison River was probably due to the concurrent but unrelated changes in these parameters downstream from station 4.

The correlations with depth and substrate texture were almost certainly meaningless.

Correlations with Temperature

The correlations of temperature with depth, velocity, and substrate texture were almost certainly the meaningless results of concurrent but unrelated changes.

Correlations with Depth

The negative correlations with current speed could have been expected for the reasons previously discussed.

The positive correlations with substrate could also have been expected for the reasons previously discussed.

Correlations with Velocity

The correlations with substrate texture could have been expected for the reasons previously discussed.

Correlations with Total Per Cent Canopy Cover

When all rivers were considered only free carbon dioxide, specific conductance, and temperature were not significantly correlated with total per cent canopy cover at the 1% level of probability. However, the latter two variables were significantly correlated with total per cent canopy cover at the 10% level. The largest correlations were with depth, substrate texture, and velocity.

When only the Madison River was considered, only total alkalinity was not significantly correlated with total per cent canopy cover at the 1% level of probability. The highest correlation coefficients were with substrate texture, depth, pH, and temperature.

MULTIPLE CORRELATIONS WITH TOTAL PER CENT CANOPY COVER

The coefficient of determination (R^2) when all rivers were considered was 0.781 (Table VIII). This indicates that about 78% of the variation of the total per cent canopy cover was associated with the nine environmental factors considered in this part of this study. The factors which had the largest partial correlation coefficients with total per cent canopy cover were (in descending order) current speed, temperature, pH, substrate texture, and total soluble inorganic carbon.

When only the Madison River was considered the coefficient of deter-

mination was 0.903 indicating that about 90% of the variation in the total per cent canopy cover was associated with the environmental factors considered. Only substrate texture and total soluble inorganic carbon had significant partial correlation coefficients with total per cent canopy cover (Table VIII).

TABLE VIII. PARTIAL CORRELATION COEFFICIENTS BETWEEN TOTAL PER CENT CANOPY COVER AND PHYSICAL AND CHEMICAL FACTORS

	Madison River Only (N = 40)		All Rivers (N = 55)	
	T	Par R	T	Par R
CO ₂	.04	.009	.06	.009
TC	1.60*	.281	2.24*	.317
TA	- .99	-.179	-1.22	-.179
SC	- .48	-.088	-1.26	-.186
pH	- .45	-.084	2.49**	.348
T ^o	- .29	-.054	2.75**	.379
D	.12	.023	.80	.119
V	-.44	-.081	-3.38**	-.451
ST	3.88**	.578	2.31*	.326
	$R^2 = .903$		$R^2 = .781$	
	ST error of est - 2430		ST error of est - 1088	
	F = 31.10**		F = 17.81**	
* significant to 10% level		T = value for "Student's" t distribution		
** significant to 1% level				

FACTORS AFFECTING THE DISTRIBUTION AND ABUNDANCE OF TAXA

The relationships between the considered environmental factors and the distribution and abundance of the taxa, as well as the relationships between taxa, will now be discussed in an attempt to determine how the environmental factors are related to the distribution and/or abundance of each taxon and to elucidate some of the competitive relationships between taxa.

Berula erecta

As previously mentioned, B. erecta occurred in varying amounts at each station except stations 1 and 2 (Table I), both of which were located on the Firehole River. However, the reasons for its non-occurrence at these stations were probably different.

The coarseness and instability of the substrate at station 2 (Table I) was the most probable reason for the non-occurrence of B. erecta at this station. The partial correlation coefficient between the per cent canopy cover of B. erecta and the substrate texture indicated (Table IX), that when all other factors were held statistically constant, substrate texture was one of the most important factors affecting the distribution and abundance of B. erecta throughout the study area. (Bear in mind that due to the method of coding, a high number indicates fine substrate texture, so the foregoing implies more B. erecta on the finer textured substrates.)

The partial correlation coefficient of B. erecta with velocity in the Madison River was positive and significant, but when all rivers were considered, the partial correlation coefficient was not significant (Table IX).

TABLE IX. CORRELATION COEFFICIENTS OF ENVIRONMENTAL FACTORS WITH BERULA ERECTA

	CO ₂	TC	D	V	ST	T ^O	SC	TA	pH
<u>Simple correlation coefficients</u>									
<u>Madison River only</u>									
r =	0.602**	0.627**	0.395*	-0.111	0.551**	0.633**	0.581**	0.231*	-0.669**
<u>All Rivers</u>									
r =	0.139	0.736**	0.114	-0.300*	0.297*	0.017	0.208*	0.522**	-0.495**
<u>Multiple correlations</u>									
<u>Madison River only</u>									
t =	0.44	1.57 *	-0.22	1.66 *	2.41*	-0.23	-0.78	1.06	0.11
par. r =	0.08	0.28	-0.04	0.29	0.40	-0.04	0.14	0.19	0.02
multiple R = 0.842 R ² = 0.709 F ratio = 8.10* standard error = 858									
<u>All Rivers</u>									
t =	-3.20 **	2.99 **	0.69	0.84	2.70 **	2.03 *	-0.71	2.06 *	0.16
par. r =	-0.43	0.41	0.10	0.13	0.37	0.29	-0.11	-0.29	0.02
multiple R = 0.887 R ² = 0.787 F ratio = 18.50* standard error = 810									
*-significant to 10% level; **-significant to 1% level; ***-significant to 5% level									

These two facts together indicate that the higher velocities in the Madison River were more favorable for the establishment and maintenance of B. erecta than the slower velocities in the Madison River and that the velocity at station 2 may have been beyond its tolerance.

Other physical factors possibly limiting for B. erecta at station 2, and at station 1, were the relatively small amounts of free carbon dioxide and total soluble inorganic carbon, the relatively high temperature, and the relatively high specific conductance (Table I).

It is possible that the relatively great depth at station 1 (Table I) was limiting the occurrence of B. erecta, as this station had the greatest mean depth of all stations. However, the only significant correlation coefficient between depth and the per cent canopy cover of B. erecta (Table IX) seems to indicate that the per cent canopy cover of B. erecta increased with increasing depth at least down to the maximum depth in the Madison River. This together with the occurrence of much shallower depths near the banks at station 1 seems to discredit the possibility that the occurrence of B. erecta at station 1 was limited by depth.

Rasmussen (1968) found B. erecta growing upstream in the Firehole River at higher temperatures, at nearly the same specific conductance, at considerably higher levels of free carbon dioxide, and judging from her reported total alkalinities, considerably higher levels of total soluble inorganic carbon than the values found for these parameters at stations 1 and 2. Thus it appears unlikely that either temperature or specific conductance were limiting to B. erecta at stations 1 or 2. This leaves free carbon dioxide and total soluble inorganic carbon as possible limiting factors

for B. erecta at stations 1 and 2. The partial correlation coefficient between free carbon dioxide and the per cent canopy cover of B. erecta when just the Madison River data was considered was positive. However, when all data were considered, it was not significant. The partial correlation coefficient between these factors for the Madison River data was not significant while it was negative when all data were considered (Table IX). This negative partial correlation coefficient was probably due to the extremely large amount of free carbon dioxide and relatively small amount of B. erecta in the Gibbon River at station 3 (Tables I and IV) and thus should not be seriously considered when thinking about stations 1 and 2.

In contrast to these varied correlation coefficients between free carbon dioxide and per cent canopy cover of B. erecta, all of the simple and partial correlation coefficients between total soluble inorganic carbon and per cent canopy cover of B. erecta were positive and significant. Thus it appears that the most likely physical limiting factor for B. erecta at station 1 (and disregarding substrate texture, at station 2) was the relatively small amount of total soluble inorganic carbon present at this station.

The abundance of B. erecta at station 3 may have been limited by the relatively low temperature or the relatively low specific conductance (Table I). However, Rasmussen (1968) reports this taxon growing at a much lower specific conductance so it is not likely that the specific conductance at station 3 was limiting.

Although there were many significant simple correlation coefficients between the per cent canopy cover of B. erecta and the considered physical

factors for the remaining stations, there were only three significant partial correlation coefficients, those with soluble inorganic carbon, current speed, and substrate texture (Table IX). From the values of these partial correlation coefficients it appears that the most important factor affecting the distribution abundance of B. erecta in the Madison River (stations 4-11) was the texture of the substrate.

Thus far nothing has been said about the effects of competition with other taxa on the occurrence and abundance of B. erecta. Only the per cent canopy cover of Potamogeton strictifolius and Ranunculus aquatilis were negatively correlated with the per cent canopy cover of B. erecta (Table XXIX). Both of these taxa had their highest per cent canopy cover at station 1 where B. erecta did not occur. As both of these taxa did occur at some stations where B. erecta also occurred, it could be inferred that competition with one or both of these taxa was responsible for the non-occurrence of B. erecta at station 1. However, it must be emphasized that this is only a possibility as it is not known if competition was actually occurring. The other taxa which had positive correlation coefficients when their per cent canopy cover was compared to the per cent canopy cover of B. erecta (Table XXVIII) were probably responding similarly to the same limiting factors as B. erecta with little if any competition occurring.

Carex rostrata

Because the highest per cent canopy cover of C. rostrata was slightly less than 5 per cent and it only occurred at stations 3 and 6 (Table IV), it is felt that any inferences about factors limiting its occurrence will be of doubtful validity. However, as it had its greatest per cent canopy cover at station 3, it appears to have significant correlation coefficients with those factors which were relatively extreme at this station, i.e., high free carbon dioxide, low velocity, fine substrate texture, low temperature, low specific conductance, low total alkalinity, and low pH (Tables X and I).

The per cent canopy cover of C. rostrata was positively correlated with the per cent canopy cover of Characeae, Deschampsia caespitosa, and Glyceria borealis (Table XXIX) which may indicate some overlapping of environmental suitability for these taxa.

TABLE X. CORRELATION COEFFICIENTS OF ENVIRONMENTAL FACTORS WITH CAREX ROSTRATA

	CO ₂	TC	D	V	ST	T ^o	SC	TA	pH
<u>Simple correlation coefficients</u>									
<u>Madison River only</u>									
r =	0.076	0.182	0.161	-0.255*	0.084	0.082	0.078	0.091	-0.126
<u>All Rivers</u>									
r =	0.506**	0.077	-0.038	-0.202	0.219	-0.461**	-0.545**	-0.512**	-0.353**
<u>Multiple correlations</u>									
<u>Madison River only</u>									
t =	-0.42	-0.07	0.30	-1.15	-0.38	-0.24	0.36	0.27	0.05
par. r =	-0.08	0.01	0.06	-0.21	0.07	0.04	0.07	0.05	0.01
multiple R = 0.499			R ² = 0.249		F ratio = 1.10		standard error = 37		
<u>All Rivers</u>									
t =	0.45	0.93	0.48	-0.03	0.40	0.42	-0.49	-0.91	1.05
par. r =	0.07	0.14	0.07	-0.01	0.06	0.06	-0.07	-0.13	0.155
multiple R = 0.604			R ² = 0.365		F ratio = 2.87*		standard error = 187		
*-significant to 10% level; **-significant to 1% level; ***-significant to 5% level									

Characeae

The largest simple correlation coefficients, both in the Madison River and when all rivers were considered, were between the per cent canopy cover of the Characeae and current speed, indicating that members of this taxon do best in slow water (Table XI). The other significant simple correlation coefficients indicated that the depth, temperature, and the substrate texture were also important in determining the abundance of the Characeae.

The partial correlation coefficients obtained when all rivers were considered indicated that current speed was the most important physical factor affecting the abundance of the Characeae and that the amount of total soluble inorganic carbon, the substrate texture, and the temperature were also important. The partial correlation coefficients between the per cent canopy cover of the Characeae and the various physical factors when just the Madison River was considered seem to indicate that temperature was the most important, but that only speed and substrate texture were not important, in affecting the abundance of the Characeae (Table XI).

Thus there were indications that the speed, the amount of total soluble inorganic carbon, the substrate texture and the temperature were affecting the abundance of the Characeae when all rivers were considered and in the Madison River the speed and the substrate texture were not affecting the abundance of the Characeae. There are several possible reasons for these apparent contradictions.

One of the most obvious possibilities is that the range of some of the physical factors in the Madison River (for example, the speed and the sub-

TABLE XI. CORRELATION COEFFICIENTS OF ENVIRONMENTAL FACTORS WITH CHARACEAE

	CO ₂	TC	D	V	ST	T ^o	SC	TA	pH
<u>Simple correlation coefficients</u>									
<u>Madison River only</u>									
r =	0.087	0.123	0.503**	-0.799**	0.571*	0.370**	-0.018	-0.019	-0.287
<u>All Rivers</u>									
r =	-0.159	-0.192	0.673**	-0.726**	0.543**	0.380**	0.234*	0.130	0.105
<u>Multiple correlations</u>									
<u>Madison River only</u>									
t =	3.95 **	4.86**	2.71 **	0.53	0.67	6.82 **	5.49 **	-4.52 **	3.12 **
par. r =	0.59	0.66	0.44	0.09	0.12	-0.78	-0.71	-0.64	-0.49
multiple R = 0.972 R ² = 0.945 F ratio = 57.01 *** standard error = 509									
<u>All Rivers</u>									
t =	0.06	2.24 *	0.80	-3.38 **	2.31 *	2.75 *	-1.26	-1.22	2.49 *
par. r =	0.01	0.32	0.12	-0.45	0.33	0.38	-0.19	-0.18	0.35
multiple R = 0.884 R ² = 0.781 F ratio = 17.81* standard error = 10.88									

*-significant to 10% level; **-significant to 1% level; ***-significant to 5% level

strate texture) were so narrow compared to the range tolerated by the Characeae that these factors were limiting only when the larger and more diverse sample was considered.

Another possibility is that more than one species of Characeae was present. If this were so these different species would probably have had different optimum ranges of the various factors considered and would have been more abundant in different parts of the study area. Thus these different species would have had significant correlation coefficients with different factors.

Deschampsia caespitosa

This taxon was most abundant at station 3 on the Gibbon River and was less abundant at stations 4-6 and 8 on the upper Madison River. It was not present at stations 1 and 2 on the Firehole River or at stations 7 and 9-11 on the lower Madison River (Table IV).

The F ratio obtained for the multiple regression when only the Madison River was considered was not significant (Table XII). This indicates that the population means were not different and that any consideration of possible limiting factors based on this analysis probably not be valid.

The F ratio for the multiple regression analysis of all data was significant. The coefficient of determination for this analysis indicated that about 78 per cent of the variation of the per cent canopy cover of this taxon was associated with the physical factors which were considered.

The magnitude of these partial correlation coefficients indicated that the amounts of total soluble inorganic carbon and free carbon dioxide, current speed, the substrate texture, and the total alkalinity were the most important factors affecting the distribution of this taxon (Table XII).

These were all possible limiting factors for this taxon at stations 1 and 2. However, this taxon was abundant at stations 6 and 8 where speed and substrate texture were comparable to those at station 1 (Tables I and IV). Thus it is doubtful the tolerance limits of this taxon for either of these factors were exceeded at station 1. The values of these two factors were extreme at station 2 so it is likely the tolerance limit of this taxon for speed and substrate texture were exceeded. This leaves the low total

TABLE XII. CORRELATION COEFFICIENTS OF ENVIRONMENTAL FACTORS WITH DESCHAMPSIA CAESPITOSA

	CO ₂	TC	D	V	ST	T ^o	SC	TA	pH
<u>Simple correlation coefficients</u>									
<u>Madison River only</u>									
r =	0.390**	0.425**	0.254*	-0.116	0.335*	0.304*	0.399**	0.193	-0.405**
<u>All Rivers</u>									
r =	0.821**	0.249*	-0.051	-0.262*	0.374**	-0.654**	-0.747**	-0.687**	-0.640
<u>Multiple correlations</u>									
<u>Madison River only</u>									
t =	-0.53	-0.22	-0.71	-1.15	1.31 *	0.44	0.61	0.45	0.05
par. r =	-0.09	-0.04	-0.13	-0.21	0.23	0.08	0.11	0.08	0.01
multiple R = 0.551 R ² = 0.303 F ratio = 1.45 standard error = 529									
<u>All Rivers</u>									
t =	1.86 *	1.72 *	-0.59	-1.28 *	1.39 *	0.02	0.50	-2.21 *	1.89 *
par. r =	0.27	0.25	-0.09	-0.19	0.20	0.01	0.08	-0.31	0.27
multiple R = 0.885 R ² = 0.783 F ratio = 18.04** standard error = 496									
*-significant to 10% level; **-significant to 1% level; ***-significant to 5% level									

(Table XXIX). These two taxa, Fissidens grandifrons and Oncophorus virens, were probably not competing with D. caespitosa as both of these taxa apparently had different environmental optima than D. caespitosa (Table XXX).

Eleocharis acicularis

This taxon was present at stations 4, 7 and 8 and was most abundant at station 7.

The F ratios of both analyses were significant and the coefficients of determination indicated that when just the Madison River was considered about 48 per cent, and when all rivers were considered about 42 per cent, of the variation in the per cent canopy cover was associated with the considered factors (Table XIII). Since these two values are so similar it seems best to consider all data when discussing limiting factors in order to take advantage of the larger variation of the factors considered which were inherent in the larger sample.

The magnitude of the partial correlation coefficients indicated that only the variation in substrate texture was not associated with a comparable variation in the per cent canopy cover of E. acicularis (Table XIII).

Thus it is possible that any of the other factors were limiting for E. acicularis at the stations where this taxon did not occur.

However, as this taxon was relatively rare it is thought that the conclusions as to limiting factors and the limits of tolerance of E. acicularis are of doubtful validity and accordingly Table XIII is presented but will not be discussed.

The per cent canopy cover of this taxon was positively correlated with the per cent canopy cover of many of the other plants (Table XXIX). The positive correlations seem to indicate similar responses to the same factors but may be an indication that competition was occurring.

TABLE XIII. CORRELATION COEFFICIENTS OF ENVIRONMENTAL FACTORS WITH ELEOCHARIS ACICULARIS

	CO ₂	TC	D	V	ST	T ⁰	SC	TA	pH
<u>Simple correlation coefficients</u>									
<u>Madison River only</u>									
r =	-0.026	-0.109	0.184	-0.209*	0.125	0.230*	-0.127	-0.063	-0.069
<u>All Rivers</u>									
r =	-0.054	0.073	0.112	-0.135	0.085	0.059	0.014	0.133	-0.077
<u>Multiple correlations</u>									
<u>Madison River only</u>									
t =	-1.31 *	-1.53 *	1.22	1.50 *	-0.62	0.83	0.78	1.30 *	-2.50 **
par. r =	-0.23	-0.27	0.22	0.26	-0.11	0.15	0.14	0.23	-0.42
multiple R = 0.692 R ² = 0.479 F ratio = 3.07** standard error = 167									
<u>All Rivers</u>									
t =	-2.58 **	-1.90 *	1.80 *	2.79 **	-0.65	2.24 *	-3.63 **	2.62 **	-3.15 **
par. r =	-0.36	-0.27	0.26	0.38	-0.09	0.32	-0.48	0.37	-0.43
multiple R = 0.646 R ² = 0.417 F ratio = 3.57** standard error = 147									

*-significant to 10% level; significant to 1% level; ***-significant to 5% level

alkalinity and the relatively small amounts of free carbon dioxide and total soluble inorganic carbon as probable limiting factors at station 1. These were also possible limiting factors at station 2 but current speed and substrate texture were probably more important.

The same 5 factors were also the probable limiting factors at the stations on the lower Madison River. In this case the values of total alkalinity, speed, and the amounts of free carbon dioxide and total soluble inorganic carbon at station 7 were exceeded at other stations where D. caespitosa was present and the values of total alkalinity and current speed at stations 9-11 were exceeded at stations where this taxa was present. This leaves the amounts of free carbon dioxide and total soluble inorganic carbon as possible limiting factors at stations 9-11 and the very fine textured substrate at station 7 as a possible limiting factor.

From the magnitude of the partial correlation coefficients, it appears total alkalinity was the most important factor affecting the per cent canopy cover of this taxon.

The values in Table XXX indicate the approximate tolerance limits of D. caespitosa to the factors considered in this study.

Although there were many significant positive simple correlation coefficients between the per cent canopy cover of this taxon and the per cent canopy cover of other taxa indicating similar responses to the physical factors considered, only two taxa were negatively correlated (Table XXIX).

Fissidens grandifrons

This taxon was present at stations 2, 5, and 9-11 and its highest per cent canopy cover was at station 9 (Table IV).

The F ratios for both of the analyses were significant. The coefficients of determination indicated that only about 39 per cent and 32 per cent of the variation of the per cent canopy cover of F. grandifrons was associated with the variation of the factors which were considered in the Madison River and all rivers respectively. These low values indicate that much of the variation of the per cent canopy cover of this taxon was associated with some undetermined factor(s).

The only significant partial correlation coefficients when all rivers were considered were between the per cent canopy cover of F. grandifrons and the amount of free carbon dioxide and the substrate texture (Table XIV).

If these factors are considered at each station, it appears that the substrate texture was too fine at stations 1, 3, 4, and 6-8 for this taxon to tolerate. Thus it seems the substrate texture was the factor which determined whether or not this taxon would be present at a station but that the amount of free carbon dioxide at a station was related to the abundance of this taxon at that station. The tolerance limit of F. grandifrons for substrate appeared to be exceeded at coded substrate values between 1.92 and 2.5. These values correspond to a mean substrate texture between gravel and sand (Table I).

The per cent canopy cover of F. grandifrons was negatively correlated with the per cent canopy cover of five other taxa but was positively

TABLE XIV. CORRELATION COEFFICIENTS OF ENVIRONMENTAL FACTORS WITH FISSIDENS GRANDIFRONS

	CO ₂	TC	D	V	ST	T ^O	SC	TA	pH
<u>Simple correlation coefficients</u>									
<u>Madison River only</u>									
r =	0.008	0.089	-0.434**	0.410**	-0.464**	-0.148	-0.009	0.276*	0.123
<u>All Rivers</u>									
r =	-0.077	0.199*	-0.354**	0.344**	-0.418**	-0.346	0.086	0.267*	0.040
<u>Multiple correlations</u>									
<u>Madison River only</u>									
t =	-0.56	-0.64	-1.26	-1.24	-0.99	1.22	0.90	0.71	0.87
par. r =	-0.10	-0.12	-0.23	-0.22	-0.18	0.22	0.17	0.13	0.16
multiple R =	0.632	R ² = 0.399		F ratio = 2.21***		standard error = 311			
<u>All Rivers</u>									
t =	2.09 *	-0.28	-0.95	-0.64	-1.50 *	-0.59	0.60	0.98	0.62
par. r =	0.298	-0.04	-0.14	-0.09	-0.22	-0.09	0.09	0.15	0.09
multiple R =	0.569	R ² = 0.324		F ratio = 2.39***		standard error = 300			
*-significant to 10% level; **-significant to 1% level; ***-significant to 5% level									

correlated with only one, O. virens, which is also a moss. There may have been some competition between F. grandifrons and these other taxa but the taxa which were negatively correlated were probably responding differently to the considered factors and the taxon which was positively correlated was probably responding to the considered factors in the same manner as was F. grandifrons.

Glyceria borealis

This taxon was present at every station except stations 1-3. It was most abundant at station 6.

The F ratios were both significant. The coefficients of determination both indicated that about 66 per cent of the variation in the per cent canopy cover of G. borealis was associated with the factors considered in this study.

The partial correlation coefficients which were obtained when all rivers were considered indicated that the amount of total soluble inorganic carbon, the current speed, the temperature, and total alkalinity were the most important factors affecting the distribution and abundance of G. borealis (Table XV).

If the values of the factors above at the stations where G. borealis was not present are examined, it appears that the possible limiting factors at station 1 were the relatively small amount of total soluble inorganic carbon and the relatively low total alkalinity. The possible limiting factors at station 2 were the relatively high velocity, small amount of total soluble inorganic carbon, and the relatively low total alkalinity. The possible limiting factors at station 3 were the relatively low total alkalinity and temperature.

The lower tolerance limit of G. borealis for temperature seemed to be between 17.5°C and 14.5°C, for total alkalinity between 2.34 and 2.23 meq/l, for total soluble inorganic carbon between 28.1 and 26.3 ppm and for speed between 0.35 and 0.32 meters per second.

TABLE XV. CORRELATION COEFFICIENTS OF ENVIRONMENTAL FACTORS WITH GLYCERIA BOREALIS

	CO ₂	TC	D	Y	ST	T ^O	SC	TA	pH
<u>Simple correlation coefficients</u>									
<u>Madison River only</u>									
r =	0.368*	0.526**	0.023	-0.196	0.074	0.487**	0.232*	0.456**	-0.428**
<u>All Rivers</u>									
r =	0.057	0.539**	-0.036	-0.093	0.014	0.108	0.175	0.448**	-0.313**
<u>Multiple correlations</u>									
<u>Madison River only</u>									
t =	-0.58	0.23	2.16 *	1.14	1.50 *	0.37	0.18	0.12	-1.31 *
par. r =	-0.11	0.04	-0.37	-0.20	-0.27	0.07	0.03	0.02	-0.23
multiple R = 0.814			R ² = 0.662		F ratio = 6.53*		standard error = 752		
<u>All Rivers</u>									
t =	-0.83	2.08 **	-1.20	-2.33 *	-1.29	3.74 **	-1.27	-1.68 *	1.19
par. r =	-0.12	0.39	-0.18	-0.33	-0.19	0.49	-0.19	-0.24	0.18
multiple R = 0.818			R ² = 0.668		F ratio = 10.08**		standard error = 678		
*-significant to 10% level; **-significant to 1% level; ***-significant to 5% level									

The upper limits seemed to be above 30.1 ppm for total soluble inorganic carbon, above 2.41 meq/l for total alkalinity, between 17.9 and 18.8°C for temperature, and between 0.72 and 0.82 meters per second for velocity (Table XXX).

From the magnitude of the partial correlation coefficients it appears temperature was the most important factor affecting the per cent canopy cover of G. borealis throughout the study area (Table XV).

Only one taxon, Potamogeton strictifolius, was negatively correlated with G. borealis. Competition may have been occurring with this taxa or with the many other taxa which were positively correlated with G. borealis (Table XXIX).

Juncus ensifolius

This taxon had its highest per cent canopy cover at station 3 but was also present at stations 4-7 (Table IV).

The F ratios of both analyses were significant. The coefficient of determination for the analysis of the Madison River was .49 and for the analysis of all rivers it was .31. These relatively small coefficients of determination indicate that 51 and 69 per cent of the variation in the per cent canopy cover of J. ensifolius in the two respective analyses was not associated with the factors considered in this study. Therefore, it is likely that some undetermined factors were important in determining the distribution and abundance of this taxon (Table XVI).

Current speed was the only factor which had a significant partial correlation coefficient with the per cent canopy cover of J. ensifolius when all rivers were considered. This taxon occurred at velocities ranging from 0.39 to 0.71 meters per second (Table XXX).

Several taxa were positively correlated with J. ensifolius but only Deschampsia caespitosa was negatively correlated with J. ensifolius. However, the environmental optima of these two taxa appear to be different (Table XXX) and thus it is doubtful that competition was occurring.

TABLE XVI. CORRELATION COEFFICIENTS OF ENVIRONMENTAL FACTORS WITH JUNCUS ENSIFOLIUS

	CO ₂	TC	D	V	ST	T ^O	SC	TA	pH
<u>Simple correlation coefficients</u>									
<u>Madison River only</u>									
r =	0.337*	0.268*	0.456**	-0.137	0.115	0.350*	0.406**	-0.119	-0.408
<u>All Rivers</u>									
r =	0.491**	0.186	0.066	-0.176	0.155	-0.358**	-0.397**	-0.383**	-0.431**
<u>Multiple correlations</u>									
<u>Madison River only</u>									
t =	0.99	1.48 *	1.47 *	1.61 *	-3.05 **	-1.38 *	-1.34 *	-1.46 *	-0.57
par. r =	0.18	0.26	0.26	0.28	-0.49	-0.25	-0.24	-0.26	-0.10
multiple R = 0.702		R ² = 0.492		F ratio = 3.23**		standard error = 126			
<u>All Rivers</u>									
t =	-0.65	0.47	0.69	-0.15	-1.38 *	0.04	0.10	-1.08	-0.31
par. r =	-0.09	0.07	0.10	-0.02	-0.20	0.01	0.02	-0.16	-0.05
multiple R = 0.563		R ² = 0.317		F ratio = 2.32**		standard error = 246			
*-significant to 10% level; **-significant to 1% level; ***-significant to 5% level									

Jungermannia

This taxon occurred only at station 5 and had only 2.8 per cent canopy cover at that station (Table IV).

Because of this limited occurrence and low per cent canopy cover, it is doubtful the statistical analyses were valid. However, the results of these analyses (Table XVII) indicate significant correlations between the per cent canopy cover of this taxon and several of the parameters considered.

As this taxon occurred only at station 5 which had a relatively large amount of free carbon dioxide (5.77 ppm) and a relatively coarse substrate (code value 1.92), it is possible that this favorable combination was necessary for this taxon to occur. This combination of factors occurred at none of the other stations (Table I).

The per cent canopy cover of this taxon was positively correlated with the per cent canopy cover of Juncus ensifolius, Glyceria borealis, and Oncophorus virens. This probably indicates an overlapping of environmental optima for these four taxa, but may be an indication that competition was occurring.

TABLE XVII. CORRELATION COEFFICIENTS OF ENVIRONMENTAL FACTORS WITH JUNGERMANNIA

	CO ₂	TC	D	V	ST	T ^O	SC	TA	pH
<u>Simple correlation coefficients</u>									
<u>Madison River only</u>									
r =	0.430**	0.433**	-0.089	0.276*	-0.215*	0.246*	0.369*	0.429**	-0.335*
<u>All Rivers</u>									
r =	0.179	0.287*	-0.077	0.208*	-0.187*	0.069	0.129	0.183*	-0.215*
<u>Multiple correlations</u>									
<u>Madison River only</u>									
t =	0.89	0.41	-1.10	0.02	2.39 *	-1.04	-0.79	-0.71	-0.37
par. r =	0.16	0.76	-0.20	0.01	-0.40	-0.18	-0.14	-0.13	-0.07
multiple R = 0.674		R ² = 0.454		F ratio = 2.77***		standard error = 145			
<u>All Rivers</u>									
t =	3.04 **	-1.59 *	-1.35 *	-0.89	-2.20 *	-0.71	1.07	1.99 *	-0.74
par. r =	0.41	-0.23	-0.20	-0.13	-0.31	-0.11	0.16	0.29	-0.11
multiple R = 0.639		R ² = 0.409		F ratio = 3.45**		standard error = 123			
*-significant to 10% level; **-significant to 1% level; ***=significant to 5% level									

Myriophyllum exalbescens

This taxon occurred at every station except station 3. It had its highest per cent canopy cover at station 4 (Table IV).

The coefficients of determination indicated that about 92 per cent (Madison River) and 84 per cent (all rivers) of the variation in the per cent canopy cover of this taxon was associated with the environmental variables which were considered.

The magnitude of the partial correlation coefficients, obtained when all rivers were considered, indicated speed, temperature, substrate texture, and the amount of total soluble inorganic carbon were, in descending order, the most important factors affecting the per cent canopy cover of this taxon (Table XVIII). Of these factors it is probable that temperature or a combination of temperature with the other factors was responsible for the absence of this taxon at station 3.

The per cent canopy cover of this taxon was positively correlated with the per cent canopy cover of several other taxa. Again it is thought this indicates an overlapping of environmental optima and does not necessarily indicate competition was occurring. The per cent canopy cover of one taxon, Potamogeton gramineus, was negatively correlated with the per cent canopy cover of M. exalbescens (Table XXIX).

TABLE XVIII. CORRELATION COEFFICIENTS OF ENVIRONMENTAL FACTORS WITH MYRIOPHYLLUM EXALBESCENS

	CO ₂	TC	D	V	ST	T ^o	SC	TA	pH
<u>Simple correlation coefficients</u>									
<u>Madison River only</u>									
r =	0.494**	0.287*	0.599**	0.010	0.583**	0.396**	0.626**	-0.214*	-0.496**
<u>All Rivers</u>									
r =	0.054	0.340**	0.395**	0.046	0.423**	0.175	0.339**	0.306*	-0.269*
<u>Multiple correlations</u>									
<u>Madison River only</u>									
t =	-1.34 *	-1.04	2.44 **	0.28	5.69 **	3.13**	2.10 *	1.43 *	3.09 **
par. r =	-0.24	-0.19	0.41	0.05	0.72	0.49	0.36	0.25	0.49
multiple R = 0.918 R ² = 0.843 F ratio = 17.87** standard error = 984									
<u>All Rivers</u>									
t =	0.06	2.24 *	0.80	-3.38 **	2.31 *	2.75 **	-1.26	-1.22	2.49 **
par. r =	0.01	0.32	0.12	-0.45	0.33	0.38	-0.19	-0.18	0.35
multiple R = 0.840 R ² = 0.781 F ratio = 17.81** standard error = 1088									

*-significant to 10% level; **-significant to 1% level; ***-significant to 5% level

Mimulus guttatus

This taxon was present only at stations 5 and 6 and had a maximum per cent canopy cover of 1.3 at station 6 (Table IV).

Because of this limited occurrence and small per cent canopy cover, it is doubtful the statistical analyses were valid. However, the partial correlation coefficients may be viewed as indications of the true relationships. It appears the amount of total soluble inorganic carbon, the substrate texture, and the total alkalinity were related to the per cent canopy cover of this taxon (Table XIX).

The per cent canopy cover of many taxa were correlated with the per cent canopy cover of M. guttatus (Table XXIX). This may be an indication of similar environmental preferences or a result of the limited occurrence of this taxon.

TABLE XIX. CORRELATION COEFFICIENTS OF ENVIRONMENTAL FACTORS WITH MIMULUS GUTTATUS

	CO ₂	TC	D	V	ST	T ^O	SC	TA	pH
<u>Simple correlation coefficients</u>									
<u>Madison River only</u>									
r =	0.248*	0.382**	0.136	-0.140	0.273*	0.189	0.229*	0.265*	-0.277
<u>All Rivers</u>									
r =	0.084	0.286*	0.082	-0.089	0.211*	0.049	0.099	0.174	-0.188
<u>Multiple correlations</u>									
<u>Madison River only</u>									
t =	-0.24	0.34	-0.26	-0.64	1.33 **	-0.01	0.14	0.06	0.00
par. r =	-0.05	0.06	-0.05	-0.12	0.24	-0.00	0.03	0.01	0.00
multiple R = 0.583			R ² = 0.339		F ratio = 1.71		standard error = 73		
<u>All Rivers</u>									
t =	-0.01	3.09 **	-0.16	-1.15	1.54 *	1.25	0.34	-2.70 **	2.70 **
par. r =	-0.00	0.42	-0.02	-0.17	0.22	0.18	0.05	-0.37	0.37
multiple R = 0.559			R ² = 0.312		F ratio = 2.21***		standard error = 62		
*-significant to 10% level; **-significant to 1% level; ***-significant to 5% level									

Oncophorus virens

This taxon was present at stations 5, 7, 9, 10, and 11, and was most abundant at station 11 where it had 7.4 per cent canopy cover (Table IV).

The F ratios for the multiple analyses were significant and the coefficients of determination indicated that about 40 per cent of the variation in the per cent canopy cover of this taxon was associated with the considered variables (Table XX). Free carbon dioxide was the only factor which had a significant partial correlation coefficient with the per cent canopy cover of this taxon and thus was presumably the most important physical factor affecting the distribution of O. virens.

The per cent canopy cover of O. virens was positively correlated with the other Bryophyta (F. grandifrons and Jungermannia) and negatively correlated with many of the other taxa (Table XXIX).

The environmental optima of these taxa appeared to be different (Table XXX) so it is doubtful that competition was occurring.

TABLE XX. CORRELATION COEFFICIENTS OF ENVIRONMENTAL FACTORS WITH ONCOPHORUS VIRENS

	CO ₂	TC	D	V	ST	T ^O	SC	TA	pH
<u>Simple correlation coefficients</u>									
<u>Madison River only</u>									
r =	-0.214*	-0.102	-0.569**	0.506**	-0.516**	-0.349**	-0.204	0.161	0.340
<u>All Rivers</u>									
r =	-0.170	0.180*	-0.432**	0.373**	-0.434**	-0.120	0.035	0.299*	0.119
<u>Multiple correlations</u>									
<u>Madison River only</u>									
t =	-0.02	0.07	-0.78	0.15	-0.49	0.59	0.19	0.02	0.94
par. r =	-0.00	0.01	-0.14	0.03	-0.09	0.11	0.04	0.00	0.17
multiple R = 0.649			R ² = 0.421		F ratio = 2.42***		standard error = 385		
<u>All Rivers</u>									
t =	1.49 *	-0.09	-0.23	0.32	-0.67	-0.56	-0.11	1.16	0.88
par. r =	0.22	0.01	-0.04	0.05	-0.09	-0.08	-0.02	0.17	0.13
multiple R = 0.614			R ² = 0.377		F ratio = 3.02**		standard error = 346		

*-significant to 10% level; **-significant to 1% level; ***-significant to 5% level

Potamogeton filiformis

This taxon was present at stations 1, 4-8 and was most abundant at station 6 where it had 26.4 per cent canopy cover (Table IV).

The multiple regression analysis of the data from all rivers indicated that about 60 per cent of the variation in the per cent canopy cover of this taxon was associated with the variations of the considered environmental factors (Table XXI). Only two factors, current speed and substrate texture, had significant partial correlation coefficients with the per cent canopy cover of P. filiformis. Thus it is probable these two factors were the most important factors affecting the distribution and abundance of P. filiformis.

At the stations where this taxon was present, the coded substrate value ranged from 1.92 to 2.94 and the velocity ranged from 0.32 to 0.71 meters per second. The taxon was generally more abundant at the stations with higher substrate values (finer textured substrates) and slower velocities (Table I). At stations 2, 9, 10 and 11 the substrate textures and/or the velocities were not within these ranges of tolerance for this taxon under these conditions. However, at station 3 the velocity and substrate texture were within these ranges but this taxon was not present. It is possible temperature, specific conductance, or total alkalinity or some combination of these factors with speed and/or substrate texture, were limiting at station 3 as the values for the three former factors were all extreme at this station (Table XXX).

The per cent canopy cover of this taxon was negatively correlated with

TABLE XXI. CORRELATION COEFFICIENTS OF ENVIRONMENTAL FACTORS WITH POTAMOGETON FILIFORMIS

	CO ₂	TC	D	V	ST	T ^O	SC	TA	pH
<u>Simple correlation coefficients</u>									
<u>Madison River only</u>									
r =	0.112	0.119	0.470**	-0.702**	0.599**	0.378**	0.330	-0.066	-0.308
<u>All Rivers</u>									
r =	-0.169	-0.053	0.547**	-0.608**	0.466**	0.349**	0.265	0.207*	0.033
<u>Multiple correlations</u>									
<u>Madison River only</u>									
t =	0.59	1.01	-0.44	0.03	1.39 *	-2.48 **	-1.47 *	1.06	-3.15**
par. r =	0.11	0.18	-0.08	0.01	0.25	-0.41	-0.26	-0.19	-0.49
multiple R = 0.888 R ² = 0.789 F ratio = 12.43** standard error = 594									
<u>All Rivers</u>									
t =	-1.00	0.60	-0.71	-2.85 **	1.38 *	1.04	0.07	0.62	0.00
par. r =	-0.15	0.09	-0.11	-0.39	0.20	0.15	0.01	-0.09	0.00
multiple R = 0.776 R ² = 0.602 F ratio = 7.54** standard error = 811									

*-significant to 10% level; **-significant to 1% level; ***-significant to 5% level

F. grandifrons and O. virens and positively correlated with many other taxa (Table XXIX). The negative correlations are with Bryophytes and probably indicate different responses to similar environmental factors while the positive correlations probably indicate that all of these taxa were responding similarly to the environmental factors.

Potamogeton gramineus

This taxon was present at stations 6, 7, 8 and 10 (Table I). It had its highest per cent canopy cover (2%) at station 8 (Table IV).

Only about 34 per cent of the variation in the per cent canopy cover of this taxon in all the rivers was associated with the considered environmental factors. The largest partial correlation coefficient (negative) was with depth. Current speed and temperature also had significant negative partial correlation coefficients (Table XXII). Thus it appears these four factors were the most important of the measured factors in determining the distribution and abundance of P. gramineus. The absence of this taxon at the other stations could be explained on the basis of the values of these factors as one, or more commonly several, of these factors were outside the range(s) in which this taxon was found (Table I). It is probable, in view of the small coefficient of determination previously mentioned, that some factor(s) unmeasured were actually more important than the ones measured.

There were numerous positive correlations between the per cent canopy cover of this and other taxa but only 2 negative correlations, that with M. exalbescens when just the Madison River was considered, and with Potamogeton nodosus when all rivers were considered (Table XXIX). These correlations probably indicate similar (positive correlations) and dissimilar (negative correlations) reactions to the same environmental gradients.

TABLE XXII. CORRELATION COEFFICIENTS OF ENVIRONMENTAL FACTORS WITH POTAMOGETON GRAMINEUS

	CO ₂	TC	D	V	ST	T ^o	SC	TA	pH
<u>Simple correlation coefficients</u>									
<u>Madison River only</u>									
r =	-0.143	-0.164	0.021	-0.402**	0.175	-0.059	-0.195	-0.078	0.084
<u>All Rivers</u>									
r =	-0.116	0.073	-0.010	-0.276*	0.121	0.031	0.007	0.160	0.003
<u>Multiple correlations</u>									
<u>Madison River only</u>									
t =	0.55	-0.12	-2.35 *	-2.14 *	0.58	-1.46 *	-0.48	-0.33	-1.03
par. r =	0.10	-0.02	-0.39	-0.37	0.11	-0.26	-0.09	-0.06	-0.19
multiple R = 0.673 R ² = 0.453 F ratio = 2.76*** standard error = 91									
<u>All Rivers</u>									
t =	0.14	-1.71 *	-3.33 **	-3.26 **	0.81	-2.26 *	2.28 *	0.95	-1.69 *
par. r =	0.02	-0.26	-0.45	-0.44	0.12	-0.32	0.32	0.14	-0.24
multiple R = 0.580 R ² = 0.337 F ratio = 2.53*** standard error = 85									
*-significant to 10% level; **-significant to 1% level; ***-significant to 5% level									

Potamogeton natans

The highest per cent canopy cover for this taxon was 11.5 per cent at station 6. It was also present at stations 2, 3, 7 and 8 (Table IV).

The F ratios were not significant for either of the statistical analyses (Table XXIII). This indicates the population means were not different, and, hence, the results of these analyses could not be considered valid. However, the only significant simple correlation coefficients were with current speed and were negative. Thus speed could be considered as an important factor affecting the per cent canopy cover of P. natans. However, the coefficient of determination indicates that only about 25 per cent of the variation in the per cent canopy cover of this taxon was associated with the variables considered (Table XXIII). Therefore, some factor(s) not considered must be important in affecting the per cent canopy cover of this taxon or the assumption of linear relationships between (and among) the environmental factors and the per cent canopy cover were unrealistic. This possibility of non-linear relationships applies to all of the statistical analyses for all taxa and in particular for those with small coefficients of determination.

P. natans had significantly positive simple correlation coefficients with G. borealis and P. filiformis when just the Madison River was considered. When all rivers were considered, in addition to the two taxa already mentioned, O. virens, Utricularia vulgaris, and Sparganium angustifolium were positively correlated with P. natans (Table XXIX).

The environmental optima of these taxa appeared to be different (Table XXX) so it is doubtful that competition was occurring.

TABLE XXIII. CORRELATION COEFFICIENTS OF ENVIRONMENTAL FACTORS WITH POTAMOGETON NATANS

	CO ₂	TC	D	V	ST	T ^o	SC	TA	pH
<u>Simple correlation coefficients</u>									
<u>Madison River only</u>									
r =	-0.064	0.002	0.024	-0.318*	0.126	0.088	-0.087	-0.045	-0.002
<u>All Rivers</u>									
r =	-0.041	0.153	-0.011	-0.221	0.098	-0.019	-0.006	0.124	-0.070
<u>Multiple correlations</u>									
<u>Madison River only</u>									
t =	-0.15	0.23	-1.01	-1.70 *	0.61	0.61	0.24	0.02	0.92
par. r =	-0.03	0.04	-0.18	-0.29	0.11	0.11	0.05	0.00	0.17
multiple R = 0.511 R ² = 0.261 F ratio = 1.17 standard error = 994									
<u>All Rivers</u>									
t =	-1.12	1.75 *	-1.11	-2.12 **	0.39	0.69	0.44	-1.96 *	0.94
par. r =	-0.17	0.25	-0.16	-0.30	0.06	0.10	0.07	-0.28	0.14
multiple R = 0.496 R ² = 0.246 F ratio = 1.62 standard error = 840									
*-significant to 10% level; **-significant to 1% level; ***-significant to 5% level									

Potamogeton nodosus

This taxon was present at stations 3-8 and was most abundant at station 4 (Table IV).

The coefficients of determination indicated that about 86 per cent (Madison River) and 84 per cent (all rivers) of the variations in the per cent canopy cover of this taxon was associated with the considered environmental factors (Table XXIV).

When just the Madison River was considered, substrate texture was the only factor which had a significant partial correlation coefficient with the per cent canopy cover of P. nodosus (Table XXIV). However, when all rivers were considered, the amount of total soluble inorganic carbon, the current speed, and the substrate texture were the only factors which did not have significant partial correlation coefficients with the per cent canopy cover of P. nodosus (Table XXIV).

Only stations 1 and 2 had smaller amounts of free carbon dioxide than did those stations having P. nodosus in the study of Rasmussen (1968).

The highest velocity at which Rasmussen found P. nodosus was 0.38 meters/second while in this study 0.71 meters/second was the upper limit for the occurrence of P. nodosus.

Thus it appears P. nodosus was excluded from station 1 by the small amount of free carbon dioxide present, and from station 2 by either the small amount of free carbon dioxide present or by the high velocity-coarse substrate texture or a combination of these factors. The high velocity-coarse substrate texture at stations 9-11 was the most probable limiting

TABLE XXIV. CORRELATION COEFFICIENTS OF ENVIRONMENTAL FACTORS WITH POTAMOGETON NODOSUS

	CO ₂	TC	D	V	ST	T ^O	SC	TA	pH
<u>Simple correlation coefficients</u>									
<u>Madison River only</u>									
r =	0.449**	0.228*	0.776**	-0.294*	0.618**	0.497**	0.605**	0.432**	-0.563**
<u>All Rivers</u>									
r =	0.151	0.323**	0.504**	-0.105*	0.466**	0.111	0.221**	0.136	-0.386
<u>Multiple correlations</u>									
<u>Madison River only</u>									
t =	-0.30	0.40	0.82	0.70	1.42 *	0.30	0.31	-0.47	-0.29
par. r =	-0.07	0.07	0.15	0.13	0.25	0.06	0.06	-0.09	-0.05
multiple R =	-.929	R ² = 0.863		F ratio = 21.04**		standard error = 883			
<u>All Rivers</u>									
t =	-7.36 **	0.62	1.78 *	0.73	1.26	-2.92 **	3.92**	-4.38 **	-4.24 **
par. r =	-0.74	0.09	0.26	0.11	0.18	-0.39	0.51	-0.55	-0.54
multiple R =	0.916	R ² = 0.838		F ratio = 25.90**		standard error = 823			
*-significant to 10% level; **-significant to 1% level; ***-significant to 5% level									

factor at these stations. As both the amount of free carbon dioxide and the velocity-substrate texture appeared favorable at station 3 while in fact there was very little P. nodosus present, it is possible that the relatively low temperature was near the limit of tolerance for this taxon (Tables I and XXX).

While the per cent canopy cover of many taxa was positively correlated with the per cent canopy cover of P. nodosus, only F. grandifrons, O. virens, and P. gramineus were negatively correlated (Table XXIX). F. grandifrons and O. virens are both mosses and both were most abundant where the velocity was relatively high and the substrate relatively coarse.

Potamogeton strictifolius

This taxon was present at stations 1, 4 and 6-8 and was most abundant at station 1 (Table IV).

The coefficients of determination indicated that about 44 per cent (in the Madison River) and 81 per cent (in all rivers) of the variation in the per cent canopy cover of this taxon was associated with the variation of the considered environmental factors (Table XXV).

When all rivers were considered, the largest partial correlation coefficient (positive) was between the per cent canopy cover and the amount of free carbon dioxide. There were also significant partial correlation coefficients with depth (positive), speed (negative), and total alkalinity (positive) (Table XXV).

When all rivers were considered, the simple correlation coefficients indicated that the per cent canopy cover of this taxon was most closely correlated with depth, total soluble inorganic carbon, temperature, and velocity (Table XXV).

Rasmussen (1968) found P. strictifolius growing at considerably lower levels of free carbon dioxide and total alkalinities than any found in this study. Therefore, it is doubtful that either of these factors were limiting the occurrence of P. strictifolius in this study area.

The factors most probably limiting at station 2 were the high velocity, coarse substrate texture, and the shallow depth.

The following factors were extreme (or outside the range in which this taxon was found) at the stations noted and as such were probably limiting

TABLE XXV. CORRELATION COEFFICIENTS OF ENVIRONMENTAL FACTORS WITH POTAMOGETON STRICTIFOLIUS

	CO ₂	TC	D	V	ST	T ^O	SC	TA	pH
<u>Simple correlation coefficients</u>									
<u>Madison River only</u>									
r =	0.179	0.007	0.500**	-0.270*	0.487**	0.348*	0.230*	-0.337*	-0.294*
<u>All Rivers</u>									
r =	-0.023*	-0.590*	0.624**	-0.405**	0.194*	0.499**	0.309**	-0.095	0.418**
<u>Multiple correlations</u>									
<u>Madison River only</u>									
t =	-1.46 *	-1.31 *	0.26	0.41	1.42 *	1.27 *	1.24	1.21	-1.35 *
par. r =	-0.26	-0.23	0.05	0.08	0.25	0.23	0.22	2.22	-0.24
multiple R = 0.660			R ² = 0.435		F ratio = 2.56***		standard error = 150		
<u>All Rivers</u>									
t =	5.64 **	-0.82	1.98 *	-1.95 *	-1.05	0.07	0.08	1.98 *	2.89 **
par. r =	0.64	-0.12	0.28	-0.28	-0.16	0.01	0.01	0.28	0.40
multiple R = 0.901			R ² = 0.812		F ratio = 21.6**		standard error = 534		
*-significant to 10% level; **-significant to 1% level; ***-significant to 5% level									

TABLE XXVI. CORRELATION COEFFICIENTS OF ENVIRONMENTAL FACTORS WITH RANNUNCULUS AQUATILIS

	CO ₂	TC	D	V	ST	T ^O	SC	TA	pH
<u>Simple correlation coefficients</u>									
<u>Madison River only</u>									
r =	-0.026	-0.039	0.226*	-0.248*	0.066	0.118	-0.098	0.030	-0.023
<u>All Rivers</u>									
r =	-0.237*	-0.601**	0.545**	-0.379**	0.120	0.484**	0.288*	-0.101	0.438**
<u>Multiple correlations</u>									
<u>Madison River only</u>									
t =	-2.04 *	-1.98 *	2.63 *	-0.64	-0.06	2.46 **	2.02 *	2.32 *	-0.17
par. r =	-0.35	-0.34	0.43	-0.12	-0.01	0.41	0.35	0.39	-0.03
multiple R = 0.655 R ² = 0.429 F ratio = 2.51*** standard error = 35									
<u>All Rivers</u>									
t =	6.38 **	-0.39	3.47 **	-1.32 *	-2.40 **	1.15	-1.23	2.34 *	3.84 **
par. r =									
multiple R = 0.920 R ² = 0.846 F ratio = 27.54** standard error = 139									

*-significant to 10% level; **-significant to 1% level; ***-significant to 5% level

in excluding R. aquatilis from these sites as the environmental optimums for these taxa appear to overlap and there were significant correlations between the per cent canopy cover of these taxa (Tables XXIX and XXX).

It is probable that R. aquatilis was excluded from stations 2 and 9-11 by unfavorable velocity and/or substrate texture (Table XXX).

Sparganium angustifolium

This taxon was present at stations 2 and 6-8 and was most abundant at station 8.

When just the Madison River was considered there were significant simple correlations between the per cent canopy cover of S. angustifolium and speed, depth, substrate texture, and temperature (Table XXVII).

When just the Madison River was considered there were significant partial correlation coefficients between the per cent canopy cover of this taxon and depth and speed (Table XXVII). The coefficient of determination for this analysis indicated that about 50 per cent of the variation in the per cent canopy cover of S. angustifolium was associated with the variations of the considered environmental factors (Table XXVII).

Thus, although this taxon does best in slow deep water about 50 per cent of the variation in its per cent canopy cover was not due to the considered environmental factors. Some of this variation was probably due to competition with the Characeae, P. filiformis, P. gramineus, and R. aquatilis whose environmental optimums seemed to have some overlap with those of S. angustifolium (Table XXX).

This taxon was probably excluded from stations 2, 5, 9-11 by the unfavorable depth and/or velocity (Table XXX).

TABLE XXVII. CORRELATION COEFFICIENTS OF ENVIRONMENTAL FACTORS WITH SPARGANIUM ANGUSTIFOLIUM

	CO ₂	TC	D	V	ST	T ^O	SC	TA	pH
<u>Simple correlation coefficients</u>									
<u>Madison River only</u>									
r =	0.045	-0.045	0.512**	-0.614**	0.280*	0.222*	0.022	-0.198	-0.161
<u>All Rivers</u>									
r =	-0.037	0.154	0.333**	-0.411**	0.201*	0.051	0.073	0.160	-0.142
<u>Multiple correlations</u>									
<u>Madison River only</u>									
t =	-0.09	-0.24	1.79 *	-1.62	-1.06	0.14	0.19	0.31	0.32
par. r =	-0.02	-0.04	0.31	-0.29	-0.19	0.03	0.04	0.06	0.06
multiple R = 0.708 R ² = 0.501 F ratio = 3.35** standard error = 1.95									
<u>All Rivers</u>									
t =	-2.46	0.27	0.57	-1.24	-1.39 *	0.04	0.12	0.85	-1.23
par. r =	-0.35	0.04	0.09	-0.18	-0.20	0.01	0.02	-0.13	-0.18
multiple R = 0.600 R ² = 0.359 F ratio = 2.80** standard error = 1.87									

*-significant to 10% level; **-significant to 1% level; ***-significant to 5% level

Utricularia vulgaris

This taxon was present at stations 4-8 and 10 and was most abundant at station 6.

The coefficients of determination indicated that only about 44 per cent (in the Madison River) and 34 per cent (in all rivers) of the variation in the per cent canopy cover of this taxon was associated with the variations of the considered environmental factors (Table XXVIII).

When all rivers were considered the simple correlation coefficients indicated that this taxon had its highest per cent canopy cover where there was a large amount of total soluble inorganic carbon, a low current speed, a silty substrate, and a high total alkalinity (Table XXVIII).

The partial correlation coefficients indicated that this taxon should have done best where there was a slow current, silty substrate, and a high specific conductance, if the other factors were constant (Table XXVIII).

U. vulgaris was probably excluded from stations 2, 9 and 11 by the unfavorably high current speed at these stations. It may have been excluded from station 1 by the small amount of free carbon dioxide present at that station. None of the considered factors appeared to be unfavorable at stations 3, 9 and 11 (Tables IV and XXX).

It is possible that competition from other taxa may have been wholly or partially responsible for approximately 60 to 70 per cent of the variation in the per cent canopy cover that was not associated with the considered environmental factors (Tables XXVIII and XXIX).

TABLE XXVIII. CORRELATION COEFFICIENTS OF ENVIRONMENTAL FACTORS WITH UTRICULARIA VULGARIS

	CO ₂	TC	D	V	ST	T ^O	SC	TA	pH
<u>Simple correlation coefficients</u>									
<u>Madison River only</u>									
r =	0.202	0.194	0.243*	-0.387**	0.381**	0.275*	0.141	0.069	-0.289*
<u>All Rivers</u>									
r =	0.015	0.321**	0.129	-0.239*	0.267*	0.060	0.125	0.283*	-0.226*
<u>Multiple correlations</u>									
<u>Madison River only</u>									
t =	1.53 *	1.30	-1.49 *	-0.16	0.27	-2.53 **	-1.75 *	-1.61 *	-1.12
par. r =	0.27	0.23	-0.26	-0.03	0.05	-0.42	-0.31	-0.28	-0.20
multiple R =	0.664	R ² = 0.441		F ratio = 2.65***			standard error = 289		
<u>All Rivers</u>									
t =	-0.73	-0.43	-2.11 *	-2.11	1.06	-0.68	1.35 *	-0.05	-1.22
par. r =	-0.11	-0.01	-0.30	-0.30	0.16	-0.10	0.19	-0.10	-0.18
multiple R =	0.583	R ² = 0.339		F ratio = 2.57***			standard error = 272		

*-significant to 10% level; **-significant to 1% level; ***-significant to 5% level

TABLE XXIX. MATRIX OF CORRELATION COEFFICIENTS BETWEEN TAXA, ALL RIVERS

C	C	ME	FG	OV	J	DC	CR	BE	PNA	PNO	UV	JE	GB	PS	PF	EA	SA	MG	PG	RA
ME	-.060																			
FG	-.344**	-.083																		
OV	-.368**	-.030	.437**																	
J	-.149	-.124	.102	.439**																
DC	-.082	-.054	-.201*	-.213*	-.030															
CR	-.146	-.158	-.100	-.113	-.037	.414**														
BE	.109	.565**	.060	.061	.070	.002	-.158													
PNA	.144	.031	.077	.199*	-.064	-.016	.021	.062												
PNO	.097	.735**	-.245*	-.265*	-.090	.058	-.047	.520**	.070											
UV	.285*	.076	-.006	-.273*	-.096	-.009	-.114	.360**	.201*	.308*										
JE	.077	.028	-.138	-.078	.104	.439**	-.071	.052	-.005	.174	.026									
GB	.186*	-.000	-.086	.104	.376**	-.152	-.066	.528**	.388**	.114	.220*	-.038								
PS	.534**	-.116	-.168	-.178	-.062	-.149	-.069	-.346*	-.111	-.074	-.141	-.094	-.206*							
PF	.741**	-.013	-.349**	-.342**	-.092	-.064	-.142	.229*	.198*	.199*	.399**	-.016	.177	.352**						
EA	.219*	.027	-.143	.006	-.052	-.096	-.063	.112	.004	.088	-.019	.036	.065	-.036	.204*					
SA	.315**	.115	-.199*	-.225*	-.073	-.000	-.063	.142	.213*	.234	.145	-.274*	.063	-.094	.425**	.303*				
MG	.212*	.176	-.111	-.125	-.041	.193*	.026	.339**	.070	.285	.375**	-.002	.296*	-.049	.201*	-.070	-.021			
PG	.239*	-.141	-.092	-.094	-.063	.026	-.076	.082	.142	-.915**	.320**	-.066	.007	-.121	.377**	-.023	.347**	-.084		
RA	.463**	-.172	-.149	-.169	-.055	-.136	-.065	-.373**	-.109	-.151	-.170	-.106	-.222*	.944**	.380**	-.049	-.056	-.072	-.113	

*-significant to 10% level

**-significant to 1% level

TABLE XXIX. MATRIX OF CORRELATION COEFFICIENTS BETWEEN TAXA, MADISON RIVER ONLY

C	C	ME	FG	OV	J	DC	CR	BE	PNA	PNO	UV	JE	GB	PS	PF	EA	SA	MG	PG	RA
ME	-.105																			
FG	-.418**	-.204																		
OV	-.469**	-.179	.395**																	
J	-.184	-.181	.080	.431**																
DC	.185	.339*	-.195	-.202	.018															
CR	.334*	-.017	-.089	-.108	-.033	-.059														
BE	.335*	.481**	-.139	-.229	-.002	.494**	.126													
PNA	.239*	-.042	.033	-.047	-.087	.085	.010	-.098												
PNO	.181	.718**	-.347*	-.405**	-.128	.346*	.032	.453**	.008											
UV	.440**	-.058	-.096	-.431**	-.140	.246*	-.108	.198	.148	.232*										
JE	.205	.287*	-.186	-.055	.252*	.181	-.068	.272*	.071	.489**	.173									
GB	.332*	-.203	-.025	-.050	.369*	.021	.475**	.353*	.345*	-.052	.085	.075								
PS	.166	.295*	-.255*	-.210	-.094	-.100	.152	-.019	-.056	.556**	.102	.212*	-.023							
PF	.839**	-.079	-.450**	-.473**	-.122	.346*	-.027	.330*	.239*	.230*	.483**	.246*	.195	.209						
EA	.315*	-.046	-.199	-.072	-.074	-.061	-.057	-.013	-.033	.035	-.087	.137	-.019	.374**	.235*					
SA	.460**	.022	-.281*	-.339*	-.104	.196	.081	-.039	.174	.171	.066	.028	-.058	.184	.511**	.269*				
MG	.298*	.136	-.154	-.185	-.057	.509**	.452**	.334*	.044	.257	.351*	.042	.263*	.125	.234*	.098	-.060			
PG	.349*	-.252*	-.156	-.182	-.089	.226*	-.069	-.090	.105	-.169	.268*	-.064	-.104	-.147	.449**	-.066	.308*	-.119		
RA	.127	-.122	-.089	-.108	-.033	-.060	-.026	-.238*	-.025	-.018	-.109	-.068	-.114	.413**	.245*	.362*	.621**	-.044	-.069	

*-significant to 10% level

**-significant to 1% level

TABLE XXX. MAXIMUM AND MINIMUM VALUES OF EACH FACTOR FOR EACH TAXON

	SP Conductance		Total Alkalinity		Temperature		Free Carbon Dioxide		Total Soluble Inorganic Carbon		Velocity		Depth		Substrate Texture	
	MAX	MIN	MAX	MIN	MAX	MIN	MAX	MIN	MAX	MIN	MAX	MIN	MAX	MIN	MAX	MIN
<u>B. erecta</u>	493	(80) 423	2.41	(0.50) 2.04	17.9 (2.26)	(12.9) 14.5	10.72	(0.4) 0.73	30.1	28.1	0.72	(0.29) 0.35	0.97	0.29	2.94	1.13
<u>C. rostrata</u>	497	423	2.41	2.04	17.9	14.5	10.72	5.77	30.1	28.6	0.71	0.39	0.55	0.46	2.74	1.92
Characeae	501	423	2.41	2.04	19.6	14.5	10.72	0.34	30.1	25.6	0.82	0.32	1.09	0.29	2.94	1.13
<u>D. caespitosa</u>	497	423	2.41	2.04	17.9	14.5	10.72	1.36	30.1	28.1	0.71	0.35	0.97	0.46	2.94	1.92
<u>E. acicularis</u>	493	(225) 480	2.36	(0.90) 2.31	17.9 (27.3)	17.7	3.62	(0.3) 1.36	28.6	28.1	0.48	(0.26) 0.35	0.97	(0.30) 0.60	2.94	2.16
<u>F. grandifrons</u>	497	(258) 478	2.41	(1.30) 2.24	17.9 (27.3)	16.8	5.77	0.39	30.1	26.3	0.82	(0.28) 0.32	0.55	(0.78) 0.29	1.92	1.00
<u>G. borealis</u>	497	478	2.41	2.31	17.9	16.8	5.77	0.73	30.1	28.1	0.72	0.35	0.97	0.29	2.94	1.13
<u>J. ensifolius</u>	497	423	2.41	2.04	17.9	14.5	10.72	1.98	30.1	28.4	0.71	0.39	0.97	0.46	2.94	1.92
Jungermannia	497	497	2.41	2.41	17.9	17.9	5.77	5.77	30.1	30.1	0.71	0.71	0.55	0.55	1.92	1.92
<u>M. exalbescens</u>	501	(225) 478	2.41	(0.90) 2.24	19.6 (27.3)	16.8	5.77	(0.2) 0.34	30.1	25.6	0.82	(0.26) 0.35	1.09	0.29	2.94	1.13
<u>M. guttatus</u>	497	478	2.41	2.37	17.9	17.7	5.77	3.05	30.1	29.4	0.71	0.40	0.70	0.55	2.64	1.92
<u>O. virens</u>	497	478	2.41	2.34	17.9	16.8	5.77	0.73	30.1	28.2	0.72	0.46	0.60	0.29	1.92	1.13
<u>P. filiformis</u>	501	(225) 478	2.41	(0.90) 2.31	19.6 (27.3)	17.7	5.77	(0.2) 0.34	30.1	25.6	0.71	(0.26) 0.32	1.09	(0.30) 0.55	2.94	1.92
<u>P. gramineus</u>	481	478	2.37	2.34	17.7	16.8	3.05	0.73	29.4	28.1	0.68	0.35	0.70	0.38	2.64	1.15
<u>P. natans</u>	493	423	2.31	2.04	17.9	14.5	10.72	1.36	29.4	28.1	0.48	0.35	0.97	0.46	2.94	2.16
<u>P. nodosus</u>	497	(379) 423	2.41	(1.65) 2.04	17.9 (22.6)	14.5	10.72	(0.4) 1.36	30.1	28.1	0.71	(0.30) 0.35	0.97	(0.30) 0.46	2.94	1.92
<u>P. strictifolius</u>	501	(225) 480	2.22	(0.90) 2.36	19.6 (27.3)	17.7	3.62	0.34	29.4	25.6	0.48	(0.26) 0.32	1.09	(0.30) 0.60	2.94	2.16
<u>R. aquatilis</u>	501	(80) 481	2.36	(0.50) 2.22	19.6	(12.9) 17.7	1.98	(0.2) 0.34	28.4	25.6	0.46	(0.55) (0.26) 0.32	1.09	(0.30) 0.60	2.60	2.16
<u>S. angustifolium</u>	493	478	2.37	2.31	17.9	17.7	3.62	1.36	29.4	28.1	0.48	(0.30) 0.35	0.97	0.60	2.94	2.16
<u>U. vulgaris</u>	497	(379) 478	2.41	(1.65) 2.31	17.9 (22.6)	16.8	5.77	(0.4) 0.73	30.1	28.1	0.71	0.35	0.97	(0.30) 0.38	2.94	1.15

Figures in () indicate values from Rasmussen 1968

SUMMARY AND RECOMMENDATIONS FOR FURTHER STUDY

Five transects were run across each of eleven stations, two on the Firehole, one on the Gibbon, and eight on the Madison River. Physical factors and plant taxa present at one meter intervals were determined. Some chemical factors were determined at three hour intervals for a 24 hour period on each of the 10 weeks of the study period (6 July to 7 September).

Simple and multiple regression analyses of all data were performed. Significant correlation coefficients were found between depth, current speed, and substrate texture (all combination) and between most of the chemical factors, i.e., total soluble inorganic carbon, free carbon dioxide, pH, and specific conductance.

It was established that only one community was present, and that the per cent canopy cover of this community was primarily determined by current speed and substrate texture. The diversity indices of this community were correlated with the amount of total soluble inorganic carbon present when all stations were considered and with the amount of free carbon dioxide and the total alkalinity when all the stations except the Gibbon station were considered. The per cent canopy cover of the community was also affected by temperature and by the amount of total soluble inorganic carbon. The per cent canopy cover of most of the taxa making up this community was also primarily affected by these same factors but some (the bryophytes) by the amount of free carbon dioxide and some (the taller taxa) by depth. The per cent canopy cover of at least one taxon (P. strictifolius) appeared to be primarily determined by competition from other taxa. The per cent

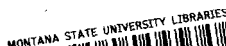
canopy cover of some taxa (in general those with a relatively low per cent canopy cover) appeared to be determined by some undetermined factor(s).

It is recommended that in any further study the time period be expanded to include at least one full year to include seasons during which other factors may be limiting. It is also recommended that a plant sampling method be used which takes into account the effects of the micro-habitat and does not assume the plants are randomly distributed across the streams.

LITERATURE CITED

- Allen, E. T. and Arthur L. Day, 1935. Hot springs of Yellowstone National Park. Carnegie Institute of Washington, D. C., Publication No. 466. 525 p.
- American Public Health Association, 1960. Standard methods for the examination of water and waste water, 11th Edition. APHA. New York. 626 p.
- Bourn, W. S. 1937. Ecological and physiological studies on certain aquatic angiosperms. Contrbs. Boyce Thompson Inst., 4 No. 4 425-496.
- Boyd, F. R. 1961. Welded tuffs and flows in the rhyolite plateau of Yellowstone Park, Wyoming. Bull. Geol. Soc. Am. 72:387-426.
- Butcher, R. W. 1933. Studies on the ecology of rivers. I. On the distribution of macrophytic vegetation in the rivers of Britain. Jour. Ecol. 21:58-91.
- Curtis, J. T. 1959. The vegetation of Wisconsin. University of Wisconsin Press, Madison. 657 p.
- Gleason, H. A. 1922. On the relation between species and area. Ecology. 3:156-162.
- Leet, L. D. and Sheldon Judson, Physical geology. Third Edition. Prentice-Hall, Inc., Englewood Cliffs, New Jersey, 406 p.
- MacFadyen, A. 1957. Animal ecology. Sir Isaac Pitman & Sons, LTD., London. 264 p.
- Margalef, R. 1950. Temporal succession and spatial heterogeneity in phytoplankton, p. 323 to 349. In A. A. Buzzati-Traverso (ed.) Perspectives in marine biology. Univ. of California Press, Berkeley and Los Angeles.
- Misra, R. D. 1938. Edaphic factors in the distribution of aquatic plants in English Lakes. Jour. Ecol., 26:411-451.
- Pearsall, W. H. 1920. The aquatic vegetation of the English Lakes. Jour. Ecol., 8:163-199.
- Pond, R. H. 1903. The biological relations of aquatic plants to the substratum. Publications of the United States Commission of Fish and Fisheries. p. 484-526.
- Rainwater, F. H. and L. L. Thatcher, 1960 Methods for collection and analysis of water samples. Geological Survey water Supply Paper #1454. United States Government Printing Office. 301 p.

- Rasmussen, S.M., 1968. Composition and structure of macrophyte vegetation of the Firehole River, Yellowstone National Park as related to physical and chemical factors. MS thesis (unpublished), Montana State University. 46 p.
- Roeder, T.S., 1966. Ecology of the diatom communities of the upper Madison River system, Yellowstone National Park. PhD thesis (unpublished), Montana State University. 85 p.
- Saunders, G.W., F.B. Trama and R.W. Bachman, 1962. Evolution of a modified C^{14} technique for shipboard estimation of photosynthesis in large lakes. Great Lakes Research Division, Institute of Science and Technology. University of Michigan, Ann Arbor. 61 p.
- Todd, E.H., 1967. Primary productivity of the Madison River in Yellowstone National Park, Wyoming. PhD thesis (unpublished), Montana State University. 120 p.
- Wright, J.C. and I.K. Mills, 1967. Productivity studies of the Madison River, Yellowstone National Park. Limnol. and Oceanog. 12:568-577.
- U.S. Geological Survey, 1966. Surface water records of Montana. U.S. Geological Survey, Washington, D.C. 301 p.



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species composition in
newly filled Bighorn Lake
Montana and Wyoming

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