



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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A thesis submitted to the Graduate Faculty in partial
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in

Botany

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TABLE OF CONTENTS

	Page
VITA	ii
ACKNOWLEDGMENTS	iii
TABLE OF CONTENTS	iv
LIST OF TABLES	vi
LIST OF FIGURES	viii
ABSTRACT	ix
INTRODUCTION	1
Description of the Study Area	1
Methods	5
Water Chemistry	5
Temperature	6
Elevations and Gradients	7
Plant Canopy Cover and Substrate Texture	8
Depth and Current Speed	8
Results and Discussion	9
Chemical Data	9
Gradients	12
Current Speed, Depth and Substrate Texture	12
Plant Data	15
PHYTOSOCIOLOGICAL CONSIDERATIONS	19
Index of Similarity	19
Index of Diversity	21
Relationships Between Diversity Indices and Environmental Factors	22
Statistical Analyses	22
Simple Correlations of Environmental Factors and Total Per Cent Canopy Cover	23

	Page
Correlations with Free Carbon Dioxide	24
Correlations with Total Soluble Inorganic Carbon	26
Correlations with Total Alkalinity	27
Correlations with Specific Conductance	27
Correlations with pH	28
Correlations with Temperature	28
Correlations with Depth	28
Correlations with Velocity	29
Correlations with Total Per Cent Canopy Cover	29
 MULTIPLE CORRELATIONS WITH TOTAL PER CENT CANOPY COVER	 29
 FACTORS AFFECTING THE DISTRIBUTION AND ABUNDANCE OF TAXA	 32
<u>Berula erecta</u>	32
<u>Carex rostrata</u>	37
Characeae	39
<u>Deschampsia caespitosa</u>	42
<u>Eleocharis acicularis</u>	45
<u>Fissidens grandifrons</u>	48
<u>Glyceria borealis</u>	51
<u>Juncus ensifolius</u>	54
Jungermannia	56
<u>Myriophyllum exalbescens</u>	58
<u>Mimulus guttatus</u>	60
<u>Oncophorus virens</u>	62
<u>Potamogeton filiformis</u>	64
<u>Potamogeton gramineus</u>	67
<u>Potamogeton natans</u>	69
<u>Potamogeton nodosus</u>	71
<u>Potamogeton strictifolius</u>	74
<u>Ranunculus aquatilis</u>	77
<u>Sparganium angustifolium</u>	80
<u>Utricularia vulgaris</u>	82
 SUMMARY AND RECOMMENDATIONS FOR FURTHER STUDY	 87
LITERATURE CITED	89

LIST OF TABLES

Table	Page
I. CHEMICAL AND PHYSICAL PARAMETERS AT EACH STATION	10
II. ELEVATIONS, DISTANCES AND GRADIENTS AT EACH STATION	13
III. PER CENT OF COVER	15
IV. PER CENT CANOPY COVER OF EACH TAXA AT EACH STATION AND TOTAL PER CENT CANOPY COVER AT EACH STATION	17
V. INDEX OF SIMILARITY	20
VI. DIVERSITY INDICES FOR STATIONS 1-11	21
VII. SIMPLE CORRELATION COEFFICIENTS BETWEEN PHYSICAL AND CHEMICAL FACTORS AND TOTAL PER CENT CANOPY COVER (ALL COMBINATIONS)	25
VIII. PARTIAL CORRELATION COEFFICIENTS BETWEEN TOTAL PER CENT CANOPY COVER AND PHYSICAL AND CHEMICAL FACTORS	31
IX. CORRELATION COEFFICIENTS OF ENVIRONMENTAL FACTORS WITH <u>BERULA ERECTA</u>	33
X. CORRELATION COEFFICIENTS OF ENVIRONMENTAL FACTORS WITH <u>CAREX</u> <u>ROSTRATA</u>	38
XI. CORRELATION COEFFICIENTS OF ENVIRONMENTAL FACTORS WITH CHARACEAE	40
XII. CORRELATION COEFFICIENTS OF ENVIRONMENTAL FACTORS WITH <u>DESCHAMPSIA CAESPITOSA</u>	43
XIII. CORRELATION COEFFICIENTS OF ENVIRONMENTAL FACTORS WITH <u>ELEOCHARIS ACICULARIS</u>	46
XIV. CORRELATION COEFFICIENTS OF ENVIRONMENTAL FACTORS WITH <u>FISSIDENS GRANDIFRONS</u>	49
XV. CORRELATION COEFFICIENTS OF ENVIRONMENTAL FACTORS WITH <u>GLYCERIA BOREALIS</u>	52
XVI. CORRELATION COEFFICIENTS OF ENVIRONMENTAL FACTORS WITH <u>JUNCUS ENSIFOLIUS</u>	55

Table	Page
XVII. CORRELATION COEFFICIENTS OF ENVIRONMENTAL FACTORS WITH <u>JUNGERMANNIA</u>	57
XVIII. CORRELATION COEFFICIENTS OF ENVIRONMENTAL FACTORS WITH <u>MYRIOPHYLLUM EXALBESCENS</u>	59
XIX. CORRELATION COEFFICIENTS OF ENVIRONMENTAL FACTORS WITH <u>MIMULUS GUTTATUS</u>	61
XX. CORRELATION COEFFICIENTS OF ENVIRONMENTAL FACTORS WITH <u>ONCOPHORUS VIRENS</u>	63
XXI. CORRELATION COEFFICIENTS OF ENVIRONMENTAL FACTORS WITH <u>POTAMOGETON FILIFORMIS</u>	65
XXII. CORRELATION COEFFICIENTS OF ENVIRONMENTAL FACTORS WITH <u>POTAMOGETON GRAMINEUS</u>	68
XXIII. CORRELATION COEFFICIENTS OF ENVIRONMENTAL FACTORS WITH <u>POTAMOGETON NATANS</u>	70
XXIV. CORRELATION COEFFICIENTS OF ENVIRONMENTAL FACTORS WITH <u>POTAMOGETON NODOSUS</u>	72
XXV. CORRELATION COEFFICIENTS OF ENVIRONMENTAL FACTORS WITH <u>POTAMOGETON STRICTIFOLIUS</u>	75
XXVI. CORRELATION COEFFICIENTS OF ENVIRONMENTAL FACTORS WITH <u>RANNUNCULUS AQUATILIS</u>	78
XXVII. CORRELATION COEFFICIENTS OF ENVIRONMENTAL FACTORS WITH <u>SPARGANIUM ANGUSTIFOLIUM</u>	81
XXVIII. CORRELATION COEFFICIENTS OF ENVIRONMENTAL FACTORS WITH <u>UTRICULARIA VULGARIS</u>	83
XXIX. MATRIX OF CORRELATION COEFFICIENTS BETWEEN TAXA:	
All Rivers	84
Madison River Only	85
XXX. MAXIMUM AND MINIMUM VALUES OF EACH FACTOR FOR EACH TAXON ..	86

LIST OF FIGURES

Figure	Page
1. Map of the Study Area	3

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.

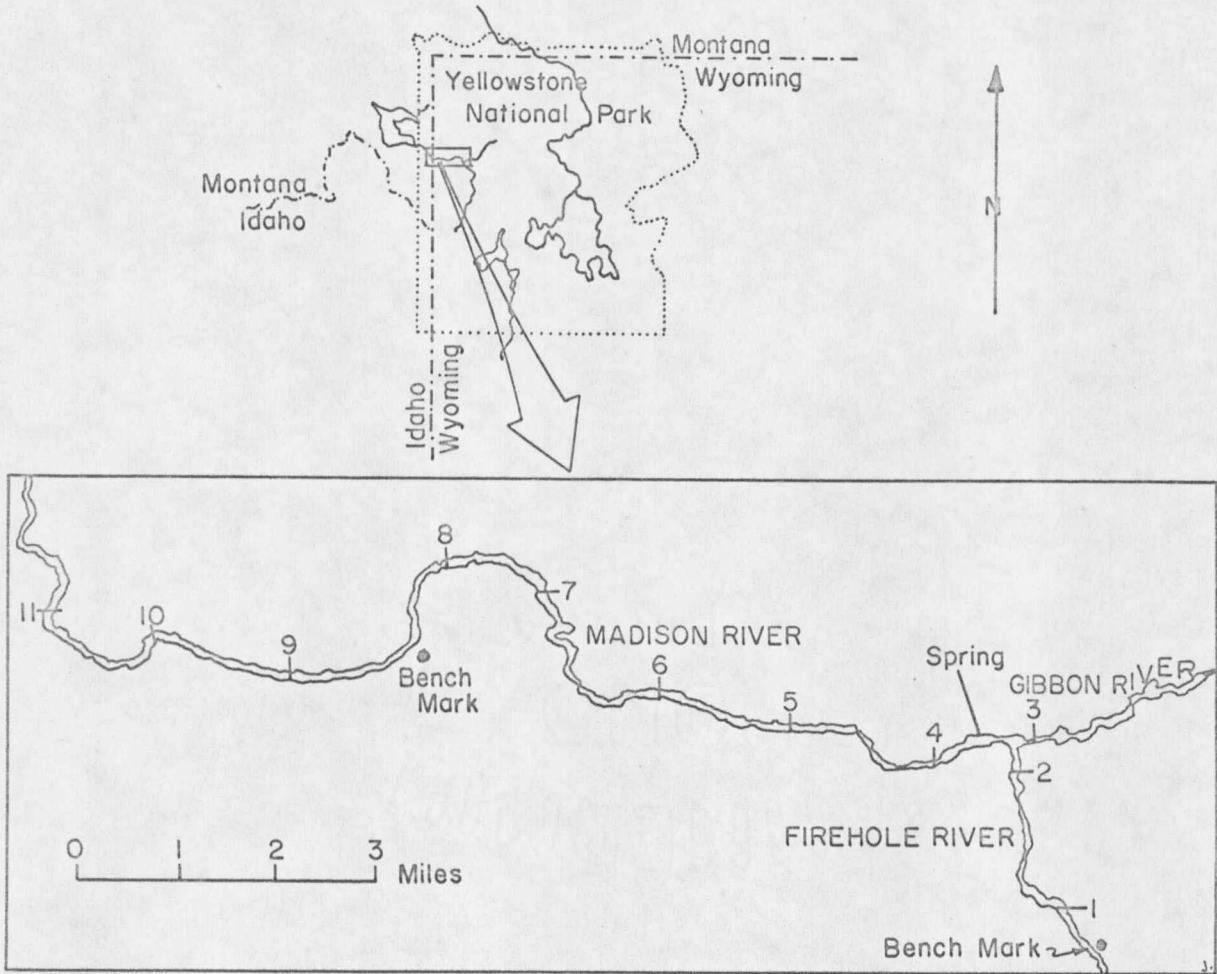


Figure 1: Map of study area

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:

$$G = \frac{E_u - E_d}{D}$$

Where G = gradient,

E_u = the elevation at the nearest upstream station,

E_d = 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^o = 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>	<u>134.1</u>	<u>11.6</u>	<u>57.4</u>	<u>201.0</u>	<u>122.9</u>	<u>221.1</u>	<u>119.4</u>	<u>114.2</u>	<u>76.0</u>	<u>37.0</u>	<u>43.1</u>

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).

