



Physiological ecology of aquatic macrophytes in the Madison River of Yellowstone National Park, Wyoming
by Duane Andrew Klarich

A thesis submitted in partial fulfillment of the requirements for the degree of DOCTOR OF PHILOSOPHY in Botany
Montana State University
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Abstract:

A distinct decline in free carbon dioxide concentration occurs through a twenty-three kilometer reach of the Madison River in Yellowstone National Park. Several investigators found a corresponding decrease in primary production which was attributed, in part, to this decline in carbon dioxide; positive and significant partial correlation coefficients were obtained between primary production and this variable. A portion of the primary production in the Madison River is due to a relatively luxurious and diverse aquatic macrophyte community in the stream.

Photosynthetic and respiratory rates of twenty-two species of macrophytes (including three species of Musci, several species of Potamogeton and other monocots, Myriophyllum-Berula and other dicots, and Chara) were determined in Madison River water collected at three stations along the carbon dioxide gradient. A photosynthetic rate response to differences in carbon dioxide concentrations was evident in all species. Greater rates and photosynthetic rate/respiratory rate ratios consistently were obtained in the high carbon dioxide water; intermediate and relatively low photosynthetic rates and ratios were obtained in the medium and low carbon dioxide samples respectively. However, respiratory rates for a species were similar in all treatments.

The photosynthetic-carbon dioxide responses of the species were substantiated by artificially removing carbon dioxide or adding it to appropriate water samples. Direct correlations consistently were obtained between these manipulations and photosynthetic activity, similar to those obtained from the unaltered river samples. However, this photosynthetic response to free carbon dioxide varied considerably among species.

Distributional patterns of aquatic macrophytes in the Madison River were determined by previous investigations. One group of species was found to be restricted to the upper, high carbon dioxide reach of the river whereas a second group was found throughout the river. This latter group was quite abundant in the lower, low carbon dioxide reach.

A distinct parallel was evident between species distribution and their photosynthetic sensitivity to carbon dioxide. Species found to be abundant in the low carbon dioxide reach demonstrated relatively small photosynthetic rate responses to variations in carbon dioxide concentrations whereas species restricted to the upper reach of the river demonstrated much more pronounced responses in photosynthetic rates.

These results indicate that carbon dioxide levels have a definite but variable influence on the photosynthetic activities of aquatic macrophytes in the Madison River. The relationships between the magnitude of the species' photosynthetic responses to carbon dioxide and their distributions in the stream indicate that this variable could act as a limiting factor to river production and macrophyte distribution

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OF YELLOWSTONE NATIONAL PARK, WYOMING

by

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A thesis submitted in partial fulfillment
of the requirements for the degree

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in

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ABSTRACT

A distinct decline in free carbon dioxide concentration occurs through a twenty-three kilometer reach of the Madison River in Yellowstone National Park. Several investigators found a corresponding decrease in primary production which was attributed, in part, to this decline in carbon dioxide; positive and significant partial correlation coefficients were obtained between primary production and this variable. A portion of the primary production in the Madison River is due to a relatively luxurious and diverse aquatic macrophyte community in the stream.

Photosynthetic and respiratory rates of twenty-two species of macrophytes (including three species of Musci, several species of Potamogeton and other monocots, Myriophyllum-Berula and other dicots, and Chara) were determined in Madison River water collected at three stations along the carbon dioxide gradient. A photosynthetic rate response to differences in carbon dioxide concentrations was evident in all species. Greater rates and photosynthetic rate/respiratory rate ratios consistently were obtained in the high carbon dioxide water; intermediate and relatively low photosynthetic rates and ratios were obtained in the medium and low carbon dioxide samples respectively. However, respiratory rates for a species were similar in all treatments.

The photosynthetic-carbon dioxide responses of the species were substantiated by artificially removing carbon dioxide or adding it to appropriate water samples. Direct correlations consistently were obtained between these manipulations and photosynthetic activity, similar to those obtained from the unaltered river samples. However, this photosynthetic response to free carbon dioxide varied considerably among species.

Distributional patterns of aquatic macrophytes in the Madison River were determined by previous investigations. One group of species was found to be restricted to the upper, high carbon dioxide reach of the river whereas a second group was found throughout the river. This latter group was quite abundant in the lower, low carbon dioxide reach. A distinct parallel was evident between species distribution and their photosynthetic sensitivity to carbon dioxide. Species found to be abundant in the low carbon dioxide reach demonstrated relatively small photosynthetic rate responses to variations in carbon dioxide concentrations whereas species restricted to the upper reach of the river demonstrated much more pronounced responses in photosynthetic rates.

These results indicate that carbon dioxide levels have a definite but variable influence on the photosynthetic activities of aquatic macrophytes in the Madison River. The relationships between the magnitude of the species' photosynthetic responses to carbon dioxide and their distributions in the stream indicate that this variable could act as a limiting factor to river production and macrophyte distribution.

INTRODUCTION

In the past, ecological studies of lentic environments have largely exceeded those on flowing waters. The various studies of Butcher (1932, 1933, 1945, 1948, among others) on the taxonomy and ecology of English rivers provide a major exception. Butcher's attention was focused primarily upon the microflora of these streams. In recent years, with the rising demand for usable water and with the development of suitable and applicable methods, increasing attention has been directed to the lotic side of the limnological spectrum. With the publication of Odum's (1956) paper, methods became available by which to effectively determine the productivity of running water under a variety of conditions. As a result, biological investigations of creeks and rivers, including considerations of the macrophyte component of the lotic ecosystem, have significantly increased in recent years.

Armitage (1958) demonstrated that the average yearly standing crop of riffle insects in the Firehole River of Yellowstone National Park and their relative abundances were correlated with bicarbonate alkalinity and temperature. Similar results were obtained by Vincent (1967) for the Gibbon River. These findings plus the availability of Odum's (1956) paper stimulated additional interest towards studying the Madison, Firehole, and Gibbon Rivers since this particular river "...system offered an ideal situation to study the effects of natural thermal and chemical enrichment on flowing water communities and their productivity

(Wright 1969)."

Chemical analyses by several investigators have demonstrated a definite carbon dioxide gradient in the Madison River of Yellowstone National Park. Work by Todd (1967) and by Wright and Mills (1967) suggested that this factor was the major cause of the downstream decline in primary productivity. Horpestad (1969) found definite relationships between carbon dioxide concentrations and various distributional features of the aquatic macrophytes in the stream. As a result, this study was undertaken to ascertain the effects of the carbon dioxide differences in the Madison River upon the photosynthetic activities of the large aquatic plants. A physiological-ecological approach was adopted for the study.

Phinney (1969) suggested that physiological ecology is a study of physiological responses in relation to potential environmental variables. Billings (1960) defined this field of science as "...the study of plant (and animal) processes under natural or simulated environmental conditions." Examples of these processes include growth, germination, reproduction, respiration, photosynthesis, and movement. Of added value is the demonstration of some correspondence between an induced change in a process and some ecological manifestation such as abundance changes, distributional irregularities, and/or alterations in diversity and community composition. With the demonstration of a quantitative relationship between these three components, some insight might be gained

towards an explanation of "why organisms live where they do" in any particular study area (Phinney 1969).

In this study, the environmental variable of major interest is the carbon dioxide gradient in the Madison River, and the ecological aspects are the differences in species abundance and distribution through the river study area and the downstream decline in primary production. Emphasis is directed primarily towards the photosynthetic rates of the aquatic macrophytes as a function of variable carbon dioxide concentrations in the river, because, if carbon dioxide is an important factor, photosynthesis would be expected to significantly respond to alterations in its availability. However, if carbon dioxide proved to be a noncritical factor for a particular species, then the photosynthetic response to changes of carbon dioxide levels would be expected to be absent or negligible.

Species restricted to different localities in the river might show considerable variations in their photosynthetic responses to carbon dioxide; thus the demonstration of a correlation between the magnitude of these responses and the species' distribution would provide evidence that this variable operates as a limiting factor in the stream. In addition, a predominance of one species type ("responder" or "non-responder") over the other would support or refute the suggestion that carbon dioxide influences primary production. That is, if the case were realized where most of the major taxa in the river were found to be

"non-responders", this would tend to refute the hypothesis that the carbon dioxide gradient in the Madison River is a major factor affecting the decline in primary production downstream.

LITERATURE REVIEW

MADISON RIVER

Initial studies in the Madison River headwaters area considered the periphyton, primarily diatoms, associations in the major rivers of the system (Roeder 1966). Subsequently, attention was directed towards the identification, distribution, abundance, and ecology of the macrophytic flora in the Firehole River (Rasmussen 1968) and in the Madison and lower Gibbon Rivers (Horpestad 1969). Productivities of the Firehole River, lower Nez Perce Creek, the lower Gibbon River (Wright 1969), and the Madison River (Wright and Mills 1967, Todd 1967, and Wright 1969) were studied as were heat budgets of the Madison River (Wright and Horrall 1967). Included as a part of these various investigations were extensive chemical and physical-hydrological analyses. In addition, macrophyte standing crop and chlorophyll accrual assessments were made. Similar data are also available from a more recent study in the area (Klarich and Wright 1974). As a result, a considerable amount of information is available on the aquatic macrophytes of the rivers and on the associated chemical, physical, and environmental factors that might conceivably influence these plants.

Information on the abundance and distribution of aquatic macrophytes in the Madison headwaters is available from several studies. Horpestad (1969) attempted to relate the distribution of these plants in the Madison River and in the lower Firehole and Gibbon Rivers of

Yellowstone National Park to various chemical and physical parameters using multiple regression methods. He determined the percent canopy cover of twenty macrophyte species at eight locations on the Madison River. Rasmussen (1968) did similar studies on the entire length of the Firehole. Todd (1967) utilized harvest methods and obtained standing crop data for various macrophyte taxa at intervals along the Madison River. Wright and Mills (1967) also obtained standing crop and distribution data for plants in the river in addition to productivity estimates of five sequential reaches of the river which were attributable at least in part to the activities of macrophytes.

Horpestad (1969) obtained a positive correlation between carbon dioxide concentrations and the diversity index of aquatic macrophytes and observed a decline in both towards the lower reach of the river. He also found significant correlations between percent canopy cover and carbon dioxide for certain of the species but not for others. In addition, Horpestad (1969) found that total canopy cover was related in part to the soluble inorganic carbon (including carbon dioxide) present within any given reach of the river. Todd (1967) and Klarich and Wright (1974) observed positive correlations between periphyton-chlorophyll accrual rates and free carbon dioxide concentrations. The latter investigators demonstrated that 93% of the variation in chlorophyll accrual rates between eight sites on the river could be accounted for by the associated variations in carbon dioxide and temperature. Similarly,

Wright and Mills (1967) found that downstream decreases in primary productivity in the Madison River were best correlated with downstream declines in carbon dioxide. Similar observations were made by Todd (1967) and Klarich and Wright (1974). All of these results point to the likelihood that free carbon dioxide functions as an important ecological variable in the stream.

The importance of substrate, current, and interspecific competition in regulating the growth, abundance, and distribution of aquatic plants in flowing water have long been recognized by aquatic scientists (Pond 1903, 1918; Pearsall 1920; Butcher 1933; Bourn 1937; Misra 1938; Curtis 1959). The importance of substrate has been noted by several workers such as Pearsall (1920) and Curtis (1959) and as early as 1903 by Pond. Butcher (1933) considered current velocity to be the major factor controlling the distribution of aquatic macrophytes in English streams. He recognized several distinct communities of aquatic plants relative to current and therefore the substrate characteristics of a river reach. These range from a "torrential community" influenced by high velocities and a bedrock-boulder substrate through several intermediate communities to a "littoral-type" characterized by very deep, slow-moving water and a mud substrate. Depth therefore also becomes an important factor in plant distribution, especially in view of the large size of certain of the aquatic plants such as the pondweeds (e.g., Potamogeton natans). The habitat of the "torrential community" is colonized

primarily by mosses while the deeper "littoral-type community" possesses vegetation similar to that of a pond.

Data on depth, current, substrate, and width are available for the Madison River through previous investigations (Wright and Mills 1967, Todd 1967, and Horpestad 1969). Results from these studies indicate a distinct downstream change in the physical nature of the river; this is qualitatively evident through the development of a long riffle that occurs in the lower reaches of the stream. Both Rasmussen (1968) and Horpestad (1969) noted the potential importance of these factors in regulating the occurrence and distribution of aquatic macrophytes in the Firehole and Madison Rivers. Regardless of the correlations between inorganic carbon and macrophyte diversity-canopy cover in the Madison River, Horpestad (1969) concluded that "...the percent canopy cover of this community was primarily determined by current speed and substrate texture."

CARBON DIOXIDE AS A LIMITING FACTOR IN AQUATIC ECOSYSTEMS

In contrast to the acceptance of substrate and current as important environmental factors, the relative roles of carbon dioxide and bicarbonate as photosynthetic carbon sources for aquatic plants and the importance of carbon as a limiting nutrient in aquatic systems have provoked disagreements among scientists since it was first suggested by Anglestein in 1911 that bicarbonate might be utilized in photosynthesis (Sculthorpe 1967). The supply of carbon dioxide, including the

"half-bound" component in bicarbonate reserves, was considered long ago by Birge and Juday (1911) to be probably the chief controlling factor in primary productivity. However, with the general acceptance of bicarbonate as a carbon source for photosynthesis in aquatic systems, the tendency has been to assume that primary productivity is related mainly to an adequate supply of this constituent rather than to free carbon dioxide.

Bicarbonate ions are often in high concentrations in many waters, and as a result, the role of carbon as a factor in eutrophication has often been overlooked; instead, attention has been directed to those nutrients in much smaller concentrations (e.g., the nitrogen and phosphorous species) as limiting factors to primary production. A variety of studies have suggested that an adequate supply of suitable carbon sources probably is not the general case for many aquatic systems. As a result, the concept that phosphorous is the most limiting nutrient to primary production in natural waters has been questioned in recent years (Goldman et al 1972).

Kerr et al (1970) concluded that the addition of phosphorous and nitrogen to waters with little available carbon dioxide and bicarbonate did not stimulate algal growth. Welch (1968) suggested that the high productivities of some lakes must be related to the large amounts of available carbon present in these systems. Waters (1957) found that the addition of lime to bog lakes increased bicarbonate concentrations,

carbon dioxide utilization, and phytoplankton yields. Myers (1947) stressed the importance of carbon dioxide in regulating algal growth. Martin et al (1969) showed that bicarbonate concentrations in Pickwick Reservoir were important in controlling the growth of Najas sp. Bristow (1969) concluded that concentrations of carbon dioxide greater than that at air saturation may be essential for the optimum development and growth of submerged higher plants.

In another study, increased phytoplankton populations were not always obtained with the addition of inorganic nitrogen and phosphorous to fish ponds; carbon dioxide was more directly involved in the control of phytoplankton growth (Thomaston and Zeller 1961). Wright (1960) has suggested that photosynthetic rates become limited by carbon dioxide once phytoplankton populations have fully utilized the nutrient pool in an aquatic system for chlorophyll synthesis. He concluded that the density dependence between photosynthesis and biomass, as observed in Canyon Ferry Reservoir, Montana, was due to decreases in available carbon dioxide concomitant with increases in standing crop.

For streams receiving wastewater effluents, Odum (1956) pointed out that increases in productivity are often common in recovery zones due to the addition of various nutrients such as nitrogen and phosphorous. However, this is also accompanied by enhanced carbon dioxide concentrations due to the oxidation of organic matter. Kerr et al (1970) suggested that the bacterial oxidation of organic matter is the

principle source of carbon dioxide in most aquatic systems. Carbon dioxide enrichment also occurs in the Madison River, but in this case, primarily via point source inputs from a thermal spring. Wright and Mills (1967) indicated that the enrichment of water with photosynthetically available carbon dioxide may be as important as other nutrients in enrichment causing eutrophication. They further suggest that the tendency for streams to become more productive downstream could not continue without a continued accrual of available carbon dioxide (by respiration and organic matter decomposition or by ground water recharge). In the Madison River, carbon dioxide evasion and utilization by aquatic plants below the thermal spring exceeds accrual. Thus, there is not a gain but rather a decline in this constituent, and correspondingly, productivity declines downstream.

CARBON DIOXIDE AS A LIMITING FACTOR TO PHOTOSYNTHESIS IN AQUATIC PLANTS

Various species of algae have been shown to have different carbon source requirements. As classical examples, Osterlind (1949, 1950, 1951) and Steemann Nielsen (1955) demonstrated that bicarbonate was preferred by young Scenedesmus quadricauda cultures, whereas carbon dioxide was the only carbon source available to Chlorella pyrenoidosa. Briggs and Whittingham (1952) also found that Chlorella sp. could utilize only dissolved carbon dioxide. Other examples and the importance of carbon dioxide and bicarbonate in algal photosynthesis have been thoroughly discussed in several review papers (King 1970, Kerr et al

1972, Goldman 1972, Goldman et al 1972, Likens 1972). Goldman et al (1972) concluded that free carbon dioxide, bicarbonate, carbonate "... and organic compounds can all serve as a carbon source for algae under specific conditions. Under normal conditions where free CO₂ is available it is often the preferred form of carbon used by the photoautotrophic algae (Myers 1951)."

Steeman Nielsen (1944, 1946, 1947) studied several species of aquatic angiosperms and an aquatic moss, Fontinalis sp. He concluded that bicarbonate could be utilized photosynthetically by Myriophyllum spicatum and other angiosperms but not by Fontinalis sp.; both the moss and the angiosperms could utilize carbon dioxide whereas neither taxon could use carbonate as a carbon source. Arens (1936) found that bicarbonate was actually absorbed by submerged leaves. A similar observation was made by Steeman Nielsen (1952). However, doubts as to the ability of aquatic macrophytes to utilize bicarbonate in photosynthesis have been expressed by a variety of physiologists, e.g., Wilmott (1921), Rabinowitch (1945), Briggs (1959).

Ruttner (1969) obtained results similar to those of Steeman Nielsen. He found that the aquatic moss Fontinalis antipyretica was able to use free carbon dioxide in photosynthesis at low pH values but that photosynthetic rates markedly declined as the pH of the medium increased to near 8.5 consequent to this carbon dioxide utilization. Carbon dioxide concentrations in water are quite low at this pH. Eloдея canadensis

was also able to photosynthesize at low pH-high carbon dioxide levels, but this plant continued to be active photosynthetically even after the pH of the media exceeded 8.5 due to the photosynthetic removal of carbon dioxide. The photosynthetic utilization of bicarbonate at the higher pH's by E. canadensis would account for the continued increase in pH ($\text{HCO}_3^- \rightarrow \text{CO}_2 + \text{OH}^-$). In contrast, the inability of F. anti-pyretica to increase pH much over 8.5 and the associated reduction in photosynthetic rates would indicate the reliance of this species upon carbon dioxide as its major carbon source.

Ruttner's (1969) data also indicate that photosynthetic rates in both species become reduced at high pH's in response to the lowered carbon dioxide concentrations regardless of the apparent ability of E. canadensis to utilize bicarbonate as a source of carbon. This is in accord with Burr's (1941) work which showed that aquatic plants are adapted to low light intensities but not to low carbon dioxide tensions. Briggs (1959) pointed to the possibility that carbon dioxide may still be the actual reactant in those systems where bicarbonate is apparently utilized with bicarbonate serving merely to increase the potential concentration of carbon dioxide at the chloroplasts.

Ruttner (1969) also found that the freshwater, red alga Batrachospermum sp. is highly dependent upon free carbon dioxide for active photosynthesis. Tseng and Sweeney (1946) made a similar observation for the red alga Gelidium cartilagineum. Ruttner (1969) further

observed that the requirement of these plants and that of the aquatic mosses for free carbon dioxide corresponded with their distributions in nature--in springs and mountain streams, and in pools and the eulittoral zone of lakes where atmospheric exchange readily takes place. In all of these habitats, adequate amounts of carbon dioxide are consistently found in the water. Bicarbonate users, in contrast, are more typical of the alkaline and relatively CO₂-free littoral zone and epilimnion of lakes. These observations prompted Ruttner (1953) to develop a classification wherein two groups of plants were delineated: (1) land plants and aquatic mosses plus the freshwater red algae able to use only free carbon dioxide (the Fontinalis-Batrachospermum-type); and (2) aquatic reed plants and algae able to use both bicarbonate ion and carbon dioxide (the Elodea-type).

Recent research, however, has revealed exceptions to this classification system. Bristow (1969) reported that the higher aquatic plants Ranunculus flabellaris and Myriophyllum brasilense can use only free carbon dioxide. As noted, some green algae, e.g., Chlorella, are restricted to the use of free carbon dioxide as a carbon source as are aging Scenedesmus cultures (Osterlind 1949). Horpestad (1969) found aquatic bryophytes growing in the Madison River of Yellowstone National Park under relatively low carbon dioxide concentrations and forming a conspicuous element of the flora in this section of the river; however, these plants were found to be quite scarce in an upstream, high carbon

dioxide reach of the stream. In addition, Wright (1969) and Klarich (1969, 1971) present data for two species of aquatic angiosperms in the Firehole and Gibbon Rivers of Yellowstone National Park that illustrate wide discrepancies in their capacity to use bicarbonate and in their reliance upon carbon dioxide for photosynthesis. Apparently the carbon source preferences of at least some aquatic plants cut across the broad taxonomic categories presented in Ruttner's (1953) classification.

Kerr et al (1972) concluded that the "availability and rate of supply of specific molecular forms of carbon (CO_2 , HCO_3^- , CO_3^{2-} , and organic) can regulate the extent and rate of biological activity." However, very little specific information is available concerning the carbon source requirements and preferences of most species of aquatic macrophytes, or of the potential for these carbon species to act as limiting nutrients for aquatic macrophytes.

Sculthorpe (1967) has pointed out that most experimenters have directed their attentions primarily to the use of such habitual experimental subjects as Elodea sp. and Myriophyllum sp. which are widely distributed, easy to culture, and easily manipulated. Data for a large proportion of the macrophyte species are therefore not available. In addition, previous research has often involved laboratory experimentation with artificially constituted systems; as a result, relationships to a specific natural situation are often vague. Similar to the case

with the algae, such research has indicated that the carbon source requirements of aquatic macrophytes are quite variable and dependent upon species and conditions. Apparently either or both bicarbonate and free carbon dioxide can be utilized by these plants with varying degrees of efficiency. As stated by Sculthorpe (1967), the "...present state of knowledge of carbon sources is highly unsatisfactory. Previous experimental results conflict, interpretations differ, and numerous perplexing questions remain unanswered...."

DESCRIPTION OF THE STUDY AREA

GENERAL FEATURES ...

The Madison River is formed by the confluence of the Gibbon and Firehole Rivers at Madison Junction in the west-central portion of Yellowstone National Park, Wyoming, approximately 22.4 km (fourteen miles) from the western border. Unique in this Park area is the large amount of thermal activity that occurs in the form of geysers, hot springs, and mud-pots which ultimately drain into the Firehole and Gibbon Rivers. The Firehole River originates at Madison Lake and flows in a northerly direction receiving thermal discharge primarily in the lower reaches from the three main geyser basins of Yellowstone National Park. The Gibbon River begins as an outlet of Grebe Lake and flows generally in a southwesterly direction until its junction with the Firehole. The thermal discharge to this river is due primarily to the activity of the Norris Geyser Basin.

After its formation, the Madison River flows in a westerly direction and exits Yellowstone National Park near West Yellowstone, Montana. With the exception of the extreme upper reach, the Madison River is devoid of thermal activity. Approximately 1.6 km below the origin of the Madison River, there is a large, warm spring with thermal discharges both on the shore and in the river channel. Through the upper 9.6 km (six miles) of the river, the stream channel meanders through Madison Canyon. Emerging from the canyon, the river then passes through a riffle region that is characteristic of the lower, 8.0 km (five mile)

reach of the stream in Yellowstone National Park. As a result, distinct physical differences are evident in the study area between the upper Madison Canyon reach and the lower, riffle segment.

The discharge of the Madison River varies seasonally and is distinctly greater in May and June corresponding to the increased runoff after snow melt in this mountainous region. Generally, the stream recedes to a constant level by mid-July. No major tributaries enter the Madison within the defined study area.

CHEMISTRY

Ionic Constituents

Since the Madison River is formed by a union of the Firehole and Gibbon Rivers, the chemistry of the river is a reflection of that of the two headwater streams. The lower Firehole River, as the name implies, is a warm stream as the result of thermal discharges. It has a relatively high concentration of dissolved ionic constituents, a high conductivity, a relatively high total alkalinity, but it has a high pH and therefore a low free carbon dioxide content. In contrast, the Gibbon River is typically a colder stream with a lower conductivity. Total alkalinity and therefore bicarbonate concentrations also are lower than those found in the Firehole River. In addition, the sulfate concentration of the lower Gibbon River is relatively high due to a sulfate-water inflow from several thermal drainages along the lower reaches of the river. As a result of these acid drainages, pH values for

the Gibbon River are markedly lower than those of the Firehole with a concomitantly greater free carbon dioxide content. Although the lower Firehole has a greater total concentration of dissolved ionic constituents, Roeder (1966) and Wright and Mills (1967) observed that the lower Gibbon River has a greater concentration of all the major cations except sodium, which is markedly higher in the Firehole (Table 1).

Since the volume of the Firehole River is greater than that of the Gibbon, the chemistry of the Madison River more closely resembles that of the Firehole (Roeder 1966). In addition, the chemistry of the Madison River is influenced by the discharge of the thermal spring that is located immediately below its origin. This spring not only adds quantities of dissolved ions, but also has a high free carbon dioxide content (low pH) which therefore enhances the free carbon dioxide concentration of the upper Madison reaches. Because of the scarcity of calcium-magnesium-containing rocks in the region, concentrations of these cations are quite low. Sodium is by far the most dominant cation in the Madison River (Table 1). Roeder (1966) found silicate concentrations generally to be near saturation. In order of prevalence, bicarbonate, chloride, and fluoride are the predominant anions in the Madison. Run-off from thermal areas tends to enrich the waters in these constituents. As a result of rhyolite decomposition and thermal input, the Madison River and its headwater streams can be chemically classified as sodium-bicarbonate-chloride waters.

Table 1. Chemistry of river water in ppm at selected stations established within the Madison River drainage system. Stations are described by their distances from the confluence of the Firehole River (FH) and Gibbon River (G) to form the Madison River (M) at Madison Junction in Yellowstone National Park. Data taken from Wright and Mills (1967) and from Klarich and Wright (1974).

Station	Distance (km)	Na	K	Ca	Mg	HCO ₃	Cl	SO ₄	F	B	Fe	CO ₂	pH
<u>Wright and Mills</u>													
FH	mouth	187.0	6.3	2.0	0.8	140.3	76.9	2.2	9.3	<0.1	0.06	0.8	8.4
G	mouth	86.3	11.3	3.9	1.0	115.9	59.9	4.3	5.0	<0.1	0.10	14.6	7.1
M1	1.6	103.5	10.2	2.7	1.0	137.3	73.8	2.8	7.6	0.4	0.20	5.5	7.6
M2	4.9	96.6	10.2	2.7	1.0	146.4	73.8	2.9	7.8	0.5	0.12	7.3	7.5
M3	7.5	96.6	10.2	3.9	1.0	152.5	70.2	2.7	7.1	0.4	0.12	4.9	7.7
M4	10.8	96.6	9.8	3.3	1.0	146.4	72.0	2.7	7.3	0.3	0.12	4.7	7.7
M5	15.9	92.0	9.8	2.7	1.0	146.4	72.0	2.8	7.1	0.2	0.10	2.3	8.0
M6	21.0	92.0	9.8	2.7	0.9	146.4	73.8	2.7	8.0	0.2	0.10	1.9	8.1
<u>Klarich and Wright</u>													
FH	3.2	91.5	7.4	5.0	0.1	125.7	59.3	10.1	8.7	---	0.05	0.4	8.7
G	2.4	56.8	10.1	7.8	1.0	93.9	39.4	17.3	3.6	---	0.13	16.3	7.0
M1	1.6	82.6	9.0	6.0	0.6	123.8	53.6	11.5	6.8	---	0.07	5.6	7.5
M2	4.9	83.0	9.4	6.0	0.5	125.7	53.3	12.0	6.8	---	0.07	5.3	7.6
M3	7.5	81.4	9.0	6.0	0.5	126.3	52.2	11.5	6.8	---	0.07	5.8	7.5
M4	10.8	81.0	9.0	6.0	0.5	125.1	50.4	11.0	6.7	---	0.07	3.5	7.8
M5	15.9	78.4	9.0	6.0	0.4	126.3	50.1	11.0	6.5	---	0.07	1.8	8.0
M6	21.0	80.7	9.0	5.8	0.5	126.9	50.4	10.6	6.5	---	0.07	1.1	8.3

Concentrations of dissolved constituents in the river vary seasonally in response to yearly variations in stream discharge. Concentrations are lowest in the spring because of dilution from snowmelt and enhanced runoff at this time. However, during the period of sampling on the river, a stabilization of concentration was evident relative to the attainment of base flow volumes by mid-July.

In addition, fluctuations of various chemical parameters are feasible diurnally and longitudinally through successive reaches of the river. Of importance to this particular study in relation to affects on macrophyte distribution and production was the recognition of any parameter that might distinctly vary longitudinally along the Madison River at any particular season and at any specific time of the day. As indicated in Table 1, apparently none of the major cations and anions fit into this category since their concentrations remain quite constant through all reaches of the river within Yellowstone National Park.

Phosphorus and Nitrogen

Wright and Mills (1967) found concentrations of phosphate much higher than those typically observed in eutrophic waters. However, except for a slight downstream decline, this was the case for all reaches of the Madison River. Roeder (1966) in turn found a slight downstream increase in orthophosphate concentrations as expressed through yearly sampling means and maximum-minimum values. Klarich and

