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The Role of Calcification in Macrophyte Photosynthesis in Williams Lake

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INTRODUCTION

Many of the submersed aquatic macrophytes in Williams Lake become encrusted with marl (calcium carbonate) during the summer. Alkalinity and calcium concentrations meanwhile decrease by about 15 and 25 percent respectively, after dilution effects and replenishment from ground water are taken into consideration. These observations prompted an examination into the causes of marl precipitation and its roles in plant growth and lake carbon cycling.

A whole-lake carbon budget constitutes the foundation for this analysis. Boundary fluxes include ground-water inputs and outputs and carbon dioxide exchange with the atmosphere. Calcification and calcium carbonate dissolution are estimated from changes in lake storage of calcium (or alkalinity), plus additions from ground-water. Net photosynthesis is estimated from changes in inorganic carbon storage, plus boundary fluxes, minus calcification. The rates and mechanisms of calcification are then addressed through carbonate saturometry for calcification within the water column, and plant incubation experiments for biological calcification. A more comprehensive account of this work has been published (McConnaughey and others, 1994).

Hydrology, geology, plant physiology, ecology, and more than a decade of research all contribute to the analysis. Without the interdisciplinary, cooperative attributes of the Interdisciplinary Research Initiative effort, this analysis would not have been possible.

METHODS

Water samples were obtained from depths of 1 m and 8 m, and temperature, specific conductance, pH, and dissolved oxygen were measured in situ at 1-m depth intervals. Sampling was conducted approximately biweekly during the ice-free part of the year and monthly when the lake was ice covered. Data from 11 years (1980-1990) were composited to produce annual chemical cycles at 1 m and 8 m, and chemistry at other depths was interpolated, based on specific conductance. From these data we calculated water-column chemical inventories.

Two versions of the stagnant film model with and without chemical enhancement of CO_2 diffusion through the surface film were used to calculate carbon dioxide fluxes across the lake surface. Stagnant film thickness was calculated from regressions against windspeed, using wind data collected over Williams Lake.

Ground-water chemical fluxes were estimated from ground-water chemical compositions measured upgradient from the lake, and ground-water flow rates were calculated from hydraulic gradients and hydraulic conductivities. Isotopic methods were also used to estimate ground-water contributions over limited periods (McConnaughey and others, 1994; LaBaugh and others (1995).

Macrophyte biomass was estimated by transect sampling (Carter and others, this volume), and rates of macrophyte calcification and photosynthesis were calculated from changes in pH and alkalinity measured during incubations in shallow water. Authigenic calcification was monitored by repeated weighings of calcium carbonate crystals and blocks suspended within dialysis bags at various points in the lake.

RESULTS

Williams Lake contains a diluted version of upgradient ground-waters. Magnesium and sodium pass through the lake with relatively little chemical

reaction; hence, their concentrations in lake waters fall along a mixing line connecting upgradient ground-waters with meteoric waters (fig. 46). Seasonal and interannual chemical variability is evident in both shallow regional ground waters and lake waters. Seasonal variations within the lake can be largely attributed to the springtime melting of ion-depleted snow and ice. All major dissolved chemicals display this springtime dilution (fig. 47). Reactive elements such as carbon, calcium, and potassium exhibit further depletion during summer, which is caused by plant growth and calcification. These nonconservative attributes are more evident when dilution effects are removed by normalizing ion concentrations to a constant magnesium concentration.

Dilution-adjusted calcium and alkalinity concentrations increase from autumn until early spring, then decline rather abruptly during summer (fig. 48B). Calcium and alkalinity display nearly equal rates of wintertime accumulation and summer-time depletion, consistent with control by calcium carbonate precipitation and dissolution. When ground-water replenishment is factored in, it appears that the lake loses about 15 percent of its alkalinity and 25 percent of its calcium between late May and August. Calcification rates, calculated from changes in calcium and alkalinity, peak at about 700 micromoles per liter per year from about late June to late July (fig. 48C).

The epilimnion is mildly supersaturated with respect to calcite during summer (fig. 48A); hence, inorganic calcification is possible. However, calcite crystals and blocks suspended in the epilimnion exhibited little or negative changes in weight, aragonite crystals lost weight, and all carbonates suspended in the hypolimnion lost weight. These carbonate saturometry experiments indicated that little authigenic calcification occurs within the water column.

Plant calcification is an obvious alternative, since several submersed macrophytes accumulate visible carbonate encrustations during summer. When incubated in jars containing calcium-supplemented lake water, several species exhibited nearly equal rates of calcification and photosynthesis (fig. 49), as is characteristic of calcify as a precursor to bicarbonate
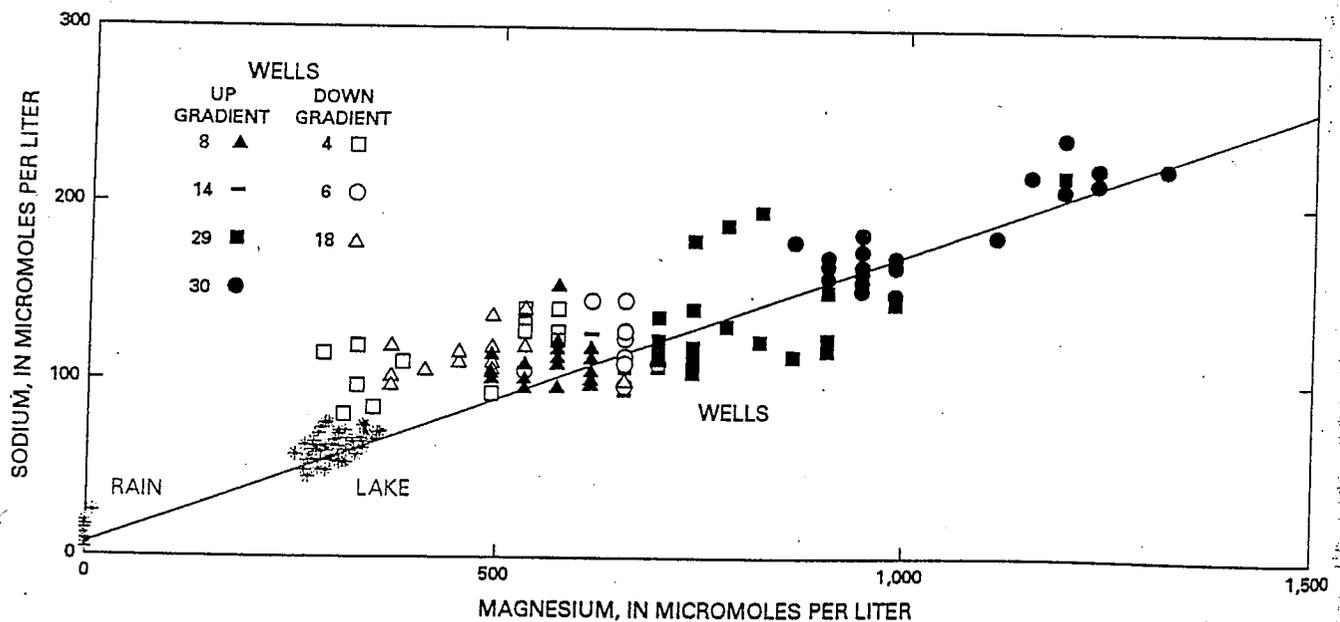

Figure 46. Magnesium and sodium concentrations in Williams Lake, nearby wells, and rain.

assimilation (McConnaughey, 1994). Also shown in figure 49 are contours of pH, carbon dioxide concentrations, and calcite saturation for lake waters subjected to various amounts of calcification and photosynthesis. Large amounts of carbon can be removed from the water, with minimal effect on pH, CO_2 concentrations, or calcite saturation state, under a 1:1 stoichiometry of calcification to photosynthesis.
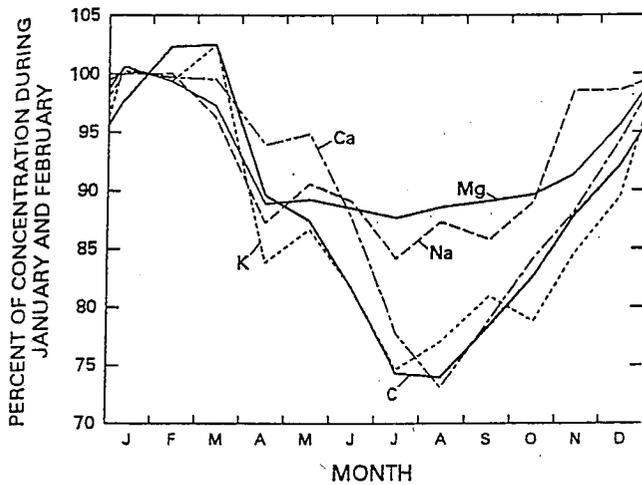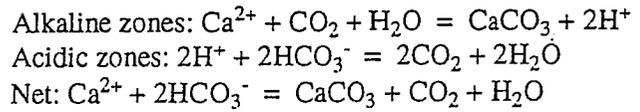

Figure 47. Seasonal cycles of Mg^{2+}, Na^+, K^+, Ca^{2+}, and dissolved inorganic carbon (C) in Williams Lake, expressed as a percentage of average concentrations during January and February.

The physiology linking calcification to photosynthesis in these plants is rather interesting (McConnaughey and Falk, 1991; McConnaughey, 1991). Calcareous plants typically develop spatially alternating alkaline and acidic surfaces, and the alkaline regions become calcified. The giant cells of characean algae commonly display alternating calcified and noncalcified bands, while the submersed leaves of *Potamogeton* become calcified on their upper surfaces but not on their lower surfaces. The calcified surfaces can exhibit pH values as high as 10.5. Carbon dioxide leaks from the plant into these alkaline regions and rapidly precipitates as calcium carbonate. The plant translocates the protons generated during calcification to its acidic surfaces and ejects them into the water, where they convert bicarbonate to carbon dioxide, which the plant absorbs. In mildly alkaline waters, this process nets the plant one carbon dioxide molecule, for photosynthesis, for each carbon dioxide molecule precipitated as calcium carbonate.

Alkaline zones: $Ca^{2+} + CO_2 + H_2O = CaCO_3 + 2H^+$
Acidic zones: $2H^+ + 2HCO_3^- = 2CO_2 + 2H_2O$
Net: $Ca^{2+} + 2HCO_3^- = CaCO_3 + CO_2 + H_2O$

In this sequence, calcification generates the protons needed to convert bicarbonate to carbon dioxide, and functionally precedes photosynthesis.

In the lake carbon budget, net photosynthesis can be calculated from the rate of carbon removal, after allowances have been made for boundary fluxes and calcification. Boundary fluxes include imports and exports through ground-water flow, recycling within the lake-sediment system, and carbon dioxide exchanges with the atmosphere.

Treating magnesium as a non-reactive constituent in the system, the net ground-water influx of carbon to the lake can be estimated as the difference between carbon to magnesium ratios in upgradient ground waters and lake waters, times the magnesium flux through the system. To a first approximation this term is constant throughout the year. Sediment fluxes are estimated as the difference between this number and the total rate of carbon accumulation in the lake. The latter is calculated from the rate of change of water-column carbon inventories during the winter, when biological fluxes are relatively small. (See dashed lines on fig. 48B for the analogous accumulation of calcium and alkalinity in the water column during winter.)

Carbon dioxide exchanges with the atmosphere reverse seasonally (fig. 50). Results from two versions of the stagnant film model are illustrated in figure 50: a standard Fickian version, and a chemically enhanced version, which considers the rate of carbon dioxide reaction within the surface boundary layer. Large losses to the atmosphere during spring and fall bracket a summertime period of carbon uptake by the lake. Carbon dioxide reactions within the surface microlayer significantly enhance summertime carbon dioxide uptake. Whole-lake net photosynthesis (fig. 51) peaks at around 8 moles per square meter per year in early summer.
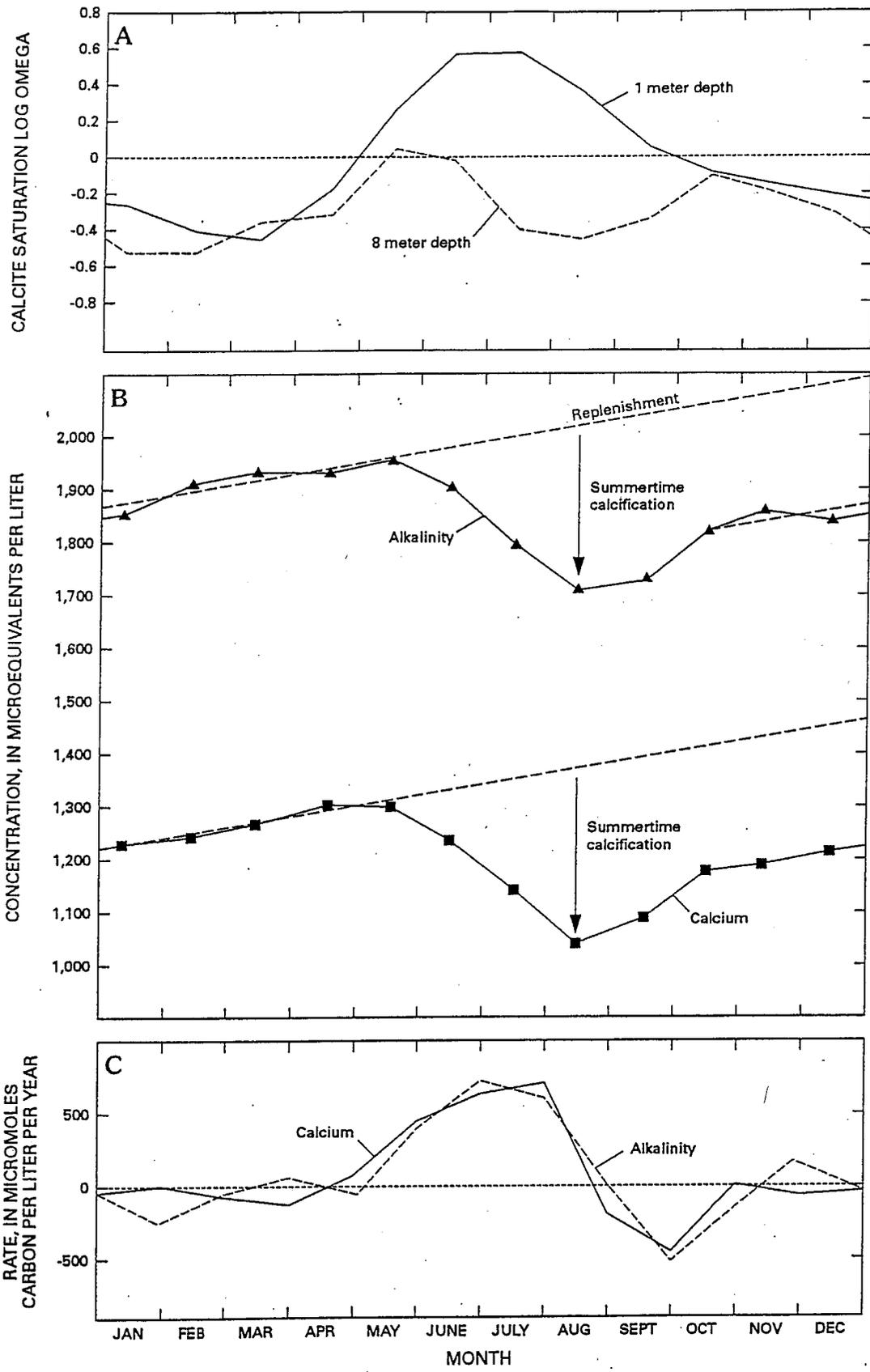
When plants calcify in order to generate protons for the photosynthetic assimilation of bicarbonate, they typically produce approximately equal molar quantities of calcium carbonate and organic carbon. Summertime photosynthesis can therefore be divided into calcification dependent and independent fractions, which utilize bicarbonate and carbon dioxide, respectively based on rates of calcification. Calcification-dependent photosynthesis accounts for about 40

percent of whole-lake net photosynthesis during the growing season, and more than 50 percent during the midsummer period of maximum plant growth (fig. 51). Calcification-dependent photosynthesis, which uses bicarbonate as its carbon source, occurs mainly during the summertime period of high pH and depressed carbon dioxide partial pressures. It represents an important adaptation to aquatic carbon dioxide depletion.

Ground-water inseepage, augmented considerably by dissolution of sedimentary marls (McConnaughey and others, 1994), supplies the calcium (and alkalinity) needed to support calcification-dependent bicarbonate-based summertime net photosynthesis. From 1980 to 1991 ground water supplied between 654 and 837 thousands of moles per year of calcium and 1,613 and 2,228 thousands of equivalents per year of alkalinity (LaBaugh and others, 1995). This input from ground water represented nearly 100 percent of the annual input of calcium and alkalinity to the lake. Without this seepage input, a significant component of lake productivity would rapidly cease to function.

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Figure 48. Annual dynamics of calcium carbonate in Williams Lake: (A) Calcite saturation, (B) Alkalinity and calcium concentrations, adjusted for dilution, and (C) Calcification rates calculated from the rates of change of calcium and alkalinity.
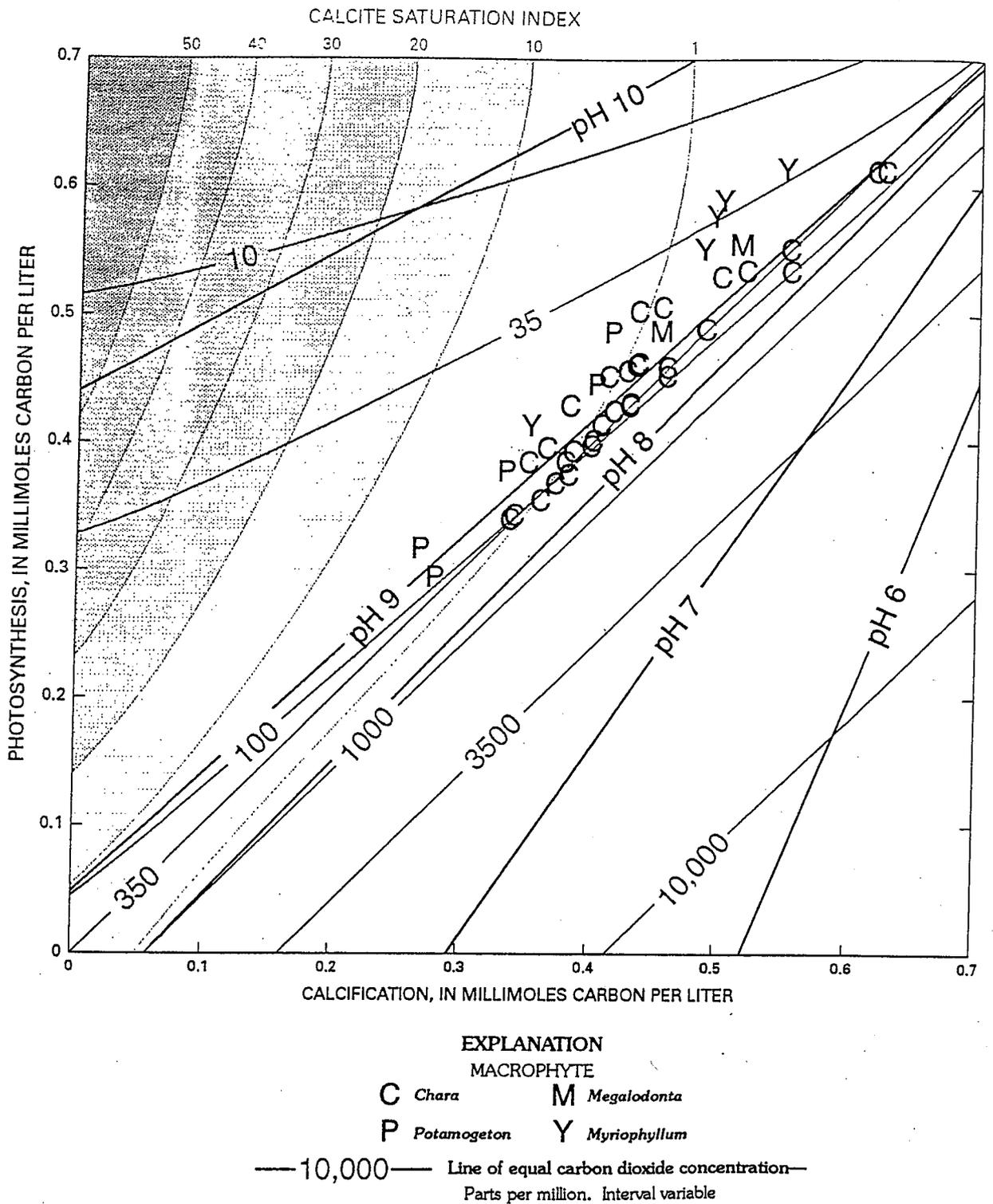
Figure 49. Rates of calcification and photosynthesis by several aquatic macrophytes incubated in calcium-enriched lake water. Also shown are contours of pH, carbon dioxide concentrations, and calcite saturation (shaded) for lake waters subjected to various amounts of calcification and photosynthesis.
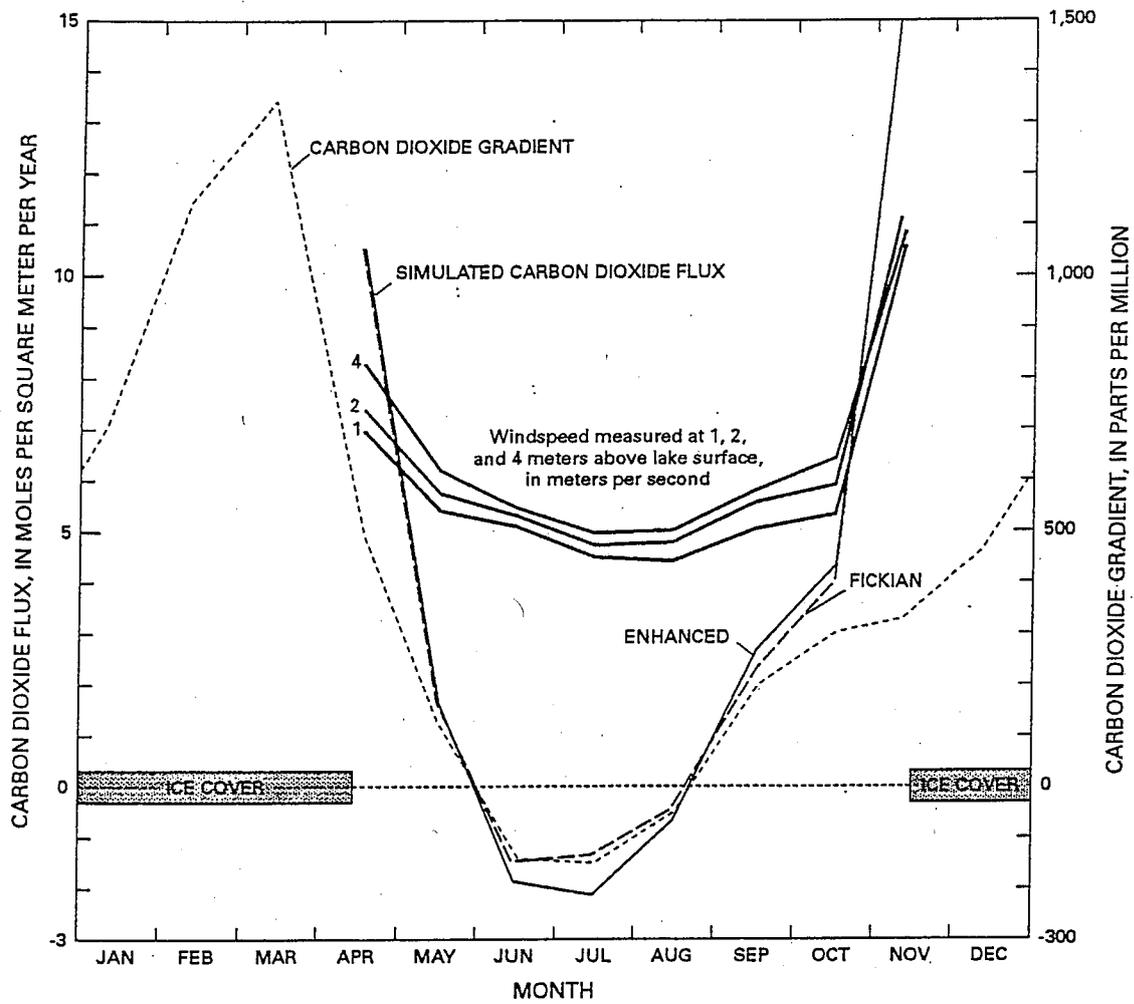
Figure 50. Carbon dioxide exchange between the lake and atmosphere calculated from the gradient in CO_2 partial pressure and windspeed. Results from two versions of the stagnant film model are illustrated: a standard Fickian version, and a chemically enhanced version, which considers the rate of carbon dioxide reaction within the surface boundary layer.
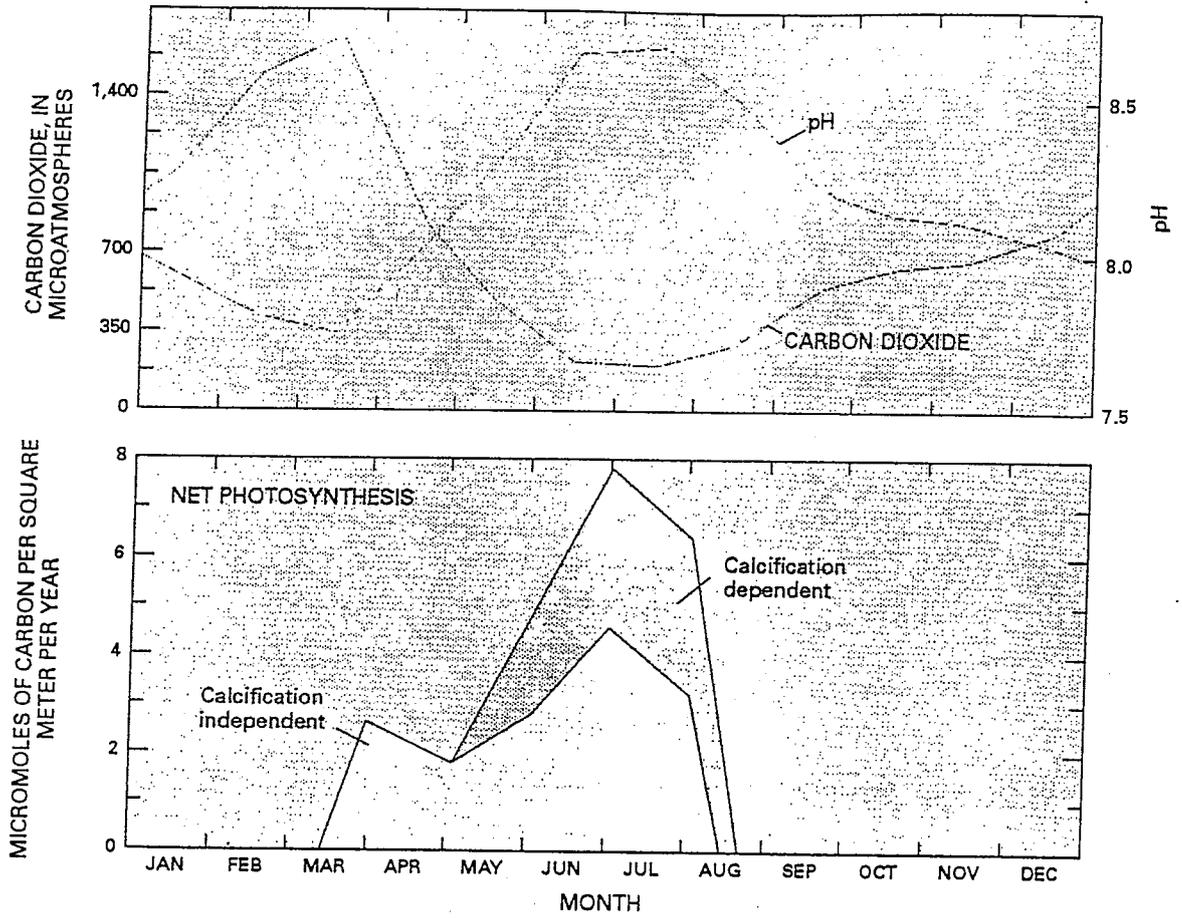
Figure 51. Seasonal cycle of photosynthesis in Williams Lake, calculated using the carbon budget approach and its relation to seasonal variation in CO_2 and pH in the epilimnion.