Stable carbon isotope ratio variations in marine macrophytes along intertidal gradients

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Summary. The hypothesis that relative water motion and boundary layer diffusion processes affect carbon isotope ratios of aquatic plants was tested in tidal pool and surge zone comparisons of the surfgrass Phyllospadix spp. No evidence was found that submerged plants growing in still upper tidal pools were isotopically different from those growing submerged in lower tidal surge zones. Significant decreases in $^{13}\text{C}/^{12}\text{C}$ ratios for plants growing emerged in the intertidal may have been caused by uptake of atmospheric carbon dioxide. Marine algae (Egregia menziesii and Halosaccion americanum) growing at the same location and tidal elevations as the seagrasses showed somewhat different isotopic fractionation patterns, suggesting that causes of isotopic variability in the seagrasses were not necessarily the same as those in the two marine algae.

Key words: Seagrasses – Phyllospadix – $\delta^{13}\text{C}$ – Halosaccion – Egregia

Fluid dynamics, as applied to aquatic plant photosynthesis, predicts that key elements influencing the magnitude of boundary layers include relative water motion and the size of the cell, leaf or thallus around which the boundary layer is located (Conover 1968; Drumgoole 1978; Wheeler 1980; Smith and Walker 1980; Raven 1981). Osmond et al. (1981) and Raven et al. (1982) tested the relationship between water motion and stable carbon isotope ratios of plants growing in different water flow regimes, while monitoring dissolved inorganic $\delta^{13}\text{C}$ source values. The hypothesis was that plants growing in fast-flowing streams are associated with smaller boundary diffusion barriers and hence, these plants should be isotopically lighter (exhibit more negative $\delta^{13}\text{C}$ values) than plants growing in still water. The more negative $\delta^{13}\text{C}$ values expected would be consistent with the known isotopic discrimination behavior of ribulose-1,5 bisphosphate carboxylase (Park and Epstein 1960). This discrimination was hypothesized to be masked in aquatic plants because of diffusion boundary layers affecting the transport of inorganic carbon to the plant (Raven 1981). The findings of Osmond et al. (1981) and Raven et al. (1982) tended to validate this hypothesis, although both studies can be criticized on the basis of two points: the great diversity of plants examined and the use of freshwater plants.

Plants sampled previously (Osmond et al. 1981; and Raven et al. 1982) were of diverse taxonomic groups, including red and green algae, mosses and several angiosperms. Taxonomic diversity complicates interspecific comparisons because physiological factors unique to an individual species could also affect isotopic fractionation.

Although there are no carbon isotope data available for marine plants with respect to water motion, there are advantages to using such plants to test the water motion hypothesis. Isotopic comparisons among marine plants are not complicated as among freshwater plants by spatial and temporal variations in dissolved inorganic carbon isotope variability because ratios are relatively constant throughout the marine environment (Broecker 1982; Galimov 1985). Although it has been shown that total CO$_2$ in still water tidal pools can be decreased by photosynthetic activity (Truchot and Duhamel-Jouve 1980; Morris and Taylor 1983) and that dissolved inorganic carbon $\delta^{13}\text{C}$ values can be made slightly more positive as a result, (~1‰; Parker and Calder 1970) this change would only serve to intensify the hypothesized boundary layer effect on carbon isotope ratios. While water temperatures could also affect fractionation in inorganic carbon available to plants in tidal pools, this effect was minimized here by the nature of the sampling locations: cool and maritime, with maximum spring tides occurring at dawn during the summer. These distinctions from freshwater systems allowed for an effective test of the influence of relative water motion on carbon isotope fractionation.

In this study, stable carbon isotope ratio variations were examined in two species of the seagrass Phyllospadix spp. growing along tidal elevation and water motion gradients. The genus grows in rocky marine habitats, exposed to surf, along the perimeter of the northern Pacific Ocean from Baja California to Japan (den Hartog 1970). Submerged plants in still water pools in the upper intertidal were compared with submerged plants growing in surge zones at the same locations.

Plants uncovered by the tide, rather than submerged in intertidal pools, also were compared isotopically. The isotopic consequence of emersion was examined because, while dissolved carbon dioxide differs little from atmospheric carbon dioxide, both are 8‰ to 11‰ lighter isotopically than oceanic bicarbonate at seagrass growth temperatures (Thode et al. 1965; Deuser and Degens 1967; Wendt 1968; Mook et al. 1974). Since some aquatic plants, including seagrasses, can utilize bicarbonate (Raven 1970; Stee-
man-Nielsen 1975; Beer et al. 1977; Beer and Waisel 1979; Millhouse and Strother 1986), it is possible that plants utilizing dissolved or atmospheric carbon dioxide could be isotopically lighter solely for that reason. This effect was separated from that of water flow by comparing plants submerged in upper intertidal pools with adjacent emerged plants growing at the same tidal elevations. Variability in isotope ratios was also measured in two macroalgae growing along the same elevation gradients to examine fractionation effects due to individual species differences independent of atmospheric exposure.

Two hypotheses were thus examined to account for variability of carbon isotope ratios: 1) Variations observed were related to relative water motion around the plants and size of the diffusion boundary layer; 2) Variations observed were related to tidal elevation and consequently proportions of exposure to air.

Material and methods

Leaves of Phyllospadix serrulatus Rupr. ex Aschers. were collected at Sandy Beach, Sitka, Alaska (57°03'N, 134°14'W) on 9 and 10 August 1983 along an intertidal transect extending from −0.88 m to +0.88 m, mean lower low water (MLLW). Leaves of the seagrasses P. serrulatus and P. torreyi S. Watson and thallus tissue of the algae Egregia menziesii (Turn.) Aresch. and Halosaccion americum I.K. Lee were collected at North Cove, Cape Arago, Oregon (43°20'N, 124°22'W) on 25 to 27 August 1984. This intertidal transect extended from −0.40 m to +0.94 m (MLLW). Algal and seagrass samples were collected along this same Cape Arago transect on 3 June 1985. The seagrass sampling protocol used on this occasion was slightly different. Instead of using unsorted leaves of all ages, at each sampled elevation, 3 of the youngest leaves from 3 separate shoots were collected. Additionally 3 of the oldest leaves from these same 3 shoots were collected and analyzed separately. On two additional transects parallel to this first transect, leaves of all ages were sampled.

All of the Sitka and Cape Arago seagrass and marine algal samples were air dried in the field and within a week were further dried at 60°C for 24 hours. Samples were prepared for isotopic analysis using the methods of Dunton and Schell (1987). Mass spectrometry was performed using a VG Isogas SIRA 9™ for the Cape Arago samples and AEI MS 20™ for Sitka samples at the Institute of Marine Science, University of Alaska, Fairbanks.

The δ13C values reported are relative to the Pee Dee Belemnite standard (PDB; Craig 1953) although 2 internal standards were employed on a continuous basis to calibrate the mass spectrometers to PDB. A correction was made for the contribution of 13CO2 to the mass 45 beam as given by Craig (1957). Instrumental error determined in consecutive analyses of a single CO2 sample averaged less than ±0.05‰. Average replicate sample standard deviation for seagrass samples from Sitka on the AEI mass spectrometer, including all instrumental errors and errors of preparation, was ±0.15‰ (N=52). Average replicate sample standard deviations for seagrass and marine algal samples from Cape Arago on the VG mass spectrometer, including all instrumental errors and errors of preparation were ±0.21‰ (N=45) and ±0.24‰ (N=42), respectively.

Samples collected were free of macroscopic epiphytes. For E. menziesii, samples consisted of roughly equal portions of blades, collapsed pneumatocysts, and stipe. For H. americum, samples consisted of collapsed, shredded sacs.

Results

Isotopic ratios observed at Sitka are based on a single sampling period using unsorted leaves of all ages, so there is no seasonal variability in the data. A Friedman Test indicated that samples collected along 1 of the transects at Cape Arago at 2 different times of year (June, 1985 and August, 1984) and using 2 different sampling protocols (old and young leaves versus unsorted) were drawn from the same population (0.3<P<0.5). Although young and old leaves from the same P. serrulatus plants varied by up to 1‰, no consistent pattern was observed for leaf age with this species (Wilcoxon signed-rank test: P=0.2; N=12). As a result, seagrass isotopic data collected at Cape Arago were grouped together for age of leaf and sampling times. A Wilcoxon signed-rank test indicated that there was no significant difference between isotopic values in marine algae collected in August, 1984 and June, 1985 (P>0.5; N=14). As a result, data for marine algae collected at Cape Arago for both times were also grouped together.

The water motion hypothesis was tested at the Cape Arago site using a Mann-Whitney test that indicated no significant differences between P. torreyi growing in subtidal surge zones (below −0.2 m) and P. torreyi growing submerged in upper tidal pools, where average water motion was lower (P>0.10; N=19; Fig. 1). P. serrulatus growing in tidal pools at Sitka also were not significantly different from P. serrulatus growing at the lowest tidal elevations (P=0.27; N=6; Fig. 1). On the other hand, P. serrulatus growing in submerged tidal pools at Cape Arago were significantly heavier than other P. serrulatus plants (Mann-Whitney, P<0.001; N=57; Fig. 1). This was apparently related to atmospheric exposure rather than water motion because almost all P. serrulatus exposed to air, even for short periods, were isotopically lighter than any growing submerged in tidal pools, even at the same elevations. Furthermore, above about −0.2 m, at Sitka, emersed P. serrulatus did not continue to become significantly lighter, indicating a threshold effect and a weakening correlation above this elevation. Particularly below −0.2 m, there was a significant relationship between decreasing δ13C values and increasing tidal elevation (Fig. 1; Table 1). Indications that the −0.2 m elevation was a threshold point also were apparent at Cape Arago. Below this elevation, for P. torreyi growing at Cape Arago, and also above +0.6 m for H. americum (Fig. 2) there were significant correlations, with both species becoming isotopically lighter with increasing elevation (Table 1). To summarize the seagrass tidal elevation patterns, all emersed seagrasses, regardless of location, became isotopically lighter with increasing tidal elevation, but not above −0.2 m tidal elevation. The lack of a correlation between increasing tidal elevation and decreasing δ13C values was observed at Cape Arago, for all E. menziesii (Fig. 2).

Discussion

Variability of δ13C values within the seagrasses studied appears to be most heavily influenced by exposure to air. Continually submerged plants were consistently heavier.