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Scope for use of stable carbon isotopes in discerning the incorporation of forest detritus into aquatic foodwebs

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Abstract

Stable isotope analysis of carbon has been proposed as a means for discerning the incorporation of terrestrial forest detritus into aquatic foodwebs, and as such, has the potential to be used as a biomonitor of the aquatic effects of riparian deforestation. A synthesis of $^{13}C/^{12}C$ data from the literature indicates, however, that the scope for successful use of carbon isotope analysis in separating allochthonous and autochthonous food provenance is much more limited than was once thought. This occurs due the overlap in carbon isotope ratios between terrestrial forest detritus and those of both lotic attached algae and lentic filamentous attached algae. Only within rocky-shored, oligotrophic lakes without macrophytes, and forest-fringed estuaries and lagoons, where the carbon isotope ratios for attached algae and forest detritus are significantly different, is there any likelihood of discerning the incorporation of allochthonous carbon into aquatic foodwebs using $^{13}C/^{12}C$ values alone.

Aquatic systems are not isolated from their surrounding landscapes but are rather dependent, to varying degrees, upon the ecotonal transfer of allochthonous organic matter necessary for sustaining productivity and biological integrity (e.g. rivers – Vanote et al. 1980; lakes – France & Peters 1995; estuaries/lagoons – Teal 1962; mangrove swamps – Odum & Heald 1972). As a result, riparian deforestation and the consequent reduced input of litterfall may have the potential to negatively effect aquatic foodwebs. Demonstration of the incorporation of terrestrial forest detritus into aquatic foodwebs might therefore be used as a managerial aid in decision-making regarding the design of protective buffer strips.

Because terrestrial forest and aquatic plants differ in their mechanisms of carbon uptake, they may often exhibit dissimilar stable isotope ratios (e.g. Fry & Sherr 1984; Peterson & Fry 1987). This has led to the suggestion that carbon stable isotope analysis (SIA) can function as a simple biomonitoring tool to gauge the effects of catchment deforestation on riverine (lotic) foodwebs (Rounick et al., 1982; Winterbourn & Rounick, 1985; Rounick & Winterbourn, 1986). Despite such optimism, however, it may often be difficult to measure the effect of riparian tree removal on stream carbon dynamics due to the overlap that occurs between the ranges of $^{13}C/^{12}C$ ratios for terrestrial litter and attached lotic algae which frequently makes it impossible to discriminate between allochthonous and autochthonous carbon dependency (France, 1995a).

The purpose of the present paper was to compile $^{13}C/^{12}C$ data from the literature in order to identify those aquatic systems in which carbon SIA could most favorably be applied in investigations of the aquatic consequences of riparian clearcutting. Because localized differences may exist in carbon isotope ratios due to the ambient influences of light, temperature, plant productivity, microbial decomposition and respiration etc., it is necessary to search for and compare source differences from a global perspective which will hopefully encompass this variability (e.g. France, 1995b). Stable carbon isotope values were therefore obtained directly from tables and from figures with a digitizing reader. Data sources are listed in France (1995a–e). The emphasis of this paper is in determining if differences exist in the carbon isotope ratios of C3 forest-plants and attached algae as a potential aid in measuring subtle effects of riparian deforestation. At lower latitudes, once deforestation has occurred, C4 grasses with distinct carbon isotope ratios may colonize watersheds, thereby permitting easy identification of terrestrial inputs (e.g. Bird et al., 1992) and possibly biological incorporation as well.

Because benthic attached algae are enriched in ^{13}C compared to planktonic algae (France, 1995b), benthic consumers will consequently also have higher ^{13}C values than pelagic consumers (France, 1995b, c). There is relatively little carbon transfer from the openwater to the benthic littoral zones in most marine coastal and freshwater systems. Further, because littoral benthic consumers rely for sustenance much more heavily upon attached algae than they do upon vascular macrophytes (France, 1995d), the $^{13}C/^{12}C$ ratios for attached algae and terrestrial plant litter represent the potential isotopic food sources available to these consumers.

As Bunn et al. (1989) stated, 'the utility of stable isotope tracing of energy flow in ecosystems depends on the existence of differences in isotope ratios among potential food sources of energy available to consumers'. The severe limitation in use of carbon SIA for accurately describing carbon pathways in lotic systems is evident from Figure 1 and has been described previously (France, 1995a). Likewise, the frequency distribution of $^{13}C/^{12}C$ ratios for filamentous algae growing on either macrophytes (epiphyton) or in semi-buoyant mats (metaphyton) within lentic systems, was found to completely envelope the $^{13}C/^{12}C$ frequency distribution for terrestrial detritus (Figure 1). As shown by the individual component studies (cf. data presented in Araujo-Lima et al., 1986; Hamilton et al., 1992; Neill & Cornwell, 1992; Bunn & Boon, 1993; Forsberg et al., 1993), it may often be impossible to distinguish between allochthonous and benthic autochthonous carbon provenance in such situations.

These are very serious limitations to the endorsement and widespread use of carbon SIA as a means for biomonitoring the aquatic effects of riparian deforestation. What these results indicate is that in possibly most rivers, and all lakes which have notable macrophyte growth and/or high productivity to sustain extensive developments of filamentous algae (which is probably most temperate and almost certainly all tropical lentic systems), carbon SIA may be inadequate for measuring the incorporation of forest detritus into aquatic foodwebs.

There are, however, at least two systems in which carbon SIA still has the potential to be a powerful tool toward discriminating allochthonous and autochthonous food provenance, as well as assessing

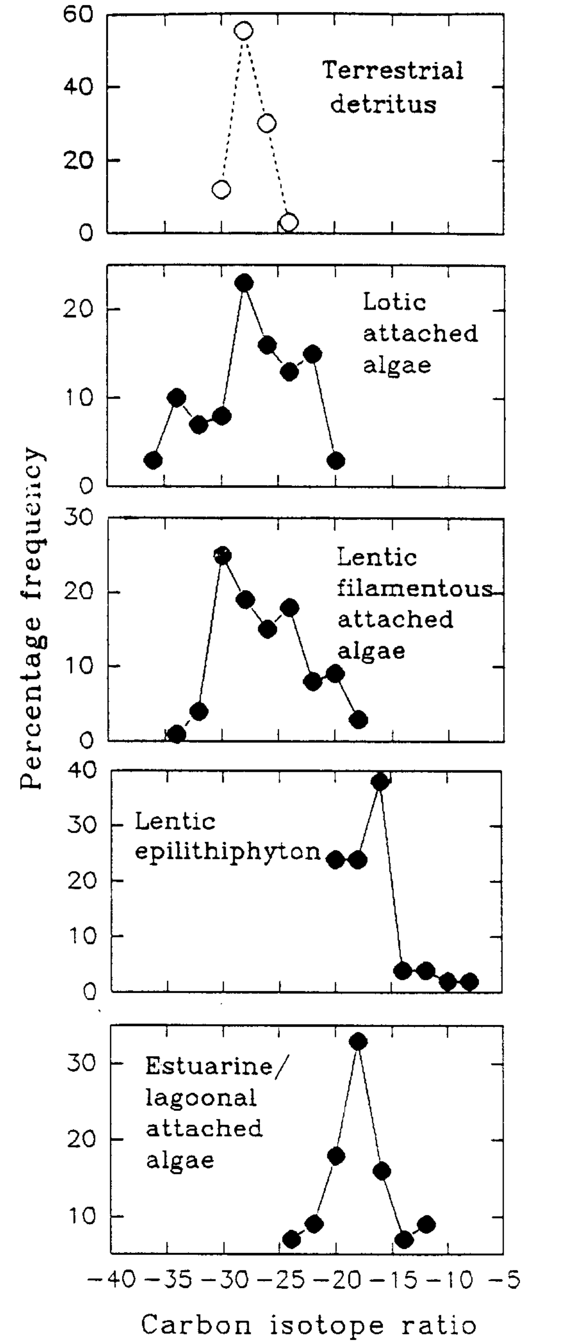

Figure 1. Percentage frequency distributions of the global extant data base for stable carbon isotope ratios for submerged terrestrial forest detritus ($n = 65$) and attached benthic algae (periphyton) in different aquatic systems: lotic (flowing waters) algae ($n = 97$), lentic (standing waters) filamentous (epiphyton and metaphyton) algae ($n = 80$), lentic epilithiphyton (rock algae, $n = 46$), and estuarine and lagoonal algae ($n = 55$). Carbon isotope ratios ($^{13}C/^{12}C$) are expressed as deviations from the recognized isotopic standard in parts per thousand. Enrichment in ^{13}C relative to ^{12}C is therefore reflected by higher (i.e. less negative) ratios; depletion in ^{13}C relative to ^{12}C is reflected reciprocally by lower (i.e. more negative) ratios.

the effects of the expected alterations in supply of the former following catchment clearcutting. These systems are: (a) northern and alpine oligotrophic lakes; and (b) forest-fringed estuaries and lagoons.

Due to the large diffusion resistance of CO_2 in water, algae with well defined boundary layers will entrap otherwise normally discriminated ^{13}C, leading to its greater enrichment within cells (Keeley & Sandquist, 1992; France, 1995b). Because of this, the low-lying diatom film growing in sheltered conditions atop submerged rocks (epilithiphyton) displays higher $^{13}C/^{12}C$ ratios than those of either epiphytic or metaphytic filamentous algae exposed to more turbulent conditions (France, 1995c). Therefore, in those rocky-shored oligotrophic lakes such as occur on the Canadian Shield or in alpine regions, which are characterized by little or no macrophyte growth, littoral benthic consumers are forced to rely upon this epilithiphyton as their sole autochthonous food source. Based on the present extant data, there is absolutely no overlap between the $^{13}C/^{12}C$ distributions for this potential food source and that for forest detritus (Figure 1). Because of this, it may therefore be possible to measure the incorporation of terrestrial carbon into resident aquatic organisms in such situations. As north-temperate regions are exposed to some of the most rapid rates and extensive magnitudes of clearcutting in the world (e.g. McLaren, 1990; McCory, 1993; Cooperman, 1993), stable isotopic measurement of the ecological significance of allochthonous carbon in these lakes has the potential for playing an important role in land management decisions.

Due to chemical discrimination with respect to atmospheric carbon, $^{13}C/^{12}C$ ratios for marine plants and animals are almost always higher compared to those for their freshwater counterparts (Fry & Sherr, 1984; Peterson & Fry, 1987). Therefore, those marine environments such as forest-fringed estuaries and lagoons, which are exposed to considerable inputs of terrestrial detritus, would be ideal systems in which to quantify the relative importance of allochthonous carbon to aquatic foodwebs due to the separation that occurs between the food source $^{13}C/^{12}C$ ratios (Figure 1; for individual component studies see Hackney & Hanies, 1980; Rodelli et al., 1984; Stoner & Zimmerman, 1988; Wada et al., 1993). Because coastal forests such as mangrove swamps are disappearing at an alarming rate (e.g. Lugo & Cintron, 1975), carbon SIA has the potential, therefore, to be used as a biomarker of aquatic disturbance resulting from such activities.

Overall, the scope for use of SIA in discerning alternate pathways of carbon flow within benthic foodwebs, and the ability to apply this information toward land management decisions, is much more limited than suggested in previous reviews (Fry & Sherr, 1984; Rounick & Winterbourn, 1986; Peterson & Fry, 1987). Because of hydrodynamic influences on ^{13}C discrimination by attached algae, it may be impossible to distinguish between benthic autochthonous and allochthonous carbon in many if not most rivers as well as those standing waters in which filamentous epiphyton or metaphyton are abundant. Nevertheless, more extensive examination of the potential for use of carbon SIA within both rocky-shored, oligotrophic lakes, as well as within forest-fringed estuaries and lagoons, would still be a profitable direction worth pursuing further.

For the other aquatic systems discussed in the present paper, it is still possible that the simultaneous analysis of multiple isotopes can improve resolution of food source provenance as has been demonstrated in studies of energy flow within complex estuarine environments (e.g. Currin et al., 1995). Secondary analysis of literature data indicates that terrestrial plants and aquatic algae/plants often differ in their respective $^{15}N/^{14}N$ ratios, thereby raising the possibility that some combination of both carbon and nitrogen SIA may be useful for measuring allochthony (France, 1995e).

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