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The Potential of Stable Carbon Isotopes in Bioarcheological Anthropology

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Analysis of the stable carbon isotope ^{13}C has been used during the past fifteen years for the correction of radiocarbon dates. However, applications to other anthropological problems are so recent, that only eight explicitly anthropological studies have been published (Brothwell and Burleigh, 1977; Burleigh and Brothwell, 1978; Craig and Craig, 1972; DeNiro and Epstein, 1978a; Herz and Wenner, 1978; van der Merwe and Vogel, 1978; Vogel and van der Merwe, 1977). Consequently, this paper shall discuss the potential of stable carbon isotopes with special reference to their most suitable use in paleonutritional and paleopathological analyses. I shall begin with a description of the nature of the ^{13}C isotope in the biological and physical environments. From an understanding of the chemical behavior of the isotope, one may deduce its relevance for anthropological studies as well as the problems inherent in such applications.

Nearly 99% of the earth's carbon is composed of the stable isotope ^{12}C. Approximately 1.1% occurs in the other stable form of ^{13}C and 10^{-12}% in the more familiar unstable isotope ^{14}C (Hammond, 1972; Smith, 1972). The distribution of ^{13}C in nature is variable. Such a phenomenon would be of little significance to anthropology had not radiocarbon labs and archaeologists discovered in the mid-1960's that dates derived from maize and sugarcane were "too young" (Hall, 1967. See also Bender, 1968; Lerman, 1972; Lerman and Troughton, 1975; Olsson, 1970; Rafter and Grant-Taylor, 1972; Stuckenrath, 1977; Stuiver, 1978; Stuiver and Polach, 1977). The dating error in corn and similar plants occurs because the ^{12}C content of these plants is "artificially" lowered due to the greater "substitution" by the plants of ^{13}C. Subsequent research in radiocarbon analysis and plant photosynthesis has expanded the anthropological implications of ^{13}C variation.

Samples of as little as 20μg of carbon (Stuiver, 1978) to be analyzed for stable carbon isotopic composition are combusted as for radiocarbon analysis. But the resulting gas is analyzed by an isotope ratio mass spectrometer, not a beta counter. The ratio of the carbon isotopes is compared to a known standard and expressed as a per thousandths (‰) value, which is always negative.

During photosynthesis, plants preferentially take up ^{12}C over ^{13}C from their immediate environments in order to metabolize energy through three major pathways: C3 (Calvin), C4 (Hatch-Slack), and CAM (Crassulacean acid metabolism) (Troughton 1972). Plant $\delta^{13}C$ values can theoretically range from 0 to -38‰ (Smith, 1972) but there is a distinct bimodal distribution of real values associated with the metabolic pathways. C4 plants discriminate less against ^{13}C than do C3 plants and therefore have higher ^{13}C ^{12}C ratios. Plants can be grouped on the basis of their $\delta^{13}C$ values alone. The mode for C4 plants is -12‰; for C3 plants it is -28‰. CAM plants are intermediate in value, depending on their growth conditions (Lerman and Queiroz, 1974).

Most non-desert plants have the Calvin or C3 pathway with a 3-carbon structure. Some plants, C4 with a 4-carbon structure, have an additional system which uses separate cells to segregate the two metabolic pathways (Black 1973; Hatch and Slack 1970; Lerman and Troughton 1975). C4 plants tend to be tropical and are uncommon in Northern temperate environments, especially where the normal July minimum temperature falls below 10°C (Teeri and Stowe 1976). Most CAM plants are succulents. Like the C4 plants, CAM plants use two metabolic pathways, but only one cell type is present. Metabolic processing is temporally separated, switching between night and day (Black, 1973; Lerman and Queiroz, 1974; Lerman and Troughton, 1975). Which metabolic pathway a plant will have is independent of the usual taxonomic criteria although consistent within species. Except for the gymnosperms (see Figure 1), one cannot predict the photosynthetic grouping of a plant above the specific level.

The carbon content of all organisms initially reflects the $^{13}C/^{12}C$ ratio of its carbon source. For terrestrial plants, the carbon source is atmospheric with a $\delta^{13}C$ value of approximately -7‰. Aquatic plants depend on either the atmospheric carbon dioxide pool or the aquatic bicarbonate or carbon dioxide pools. Bicarbonate is enriched in ^{13}C more so than carbon dioxide and therefore has a higher (less negative) $^{13}C/^{12}C$ ratio. As a general rule, adaptations in plants "leading to high $^{13}C/^{12}C$ ratios seem to be a response to life under difficult conditions" (Smith and Epstein, 1971:383) such as an aquatic or xeric environment. Studies by DeNiro (1977) and DeNiro and Epstein (1978b; 1978c) of animals fed

a controlled diet show that as the carbon is passed from one member to another in the food chain, the individual organisms continue to reflect the relative isotopic composition of their diet (see also Smith, 1972; Minson et al., 1975; Vogen and van der Merwe, 1977).

Unlike the unstable ^{14}C, the ratio of ^{13}C to ^{12}C in an organism after death will not intrinsically fractionate. Analysis of skeletons, food refuse, soil humus, or shell can therefore reflect the environment of the living organism.

Applications--Environmental

Stable carbon isotope analysis can be applied to two major areas of anthropological interest: 1) environmental reconstruction and 2), with a more direct bearing on human behavior, dietary reconstruction.

Because temperature will affect the viability and proportion of C4 plants in North America (Teeri and Stowe, 1976), the proportion of C4 plant remains in an archaeological site, even though not identifiable as to species, may yield palaeoclimatic data. The shift in $\delta^{13}C$ within the general C3 mode between datable tree rings can also be used for climatic reconstructions (Lerman and Long, 1978; Mazany, 1978). CAM plants will shift their $\delta^{13}C$ values according to temperature, light, and water regime (Lerman, and Queiroz, 1974; Lerman and Troughton, 1975; Osmond et al., 1973; Troughton et al., 1974). Troughton et al. (1974) confirmed a shift in Mojave Desert climate to a drier, warmer period between 40,000+ BP and 10,000 BP through a shift in $\delta^{13}C$ values of prickly pear remains in cave sites.

Shell, plankton, and aquatic $\delta^{13}C$ values will reflect temperature (Lerman and Troughton, 1975; Smith 1972; Troughton, 1972). The use of $\delta^{13}C$ analysis with $\delta^{18}O$ analysis may aid in oceanic and local climate reconstructions (Herz and Wenner, 1978). Microstrata within shell heaps may be distinguished by the $\delta^{13}C$ and $\delta^{18}O$ values of shell lenses. These characteristics have been useful in locating quarry sources for Greek marbles (Herz and Wenner, 1978).

The study of browsing/grazing ratios for certain animals which eat C4 grasses and C3 shrubs and trees may be aided by carbon isotopes (DeNiro and Epstein, 1978c; Tieszen et al., 1979 and Vogel and van der Merwe, 1977). Lerman and Troughton (1975) believe the ^{13}C values of fossil soil organics should reflect variation in relative biomass of coeval C3 and C4 species as in tropical

savannahs. This variation should follow climatic trends. Unidentifiable calcined bone found at Palaeo Indian sites may still be identifiable as to herbivore or carnivore because of the slight enrichment in ^{13}C of meat over the original plant biomass.

Applications--Dietary

The behavioral and microevolutionary implications of dietary and economic change are of great interest to anthropologists and human biologists. But biological research has had to rely on an insufficient archeological record and studies on living individuals of the interactions of nutrition and disease (e.g., Scrimshaw et al., 1959). Studies of clinical and ethnographic populations suffer several limitations for an understanding of a) human adaptation to changing environments, b) disease processes, and c) variation in human nutrient requirements and in social and environmental impacts on nutrition. Clinical populations generally represent a highly selected sample of individuals who are not members of the same gene pool. Clinical studies will reflect individual response but cannot reliably reflect the variation in species response. The "population" studied may have problems of bias toward the clinically ill.

Ethnographic populations offer the opportunity for examination of the finer effects of drift, flow, mutation, population and social structures, and environment in modern interactions in human variation. But hypotheses of change which are generated cannot be tested within these same populations. Anomalies which are encountered in the population, such as a negative nitrogen balance, may require that we modify our current understanding of health and disease processes or may result from anomalous conditions in the population which were present at the time of study (Norgan et al., 1974). The use of historiographical populations removes us entirely from direct contact with the individuals involved. Analysis of the history of disease is limited by literary distortions common to written texts.

Archeological populations offer historical information, i.e., time depth, to studies of human nutrition. Individuals represent social, biological and physical environments which are no longer extant. More importantly, they offer an experimental unit, with its own constraints, advantages, and configurations, which is not inherent in the use of living populations.

However, examinations of prehistoric dietary change have, in the past, been hampered by the vagaries of organic food preservation in the archaeological record or have had to rely on the indirect

evidence of technological or stylistic change. Nevertheless, analysis of nutritional quality, energy sufficiency, and implications for changing disease patterns is possible through archeological remains (Kaplan, 1973). But detailed archeological inferences of diet from floral and faunal remains have probably only a 20% accuracy; poor preservation conditions further reduce this level of accuracy. Even were we to assume near perfect preservation of food remains, such information would only tell us which classes of food were eaten, not which parts were deemed necessarily eatable nor who ate what. Coprolites add information about what was undigested rather than what was utilized. Furthermore, all sources of archeological information of diet, disease, and energy, other than human skeletal remains, are at least one step removed from the individuals who participated in the cultural organization of that information, and are at least one analytical step from the primary human data base.

Prior to chemical analyses of bone constituents, one had to infer the relationship between the biological analyses (of skeletal indicators of health and nutrition) and the archeological analyses (of dietary and cultural remains). Chemical analyses offer the potential for direct measurement and assessment of diet in individuals and the population. Studies in trace elements which reflect dietary components in the bone mineral are older than those of isotopic composition of bone collagen. But, there are many problems with a bone mineral sample, to be discussed later.

Stable carbon isotope analysis provides a new approach which offsets many of the problems of other approaches such as palaeopathology, archaeology, and mineral analyses.

$\delta^{13}C$ analysis can be applied to studies of 1) seasonal rounds, 2) coastal versus inland exploitation strategies, and 3) the introduction and evolution of horticulture in the Western hemisphere (these isotopic studies are not restricted to the New World but the environmental parameters are probably more easily controlled here). Time periods accessible to study range from the present to 10 to 20 million years BP (DeNiro, pers. comm.), thus potentially adding new information to questions related to Australopithecine diet and dimorphism. Samples for analysis of human diet can come from the plant remains themselves, other animal bones, or human skeletal remains.

For example, studies of regional site utilization in an area of good preservation such as MacNeish's sites in the Tehuacan Valley could be correlated with season through inter-site variation

in CAM plant $\delta^{13}C$ (Stuckenrath, pers. comm.). Because a marine diet will result in $\delta^{13}C$ values similar to C4 plants (that is, a high $^{13}C/^{12}C$ ratio), we could assess from skeletal remains 1) the importance of coastal-inland subsistence patterns; 2) the relative importance and consequent cultural dependence on marine resources in a marine adaptive strategy; or 3) the relative importance of anadromous fish runs in the total annual diet. We might isolate populations using only an inland, C3 subsistence from those using a coastal/inland base and trace the interactions and movements of these coeval populations in an area such as Labrador or southern New England (similar work is in progress for eastern Cape populations in South Africa; van der Merwe, pers. comm.).

Cultigens in the New World, such as maize, tend to be C4. In most temperate environments (with an abundance of C3 plants and few C4 plants), shifts in prehistoric subsistence systems from dependence on indigenous gathered plants and animals to the use of cultigens means a shift in dietary isotopic composition. As with trace elements, we may follow the introduction, migration, and evolution of horticulture (Gilbert, 1978) through bones, even when horticultural implements or adequate floral remains are absent.

Vogel and van der Merwe (1977) with a sample of ribs from seven individuals from four New York sites (2500 BC-1450 AD) demonstrated a significant shift in collagen C3-based $\delta^{13}C$ values with the dietary shift from hunting and gathering to horticulture (average $\delta^{13}C$ of -19.7‰ for gatherers; -14.43‰ for horticulturists). Isotopic evidence showed a high proportion of maize (average 40%) in the horticultural diet. The shift to intensive maize cultivation occurred within 200 years after maize introduction. The van der Merwe and Vogel (1978) study of 52 individuals from ten Midwestern sites (3000 BC-1300 AD) confirmed the earlier study (pre-maize average of -21.4 ± 0.78‰; Ohio maize average of -11.8 ± 1.3‰). Isotopic analysis of six females and four males from the Ohio horticultural site indicates a higher C3 (less maize) component in the women'd diet (approximately 64% maize for females, 75% maize for males).

Based on prehistoric human skeletal material from the Viru Valley, Peru (sample parameters not stated), DeNiro and Epstein (1978a) have eivdence that $\delta^{13}C$ values of collagen increase through time, consistent with the archeological evidence for increased use of maize in a seafood diet base. Isotopic evidence indicated maize was introduced to the region several hundred years earlier than recovered maize organic remains indicated.

MacNeish (1978) employed DeNiro's isotopic analysis of 75 individuals from several sites in the Tehuacan Valley, Mexico, in an ambitious attempt to estimate the evolution of energy flow in the cultural system. $\delta^{13}C$ was used to estimate dietary proportion of maize and animal protein. Table kcal values were assigned to the various dietary components (determined from ^{13}C analysis and preserved food remains) which were then compared to table kcal values for the estimated work expenditure within the various cultural time periods in the 10,000 year span.

Isotopic composition of other animals (Vogel and Lerman, 1969) will also indicate maize cultivation. Iowa today not only produces the best corn-fed beef but also corn-fed venison from raiding deer. Hair samples from ten prehistoric mummified Peruvian dogs, analyzed by Burleigh and Brothwell (1978), indicate maize contributed 20 to 60% of the dogs' diet. Collagen from an Ecuadorian dog indicated the presence of maize (63%) on the coast there from 3000 BC.

Thus, stable carbon isotope studies will contribute significantly to current analyses of horticultural economic change by 1) establishing the presence of maize in a population's diet; 2) segregating groups of individuals with differential access to maize; and 3) determining the proportion of maize, animal protein, and other foodstuffs within individual diets. Once diets were known, we could make inferences of status, disease, marriage patterns, or of other social and biological patterns affecting differential access to diet. For example, the weanling, the aged, and the ill of a population all require diets which may differ from the rest of the population. Wives captured from horticultural groups by hunting and gathering raiders may be observable isotopically in the hunting populations. Regional trade patterns shoudl be discernible where, for instance, maize is used as a medium of exchange, traded for Northern furs or for European goods.

Isotopic analysis can clarify whether porotic hyperostosis and infectious skeletal lesions occur more frequently in Midwestern and Southwestern horticulturalists (El-Najjar, et al., 1976; Lallo, et al., 1977; Lallo, et al., 1978; Mensforth, et al., 1978) than earlier gatherers because of a postulated heavy maize diet, per se, or from a changing social environment. Studies of dietary proportion may reveal protein deficiencies. This may have special relevance to studies of Aztec cannibalism which assume the cannibalism is a manifestation of the well-nourished elite indulging in their corn-fed masses.

Problems

As indicated, stable carbon isotope analysis can provide us with data on the original physical environment of plants and with information about the diet of humans and other animals from organic remains found at archeological sites. The analysis itself is simple and relatively cheap when compared to other techniques which could be applied to anthropology. Plants are clearly C3, C4, or CAM and animals reflect this in their diet. Any form of carbon can be analyzed. However, before you rush your bits and pieces of interest to the radiocarbon labs, you must realize the problems involved in $\delta^{13}C$ analysis. These problems, termed fractionation effects or "errors," can occur anywhere in the carbon cycle, including the actual analysis. In essence, the critical point in any research design involving stable carbon isotopes, especially those used for dietary reconstruction, is the sample which is analyzed for $\delta^{13}C$. The mass spectrometer will measure the $\delta^{13}C$ composition of the gas presented to it. It cannot distinguish whether the carbon derives from the diet of the individual tested or derives exogneously from microbiological activity or soil organic matter contaminants. It cannot compensate for differential loss of the isotopes in the sample due to groundwater dissolution or chemical preparation. The critical point in interpretation is that the measurement given is only $\delta^{13}C$ of the sample. Derivation of those carbon isotopes is not measured nor is dietary composition (the proportion of those isotopes derived from C3- and/or C4-like foods nor the specific foods ingested). This last point will be explained later.

Points in the carbon cycle where fractionation may occur can be outlined as in Figure 2.

Biosynthetic fractionation (points 1, 2, 3) is becoming quite well known in higher plants and variance is highly predictable (see Smith and Epstein 1971). Fractionation in terrestrial plants may come from 1) the source of carbon dioxide; 2) during carbon dioxide uptake and metabolsim; 3) during respiration; and 4) during reassimilation of respired carbon dioxide by photosynthesis in light before it can mix with atmospheric carbon dioxide (Troughton, 1972). Isotopic differences exist within plants and between plant parts, chemical fractions, and amino acids (Smith, 1972. See also Bender, 1971; Freyer and Wiesberg, 1974; Lerman and Troughton, 1975; Lowdon, 1969; and Troughton, 1972).

$\delta^{13}C$ values for aquatic plants vary due to 1) contribution of carbon dioxide from other biological activity in the environment; 2) carbon dioxide or bicarbonate as the source of carbon; 3) fractionation between carbon dioxide and bicarbonate because of temperature dependence (this also affects the amount of dissolved

gas present); 4) pH; 5) bicarbonate predominance in hard or sea water and carbon dioxide predominance in freshwater; and 6) use by plants grown partially in water and partially in air of carbon from both sources (Lerman and Troughton, 1975; Smith, 1972; Smith and Epstein, 1970; and Troughton, 1972).

Soil ^{13}C values will be affected by 1) type of residue returned to the soil and its differential preservation; 2) distribution of living roots and soil animals which will alter soil values; and 3) losses due to soil permeability and escaping carbon dioxide (Stout and O'Brien, 1972).

Within animals, there seems to be a slight enrichment of ^{13}C in collagen relative to soft tissues (DeNiro, 1977; deNiro and Epstein, 1978b; Vogel and van der Merwe, 1977). For example, animals feeding on a C3 diet (^{13}C of -26‰) have collagen values of -20‰. Studies of "buffalo and elephant bones show depletion of bone collagen . . . relative to the bone mineral" (Hassan, 1975: 92).

Human collagen shows a similar enrichment relative to soft tissues as do other animals (DeNiro and Epstein, 1978a; Farmer et al., 1972; Harkness and Walton, 1972; Lyon and Baxter, 1978; van der Merwe and Vogel, 1978; Vogel and van der Merwe, 1977). Like the elephant and bison, humans show variations in $\delta^{13}C$ values between skeletal components--a 37-year old Glasgow woman had values of -34.2‰ for marrow; -27.6‰ for collagen; and -17‰ for mineral (Harkenss and Walton, 1972). Why such a variation exists between tissues is as yet unknown although it will be related to the biochemical nature of the tissue and to changes in the diet over the span of tissue formation. For example, teeth (formed early in life) may reflect the carbon composition of a weanling diet which would differ from an adult diet reflected in muscle tissue or long bone.

Laboratory fractionation (points 5, 6, 7) is the easiest to control. Combustion and gas collection and purification technique have been perfected over the past 25 year history of radiocarbon dating. Techniques of isotope ratio mass spectrometry are also well established. However, between lab variation, from machinery and processing used, is substantial for radiocarbon dating and can be expected for ^{13}C (Craig and Craig, 1972; DeNiro, pers. comm.; Stuckenrath, van der Merwe). Mass spectrometry error varies from ± 0.05‰ (Craig and Craig 1972) to ± 2-3‰ (De Niro, pers. comm.). Chemical fractionation may occur due to the resistance of the heavier ^{13}C molecule (Hassan, 1975; Smith, 1972). Careful pretreatment of the sample is required to ensure that the extraneous carbon is not also analyzed. However, variations in ^{13}C content

due to lab analysis are small compared to those variations found in biosynthesis between species (Hassan, 1975).

Diagenetic fractionation (point 4) or errors include all changes in the post-mortem environment which result in loss, contamination or addition, or fractionation via chemical exchange of the initial $^{13}C/^{12}C$ material. I would like to stretch the term "diagenesis" somewhat to imply depositional and post-depositional mechanical alterations in the archeological record, but these implications will be assumed and not discussed here. Diagenetic fractionation, along with the human sub-system, are the greatest sources of unknown problems in anthropological isotopic analysis.

After death, there may be enrichment or depletion of ^{13}C through 1) physical inclusions; 2) exchange of carbon with extraneous sources such as between bone carbonate and the surrounding medium; and 3) fractionation within the decay processes of organic matter (Hassan, 1975).

Carbon in bone mineral is known to exchange with its environment; physical contamination with carbonaceous material (primarily as precipitates or inclusions of organic matter and soil minerals) is frequent in the bone interstices (DeNiro and Epstein, 1978a; El-Dahoushy et al., 1978; Hassan, 1975; Hassan and Ortner, 1977). Collagen, however, is not known to exchange with its environment (DeNiro and Epstein, 1978a; Hassan and Ortner, 1977; Ho et al., 1969; Olsson et al., 1974). But, collagen content of archeological samples decreases with time (Olsson et al., 1974; Haynes, Ortner, Stafford, von Endt, pers. comm.). Degradation, and loss of amino acids, is also a problem with Pleistocene sample; (see especially Ho, 1967). An additional complication is that laboratory demineralization of bone results in a material which is mostly collagen or collagen-derived but which also contains other proteins, hydroxybenzoeacids, polysaccharides, and fats (Olsson et al., 1974) not directly comparable to the diet-derived isotopic composition of the collagen, but which may nevertheless skew the $\delta^{13}C$, if analyzed in the sample.

For the analysis of most plant remains, the difference of $\delta^{13}C$ values between cellular components of plants, such as between lipids and cellulose of up to 10‰, will not greatly affect overall plant values. But differential preservation of those components might skew bioevolutionary studies which use fossil plant specimens (Lerman and Troughton, 1975).

Evaluation

There is hope. Most of the cargon isotope variation can be predicted. In other cases, such as diagenesis, error can be

controlled through a careful sampling design. Fractionation effects are consistent. Variance within skeletal populations is low as is the variance in the within-site diet base. But given our current state of ignorance of the carbon cycle, carbon isotope techniques are best applied to anthropological questions related to distinguishing C3 from C4 diets and inland from marine diets from skeletal populations or individuals in a C3 environment.

Questions related to the dietary variation within the population require background $\delta^{13}C$ values for indigenous foods because plants (and animals) derive their $\delta^{13}C$ values from the immediate environment. It does not seem valid at this point in our knowledge to rely heavily on average, postulated, or non-local dietary $\delta^{13}C$ for determining population variance in dietary proportion (cf., van der Merwe and Vogel 1978) of C3- and C4-like foods. (It would be very helpful if archeologists could obtain $\delta^{13}C$ values for the organic remains along with radiocarbon dates and paleobotanical or paleozoological studies from their sites). Population variation studies also require valid sample size stratified by age and sex groups. In all cases where conclusions of dietary variation are drawn from isotopic studies, these conclusions must be tested against other modes of analysis, especially the archeological record. For example, in the Burleigh and Brothwell (1978) study the C4 component of the coastal Ecuadorian dog diet was assumed to derive from maize because dogs do not feed on seafood. However, dogs do scavenge human fecal waste. Thus, the $\delta^{13}C$ of the dog collagen may ultimately derive from a human marine diet, not from a previously unsuspected early cultivation of maize.

Skeletal populations from horticultural and pre-horticultural sites, such as Dickson Mounds, are the most numerous and accessible to study. Carbon isotope analysis of these populations can test hypotheses of human cultural and biological interactions. For example, we can test the expectation that 1) synergistic interactions of nutrition, disease, and acculturation stress will not affect a population as a whole but rather specific sub-groups which may be defined on the basis of biological (age, sex, etc.) or social status. 2) It may be the requirements of critical subgroups such as the aged, ill, weanling, adolescent, or nursing individuals which will affect a) a group's choice of adaptive strategy and b) its eventual success or failure in meeting biological stresses. And 3) the associations of isotopic composition and disease should vary between populations of different biological-social-physical environments.

As long as archeological anthropology is said to deal with the material remains of human action (Reynolds, 1976), it must be founded on an understanding of the human organism behind that action. Stable carbon isotopes, when carefully used, along with the other techniques discussed in this volume, can provide an access to that understanding.

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Figure 1

Some Examples of Naturally Occurring $\delta^{13}C$ Variation

I. C3 (Calvin or Calvin-Benson); RuDPC; more negative $\delta^{13}C$ (low $^{13}C/^{12}C$ ratio) All major economic crops except *. Soybean (Glycine max.); sunflower; cattail (Typha latifolia); rice (Oryza sativa); oats (Avena sativa); some algae; some photosynthetic bacteria; wheat; barley; safflower; maple; sugar beet; squash; pea; peanut; potato; ryegrass; Leguminosae; mosses; all gymnosperms except Welwitchia

II. C4 (Hatch-Slack); PEPC; less negative $\delta^{13}C$ (high $^{13}C/^{12}C$ ratio) *Sugarcane (Saccharum officinarum); *maize (Zea mays); *sorghum (Sorghum bicolor); crab grass; Panicum maximum; P. texanum; Bermuda grass; pigweed; marine plants; freshwater aquatic plants; some desert plants; *millet; coastal marshlands--Spartina patens, S. alterniflora (cord-grass); papyrus; some sedges and grasses (fibers, thatching); some lichens

III. CAM (Crassulacean acid metabolism)

Opuntia; pineapple; agave (tequila, pulque, sisal, henequen); Lorphora spp. (peyote); cactus (Trichocereus spp., Oreocereus spp.--thatching); Aizoaceae; Cactaceae; cucurbit

IV. Genera with C3 and C4 pathways

Atriplex; Cyperus; Bassia; Kochia; Euphorbia; Panicum; Aizoaceae (some with CAM); Asclepiadaceae; Compositae;

Figure 1 (Cont'd.)

Zygophyllaceae; Euphorbiaceae; Portulacaceae; Chenopodiaceae; Cyperaceae; Graminae; Amaranthaceae

V. C3-like $\delta^{13}C$ values may include some

Fat/blubber; fish flesh; shellfish meat

VI. C4-like $\delta^{13}C$ values may include

Mammoth ivory; shell carbonate

VII. Bicarbonate is less negative than atmospheric CO_2

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