i.e., $m_i = d_i/s_i$, where d_i is the number of deaths during the time interval i, and s_i is the number of survivors at the midpoint of the time interval i.

Gehan (1969) has derived an equation which enables the variance of the midpoint age-specific mortality to be determined:

$$\mathrm{Var}[\hat{m}_i] = \frac{(\hat{m}_i)^2}{s_i q_i}\left\{1 - \left(\frac{\hat{m}_i}{2}\right)^2\right\},$$

where $q_i = \dfrac{d_i}{s_i}$, i.e.,

$$\mathrm{Var}[\hat{m}_i] = \frac{(\hat{m}_i)^2}{d_i}\left\{1 - \left(\frac{\hat{m}_i}{2}\right)^2\right\}.$$

This formula may be used to calculate 95% confidence intervals around m_i values (Fig. 1), aiding the comparison of survivorship patterns in the cohorts (Lee 1980). When this procedure is applied to the data of Pyke and Thompson (1986), the analysis shows that the mortality rates differ significantly in the two cohorts during the intervals between days 0–10, 10–20, 30–40, and 50–60, confirming the conclusions of the analysis of the residuals generated during calculation of the logrank statistic.

Conclusions

Despite the vigor with which plant demography has been pursued in the last twenty years, ecologists are still mostly ignorant of the causes of the deaths of individual plants in the field and of the reasons why mortality rates of species differ between sites and different growing conditions. Common problems in interpreting the causes of mortality and the rates of mortality in populations stem from our ignorance of the exact times at which plants have died and of variations in mortality rates through time. The analysis of residuals, and comparison of confidence intervals about mortality rates, which have been described above, are approaches that can enable very short periods of time to be identified when mortality risks differ substantially between sets of plants. Although for the field ecologist inferences about the causes of plant death will always be easier than proof, the ability to compare mortality rates over very short time intervals will allow more accurate interpretation of the causes of mortality and promote a sharper understanding of the tolerance limits of species in the field.

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STABLE ISOTOPE DIAGRAMS OF FRESHWATER FOOD WEBS

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Stable carbon and nitrogen isotopes are valuable tracers in ecological research (Rundel et al. 1988). One use of isotope measurements is to rapidly survey how

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organic matter is cycled in different ecosystems. For example, a few measurements of isotopic compositions of dissolved nutrients, aquatic plants, and animals establish a chemical outline of food web structure (Fry and Sherr 1984, Minagawa and Wada 1984). These tracer results can be used to check conventional ideas about trophic structure in well-studied systems, and to test how food web structure varies in other systems where conventional visual studies of trophic relations are difficult or lacking (Rau 1980). A dual-isotope approach is often useful in these studies, for example, with nitrogen isotope measurements functioning as trophic level indicators, and carbon isotope measurements indicating which plants are important sources of nutrition for consumers (Peterson and Fry 1987).

Ecologists from Long Term Ecological Research (LTER) sites in the United States and Puerto Rico recently used isotope analysis to test ideas about aquatic food-web structure and terrestrial nitrogen cycling. This note reports an overview of the food-web results discussed at a workshop in September 1989, and includes a $\delta^{15}N$ survey of terrestrial materials that contribute to freshwater food webs as allochthonous organic matter. A list of isotopic analyses from each site is available.[2]

Study Areas

Samples for studies of food webs were collected from streams (sites 1, 3, 8, and 17, Fig. 1) and lakes (sites 1, 10, and 16). To determine generality of $\delta^{15}N$ values in plants and soils, samples were also collected at several sites in forests (sites 2, 9, 12, 15, 16, and 17), grasslands and deserts (sites 4, 5, and 7), at a coastal dune site (site 14), and at a high-altitude tundra site (site 6).

Methods

Soils, plant leaf material, plant litter, and whole animals or muscle tissue from fish were collected in the summer of 1989, dried at 60°C, and ground to fine powders. Most samples were composites of >5 individual samples. Samples were combusted at 750°C overnight (soils) or 900°C for 1 h (plants, animals) in evacuated sealed Vycor high temperature glass tubes (Corning Glass, Corning, New York) containing 1 g of CuO and 0.5 g Cu metal (Minagawa et al. 1984). Sample sizes were typically 5 mg for animals, 15 mg for plants, and 50–1000 mg for soils. To obtain accurate $\delta^{15}N$ values, it was necessary to grind soils, but not plant or animal samples, with CuO prior to combustion.

Combustion gases were cryogenically separated and pure CO_2 and N_2 measured for carbon and nitrogen isotope values with a Finnigan 251 stable isotope ratio mass spectrometer. Molecular sieve (0.5 nm, Alltech Associates, Deerfield, Illinois) was used during collection and transfer of N_2 gas between vacuum preparation lines and the mass spectrometer. Replicates usually fell within a 0.2‰ range for both carbon and nitrogen isotope measurements; an increased range often resulted if samples had not been finely ground to a flour-like consistency.

[2] See ESA Supplementary Publication Service Document No. 9102 for 32 pages of supplementary material. This document is available on microfiche or in printed form. For a copy of this document, contact the author or order from The Ecological Society of America, 328 East State Street, Ithaca, New York 14850-4318 USA.

$\delta^{13}C$ and $\delta^{15}N$ values are reported relative to carbon in the Peedee belemnite (PDB) limestone and nitrogen in air, respectively, in parts per thousand (‰).

$$\delta^{13}C \text{ or } \delta^{15}N = \left[\frac{R_{sample} - R_{standard}}{R_{standard}} \right] \times 10^3, \text{ and}$$
$$R = {}^{13}C/{}^{12}C \text{ or } {}^{15}N/{}^{14}N.$$

High-purity tank carbon dioxide and nitrogen gases were used as working standards during sample analysis. These working standards had been calibrated against National Bureau of Standards (NBS) isotope standards NBS-20 limestone and NBS-21 graphite for $\delta^{13}C$, atmospheric nitrogen and N-1 ammonium sulfate for $\delta^{15}N$ (Coplen et al. 1983, Mariotti 1983, Minagawa et al. 1984, Nevins et al. 1985). PDB and nitrogen in air have by definition δ values of 0‰; samples enriched in ^{13}C or ^{15}N are "heavy" and have higher $\delta^{13}C$ and $\delta^{15}N$ values, while samples enriched in ^{12}C and ^{14}N have lower δ values.

Food Webs

Nitrogen isotopic compositions of plants and various types of animal consumers showed remarkable similarity in eight lake and stream sites sampled (Fig. 2). Plants had lowest $\delta^{15}N$ values of typically −4 to +3‰, and $\delta^{15}N$ values of aquatic and terrestrial plants were generally similar (Fig. 2). A broad analysis of plants and soil fractions showed that $\delta^{15}N$ values of terrestrial materials at the lake and stream sites were fairly typical and could be expected to occur at most other LTER sites where streams and lakes were often present, but not sampled (Figs. 2 and 3). Plants and soils in these relatively undisturbed LTER sites also had generally lower $\delta^{15}N$ values than previously analyzed agricultural plants and soils of North America (Feigin et al. 1974, Shearer et al. 1978). Only samples from arid sites 4 and 5 had higher average $\delta^{15}N$ values similar to those found in agricultural sites (Fig. 3).

Animals from LTER lakes and streams had higher $\delta^{15}N$ values than did plants, and animal $\delta^{15}N$ values increased with increasing trophic level (Fig. 2). There was an average $\delta^{15}N$ increase of 2–3‰ per trophic level (Fig. 2), and at all sites top predators, such as smallmouth bass and giant salamanders, had highest values (up to 9‰ higher than algae at the base of the food web). Using the assumption of a 3.3‰ increase in $\delta^{15}N$ per trophic level (Minagawa and Wada 1984), the $\delta^{15}N$ results indicate that there are 2.5–3.5 trophic levels in all stream and lake ecosystems (Fig. 2).

The estimate of 2.5–3.5 trophic levels agrees fairly well with estimates of trophic complexity in other freshwater and marine ecosystems (Macko and Estep 1984, Minagawa and Wada 1984, Estep and Vigg 1985, Fry 1988), although stable isotope studies have not yet

FIG. 1. Sampling sites in the Long Term Ecological Research (LTER) Program. (1) Arctic Tundra (Alaska), (2) Bonanza Creek Experimental Forest (Alaska), (3) H. J. Andrews Experimental Forest (Oregon), (4) Jornada (New Mexico), (5) Sevilleta (New Mexico), (6) Niwot Ridge/Green Lakes Valley (Colorado), (7) Central Plains Experimental Range (Colorado), (8) Konza Prairie (Kansas), (9) Cedar Creek Natural History Area (Minnesota), (10) North Temperate Lakes (Wisconsin), (11) W. K. Kellogg Biological Station (Michigan), (12) Coweeta Hydrologic Laboratory (North Carolina), (13) North Inlet (South Carolina), (14) Virginia Coast Reserve (Virginia), (15) Harvard Forest (Massachusetts), (16) Hubbard Brook Experimental Forest (New Hampshire), (17) Luquillo Experimental Forest (Puerto Rico).

adequately characterized possible important microbial links in aquatic food webs. Initial studies show that uptake and metabolism of nitrogen by bacteria can affect $\delta^{15}N$ values of nutrients available to plants and of detrital foods (Zieman et al. 1984, Cifuentes et al. 1988). The observation that $\delta^{15}N$ distributions are similar across a variety of sites probably indicates relatively uniform isotopic compositions of nitrogen sources and patterns of nitrogen isotopic fractionation in these fairly undisturbed freshwater systems.

Isotopic fractionation across trophic levels is much smaller for carbon isotopes (0–1‰ per trophic level, Fry and Sherr 1984), and $\delta^{13}C$ measurements primarily indicate which plant sources of carbon are important to consumers in food webs, rather than indicating trophic level. The overall survey of sites showed that terrestrial and aquatic plants that could provide carbon to consumers in food webs had broad and overlapping $\delta^{13}C$ ranges (ranges for terrestrial C_3 plants and aquatic algae were -35 to $-25‰$ and -34 to $-18‰$, respectively). This overlap occurred at only some of the sites, however, and at four of the eight sites $\delta^{13}C$ measurements were useful tools for examining plant sources of carbon to the food web. For example, at a northwest Pacific stream site consumer $\delta^{13}C$ values more closely

matched algal values than values of terrestrial vegetation, suggesting an important role of the attached stream algae in supplying carbon to consumers (Fig. 4). In an interesting contrast, consumer values did not closely match those of attached algae (epilithiphyton) in an arctic lake. There, phytoplankton and terrestrial detritus appeared most important (Fig. 4), perhaps because of the greater importance of plankton in large lakes.

Several types of freshwater sites appear favorable for $\delta^{13}C$ food-web studies because possible sources of plant carbon—aquatic algae and terrestrial plant detritus—have distinctly different $\delta^{13}C$ values. Favorable sites included streams in rain forests where terrestrial plants had low $\delta^{13}C$ values (-32 to $-35‰$ in this study, Wickman 1952), lakes where benthic metabolism contributed strongly to the dissolved CO_2 pool and plankton had low $\delta^{13}C$ values ($-37‰$ in this study, Rau 1980, Araujo-Lima et al. 1986), and some lakes and streams where attached algae had high $\delta^{13}C$ values (-15 to $-22‰$ in this study, Osmond et al. 1981, LaZerte and Szalados 1982). Other studies have also successfully used $\delta^{13}C$ measurements to study the importance of attached algae in streams and springs for consumers (Rounick and Winterbourn 1986). Combining $\delta^{13}C$ and
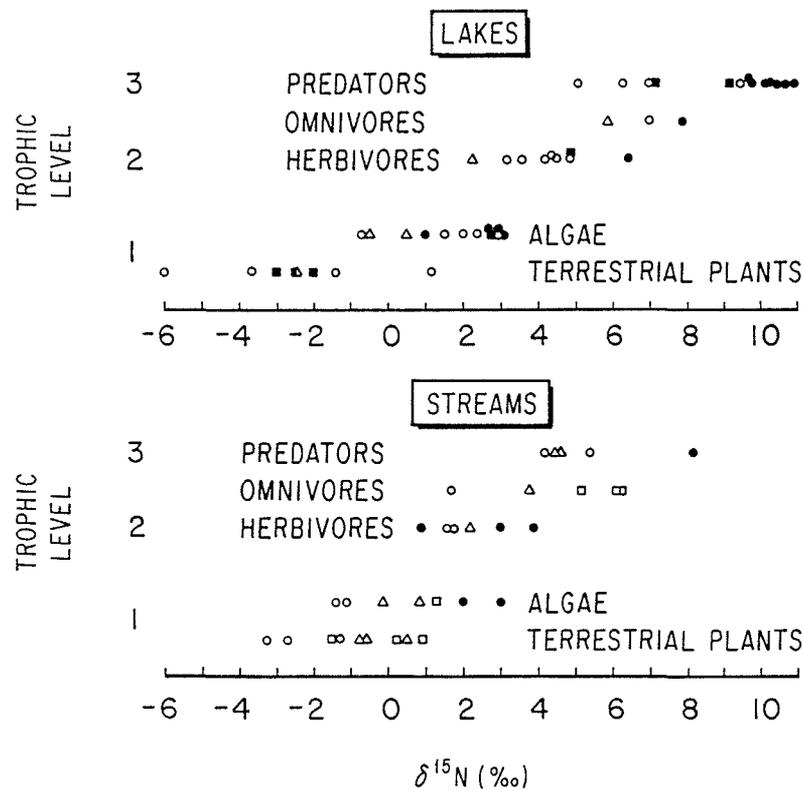
FIG. 2. $\delta^{15}N$ values of biota from lakes and streams at the LTER sites shown in Fig. 1. Trophic-level classifications are rough estimates made by workshop participants. Key to lake symbols: O = site 16, Mirror Lake; △ = site 10, Crystal Bog; ■ = site 10, Trout Lake; ● = site 1, Toolik Lake. Key to stream symbols: O = site 3, Lower Lookout Creek; △ = site 8, ephemeral creek; □ = site 17, shady forest stream; ● = site 1, Kuparuk River.

$\delta^{15}N$ studies appears to be a quick, increasingly inexpensive way to obtain a chemical outline of food web structure that can be used to check conventional ideas about the trophodynamics of natural systems.
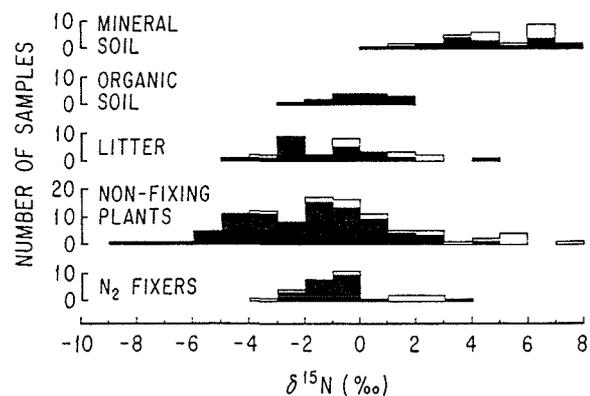
FIG. 3. $\delta^{15}N$ values of plants, litter, and soils from LTER sites 2, 3, 4, 5, 6, 7, 8, 9, 10, 12, 13, 14, 15, 16, and 17 shown in Fig. 1. Samples from deserts and arid grasslands (sites 4 and 5) shown in light boxes often had high $\delta^{15}N$ values; mesquite (*Prosopis*) and saltbrush (*Atriplex*) had highest values among N_2 fixers and non-fixers, respectively.
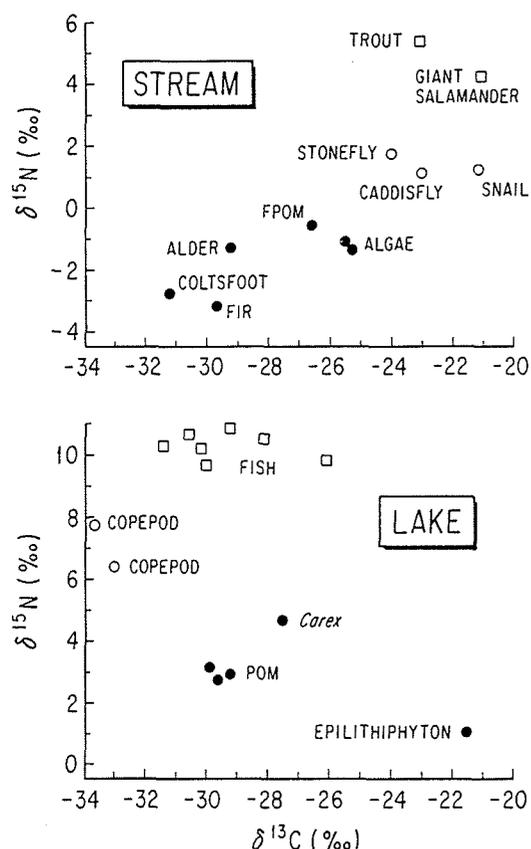
FIG. 4.   Stable isotope diagrams of a stream food web (site 3: Lower Lookout Creek, Oregon) and a lake food web (site 1: Toolik Lake, Alaska) community.

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