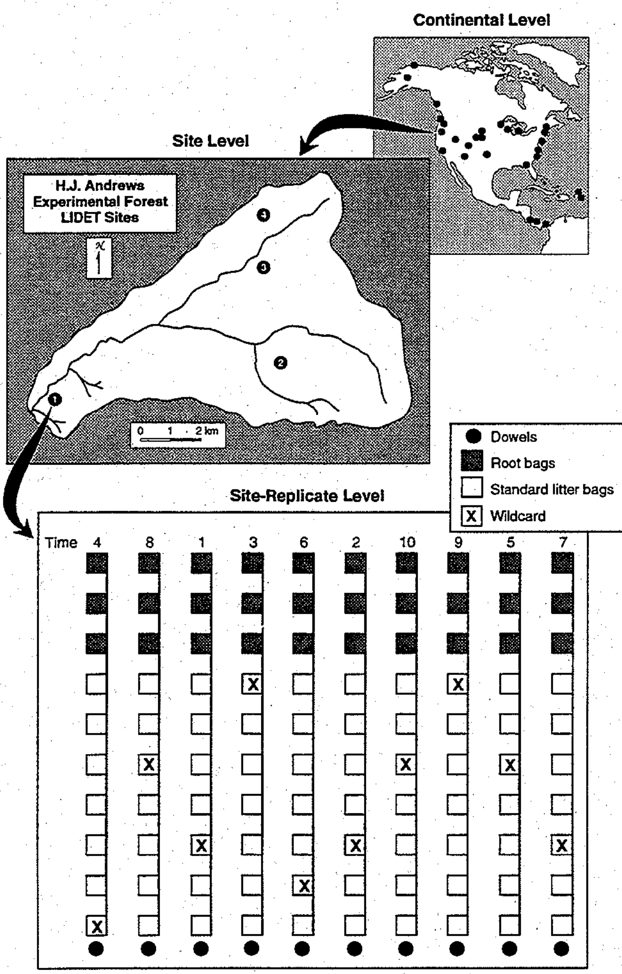

MEETING *the* CHALLENGE *of* LONG-TERM, BROAD-SCALE ECOLOGICAL EXPERIMENTS

by the

Long-Term Intersite

Decomposition Experiment Team

(LIDET)

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LTER

U.S. LTER Network Office
University of Washington
College of Forest Resources
Box 352100
Seattle, WA 98195-2100

Phone: 206-543-4853
Fax: 206-543-7295
E-mail: *Office@LTErnet.edu*

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MEETING *the* CHALLENGE *of* LONG-TERM, BROAD-SCALE ECOLOGICAL EXPERIMENTS

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(LIDET)

October 1995

PREFACE

*Long-Term Intersite Decomposition Experiment Team (LIDET) 1995**

Understanding ecological systems on the global scale will require an increase in preplanned, long-term, multisite studies. We describe an example of this type of research—a 10-year, 28-site experiment to test the effect of substrate quality and macroclimate on long-term decomposition and nutrient dynamics.

Over the last decade, it has become increasingly clear that human activities are altering ecological processes on a global scale (Clark and Holling 1985, International Geosphere-Biosphere Programme 1990). Few processes appear to be immune to human influence. Climate, the chemical composition of precipitation, rates of nutrient cycling, decomposition, and production: all appear to be affected by the combination of land-use change, resource utilization, and industrial emissions (Ojima et al. 1991, Lubchenco et al. 1991). Comprehensive understanding of how ecological systems will respond to these broad-scale changes poses a great challenge to ecologists (Levin 1992), in part because of the way ecology traditionally has been studied. The typical single-investigator, small-scale studies may not be sufficient to provide the required regional and global perspective. An alternative approach, presented here, involves a broad-scale, multi-site, multi-investigator study.

The success of the ecological community in meeting the challenges raised by research on global change depends on at least three factors. First, interesting ideas or hypotheses are essential to attract investigators. Second, increased funding will be required in order to conduct many of the measurements needed. Finally, scientists separated by long distances must be able to communicate and coordinate activities if they are to produce comprehensive tests of hypotheses. We wish to address these logistical factors in this report, drawing from five years of experience as a broad-scale, multi-investigator team examining long-term decomposition dynamics. We feel that our experience provides an example of how such studies can be conducted successfully.

*Names and affiliations of LIDET members are provided in Table I.

Acknowledgments

This research was funded in part by grants from the National Science Foundation Ecosystems Studies and LTER programs (BSR-8805390, BSR-9108329). This publication is Paper 2964 of the Forest Research Laboratory, Oregon State University. We wish to thank all the site participants, without whom this project would not be possible.

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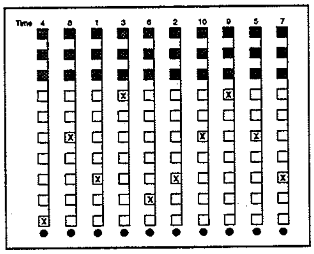
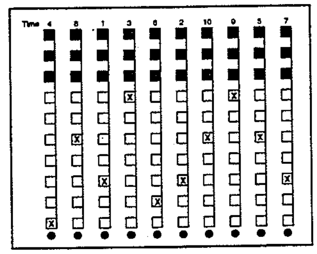


SYNTHESIS BEFORE, NOT AFTER, THE FACT

The foundation of traditional ecological research has been individuals or small teams of investigators working within a limited spatial and temporal framework. Periodically, results have been synthesized in review articles (e.g., Vogt et al. 1986) or as larger-scale efforts, such as the global carbon budget (e.g., Houghton et al. 1983).

If ecologists cooperated by minimizing methodological differences and using a planned distribution of sites, the usual problems with broader-scale projects could be avoided

These types of syntheses require very different information from that required for individual studies. In a review article, one is free to accept certain methodological and geographical disparities in search of an overall pattern that may be a qualitative, but useful, description of the system being examined. In broader-scale quantitative efforts, however, methodological and geographical disparities may severely limit the outcome. This problem is exacerbated by pressures from peers, funding sources, and publication requirements to produce unique studies. Furthermore, the tendency for investigators to work near home has resulted in a preponderance of fine-scale, temperate-zone studies. We feel these problems could be avoided if, instead of going separate ways, ecologists cooperated on broader-scale projects by minimizing methodological differences and using a planned distribution of sites. One example of such an approach is the National Atmospheric Deposition Program (NADP), a network of 200 precipitation-monitoring sites, all operating voluntarily to provide a nationwide picture of precipitation chemistry (NADP 1993). Small independent studies will always be needed, but we suggest that this should not be the only mode of research. Here, we describe another example of the alternative, broad-scale approach.

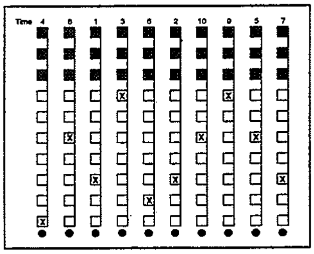


UNDERSTANDING LONG-TERM DECOMPOSITION PROCESSES

Decay of plant material in an ecosystem can be thought of as a continuum from fresh plant litter to the formation of refractory soil organic matter. The early stages of this continuum have been intensively studied over the past two decades in both laboratory studies lasting weeks to months and field studies lasting one to two years (Melillo et al. 1984, Olson 1963, Swift et al. 1979, Vogt et al. 1986). Our knowledge of the latter stages of the decay continuum is much poorer (Melillo et al. 1989). We know little about the patterns of change of the various carbon fractions and nutrient pools in litter during the later stages of decay or about the factors that control them. Those studies that have been long-term (e.g., Aber at al. 1990, Berg and Staaf 1981, Berg et al. 1984, Edmonds 1984, Lousier and Parkinson 1978) are limited geographically; thus, results might be explained by specific local conditions, rather than underlying general controls that would be expressed over large spatial areas.

We know little about the patterns of change of the various carbon fractions and nutrient pools in litter during the later stages of decay or about the factors that control them

A workshop at Woods Hole Marine Biological Laboratory in May 1989, sponsored by the National Science Foundation, was one of the first extensive attempts to address this major imbalance between short- and long-term decomposition studies. Participants agreed overwhelmingly that long-term intersite experiments would be required before general and site-specific patterns could be separated. Therefore, such an experiment was planned at this workshop. The experiment was designed to test the degree to which substrate quality and climate control the carbon and nitrogen dynamics of decomposing leaf, wood, and fine-root litter over a 10-year period.

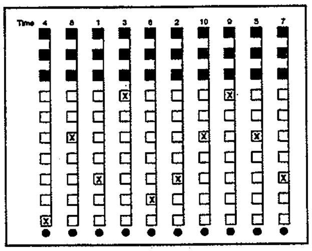


LONG-TERM PROCESSES

The decision to focus on substrate quality and macroclimate was possible because individuals recognized the greater value in a joint project with common measurements at all sites

During the workshop, it became apparent that the proposed project would be more likely to succeed if certain methodological and logistical considerations and investigator interactions were addressed explicitly. Participants felt that it was not sufficient simply to agree to conduct independent long-term decomposition studies and assemble the results in 10 years; undertaking the project as a team would yield much greater dividends. Differences in methodology were relatively easy to standardize, because generally accepted methods already existed. Logistical problems were more difficult to solve, but the infrastructure at sites participating in the Long-Term Ecological Research (LTER) Program funded by the National Science Foundation (17 of the 28 sites; Table I) provided local resources that minimized costs. Other recent infrastructural developments, such as an electronic mail network connecting most of the sites, have greatly reduced communication problems.

By far the most challenging problems involved the interactions of the scientists themselves. In our opinion, the success of most broad-scale research lies in effectively addressing such issues as personal rewards, individual versus group perspectives, and long-term stability. For example, decomposition and nitrogen dynamics of fine litter are complicated processes controlled by many factors, including substrate quality (Fogel and Cromack 1977, Howard and Howard 1974, Melillo et al. 1982, Minderman 1968), size (Swift et al. 1979), decomposer species (Heath et al. 1964, Kurcheva 1960, Witkamp and Olson 1963) edaphic conditions (McClaugherty et al. 1985), and climate (Bunnell and Tait 1977, Bunnell et al. 1977, Jansson and Berg 1985, Meentenmeyer 1978). At the Woods Hole workshop, it was decided that all factors could not be tested simultaneously; yet this excluded some investigators' areas of interest. The decision of the group to focus on substrate quality and macroclimate was possible only because individuals recognized the greater value in a joint project



LIDET SITE COLLABORATORS

Site/Task	Location	Team Member	Key No.†
*Arctic Tundra	Alaska	Jim Laundre	1
*Bonanza Creek Experimental Forest	Alaska	Keith Van Cleve	2
Juneau	Alaska	Paul Alaback	3
Olympic National Park	Washington	Robert Edmonds	4
*H.J. Andrews Experimental Forest	Oregon	Mark Harmon	5
Blodgett Research Forest	California	Steve Hart	6
Santa Margarita Ecological Reserve	California	James Reynolds	7
Curley Valley	Utah	James MacMahon	8
*Sevilleta National Wildlife Refuge	New Mexico	Carl White	9
*Jornada Experimental Range	New Mexico	Walter Whitford	10
*Central Plains Experimental Range	Colorado	Indy Burke	11
*Niwot Ridge/Green Lakes Valley	Colorado	Marilyn Walker	12
Loch Vale Watershed	Colorado	Jill Baron	13
*Konza Prairie Research Natural Area	Kansas	Tim Seastedt	14
*Cedar Creek Natural History Area	Minnesota	Dave Wedin	15
*North Temperate Lakes	Wisconsin	Tom Gower	16
*Kellogg Biological Station	Michigan	Eldor Paul	17
*Coweeta Hydrological Laboratory	North Carolina	Barry Clinton	18
*Hubbard Brook Experimental Forest	New Hampshire	Tim Fahey	19
*Harvard Forest	Massachusetts	Jerry Melillo	20
*Virginia Coast Reserve	Virginia	Linda Blum	21
North Inlet (Hobcaw Barony)	South Carolina	Jim Morris	22
University of Florida	Florida	Henry Gholz	23
*Luquillo Experimental Forest	Puerto Rico	Jean Lodge	24
Guanica State Forest	Puerto Rico	Ariel Lugo	25
Monte Verde	Costa Rica	Nalini Nadkarni	26
La Selva Biological Station	Costa Rica	Phil Sollins	27
Barro Colorado Island	Panama	Joseph Wright	28

Table I. Members of the Long-Term Intersite Decomposition Experiment Team (LIDET), their sites or affiliations, and their responsibilities in the long-term leaf and fine-root experiment.

*Long-Term Ecological Research site. †Key numbers relate to Figure 1.

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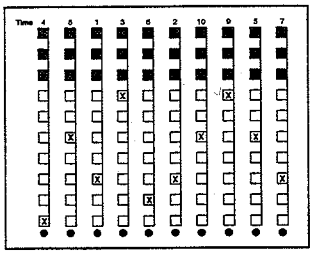


Table I. *Continued*

CENTRAL ANALYSIS		
Data Management	Oregon State University	Mark Harmon
NIR Analysis	Oregon State University	Mark Harmon
Wet Chemical Analysis	Oregon State University	Mark Harmon
MODELING		
CENTURY	Colorado State University	William Parton
GEM	Woods Hole, MA	Edward Rastetter
GENDEC	Texas Tech University	Daryl Moorhead
DODMOD	University of New Hampshire	John Aber

that had common measurements at all the sites. Other crucial investigator-related issues that were addressed included 1) clearly defining the role of the project participants, 2) developing an equitable strategy for publication credit, and 3) balancing standardization and central control against needs of individual sites.

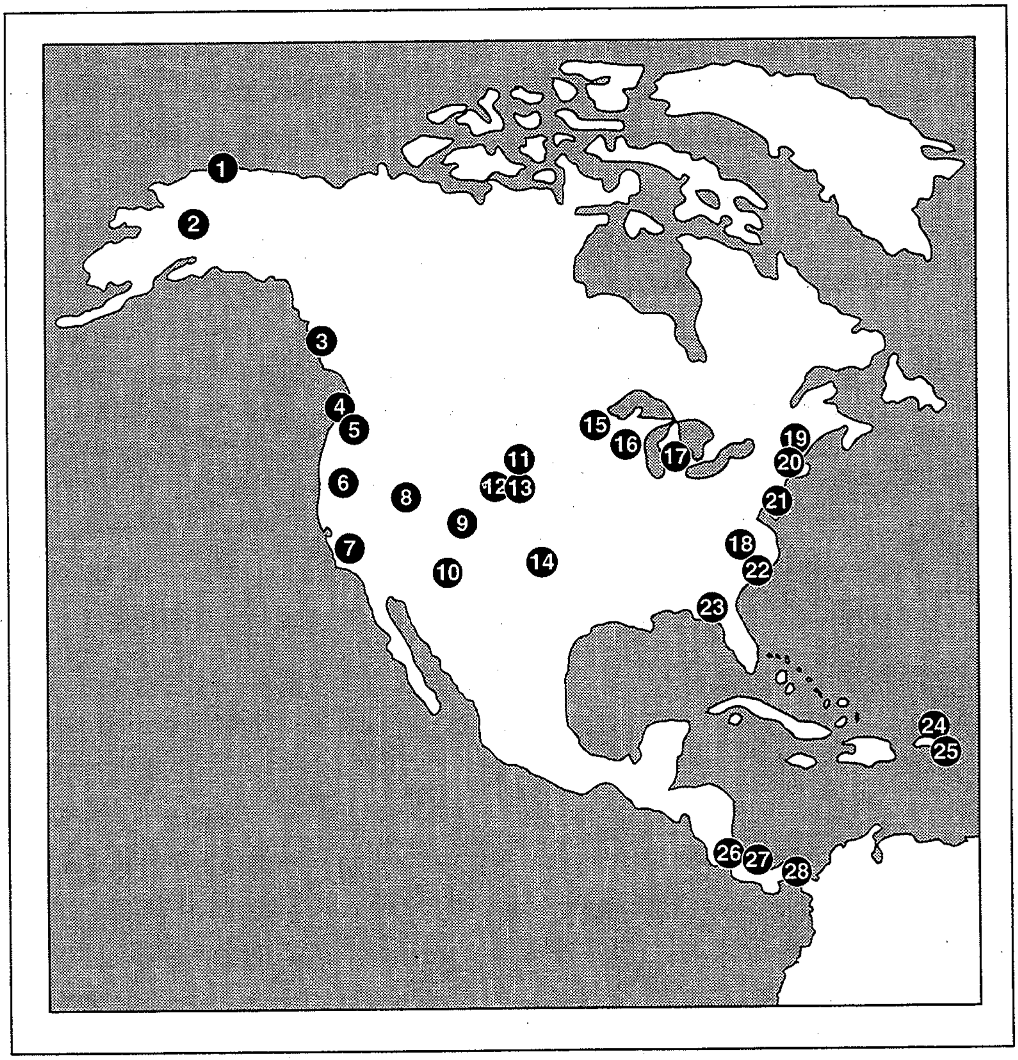
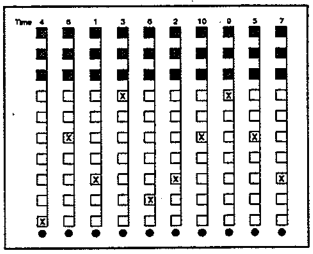


Figure 1. Location of the sites being used in long-term leaf and fine root litter experiments. The numbers correspond to the key numbers in Table I.



FORMATION OF LIDET

Explicit definition of the roles and expectations of the participants was achieved by forming a group of 35 individuals, the Long-Term Intersite Decomposition Experiment Team (LIDET), to conduct the field studies and publish the results (Table I).

LIDET is divided into three subgroups:

◆ *Field Collaborators*, whose responsibilities are to place and remove litterbags and to provide necessary background information on climate, soils, and vegetation. Each site has one collaborating investigator who is responsible for managing the project on the site level.

◆ *Central Analysis Group*, whose responsibilities include chemical analysis, data management, and preliminary data analysis.

◆ *Modelers*, whose main tasks are to synthesize mechanisms controlling C and N dynamics and to use the results of field studies to test the hypothetical controls used in the models.

Data and credit are shared according to the following guidelines. Each site annually receives a current, proofed copy of the data from that site. Site investigators then have one year in which to prepare site-specific manuscripts, usually to be published under individual names. After one year, the data become available for intersite syntheses to be published under joint LIDET authorship and for model parameterization and testing.

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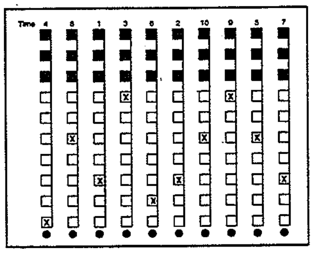


STUDY DESCRIPTION

The LIDET experiment is designed to test the effects of substrate quality and macroclimate on long-term decomposition and nutrient release dynamics of fine litter. Although other factors, such as the decomposer biota, may also influence these long-term dynamics, we felt that substrate quality and macroclimate would explain the largest proportion of the variation and would be the easiest to extrapolate geographically. The role of the decomposer biota is tested indirectly by the LIDET experiment, however, as a result of using non-native litter. If there is a large interaction between substrate quality and decomposer biota, then one would expect to see "outlier species" that decompose faster or slower than generally expected at the sites on the basis of substrate quality and macroclimate alone.

The LIDET decomposition experiments have been installed at 28 sites that span a wide array of ecosystems, from moist tundra to warm desert to shortgrass steppe to moist and dry tropical forest (Table I, Figure 1). Annual precipitation across the sites ranges from 230 to 4000 mm year^{-1}, and mean annual air temperature ranges from -7 to 26°C (Figure 2). Although many sites differ markedly in annual precipitation and mean temperature, others are

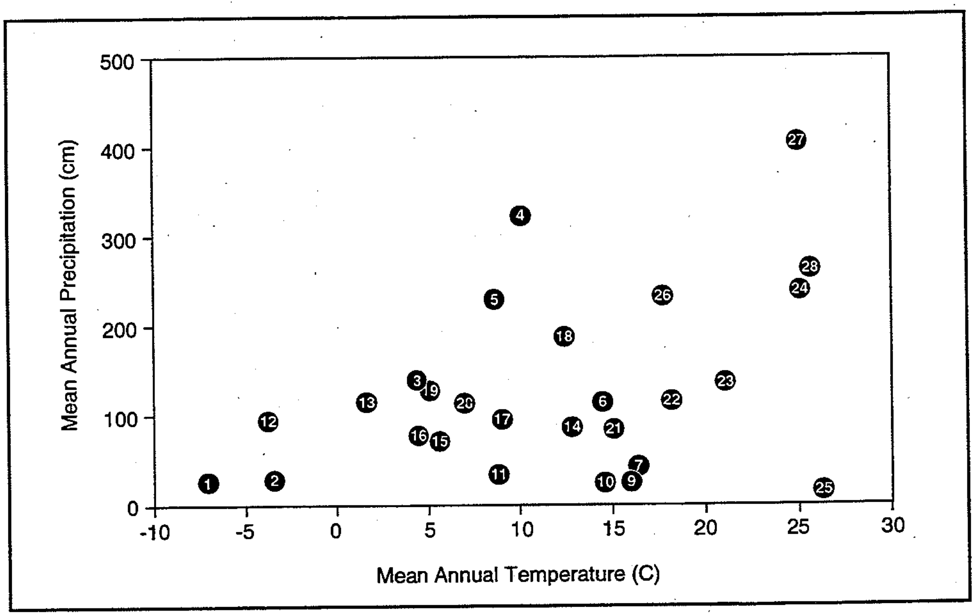
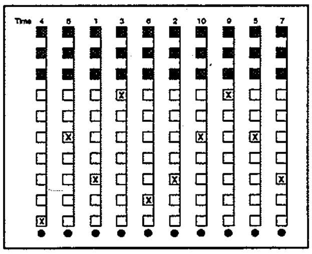


Figure 2. Mean annual temperature and precipitation of the sites used in the long-term leaf and fine root litter experiments. The numbers correspond to the key numbers in Table I.



distinguishable only by differences in their seasonal dynamics. The Konza (Kansas) and Andrews (Oregon) sites, for example, have identical abiotic decomposition indices (Parton et al. 1987)* but distinctly different precipitation patterns, with more winter rainfall at Andrews and more summer rainfall at Konza.

The experiment was set up as shown in Figure 3. Each site received 10 types of litter: nine "standard" litters and a "wildcard." The standard litters included three types of fine roots—graminoid, hardwood, and conifer—and six types of leaf litter, ranging in lignin/nitrogen ratio from 6 to 43 (Table II and Figure 4); all wildcard samples were leaf litter. In addition to leaves and

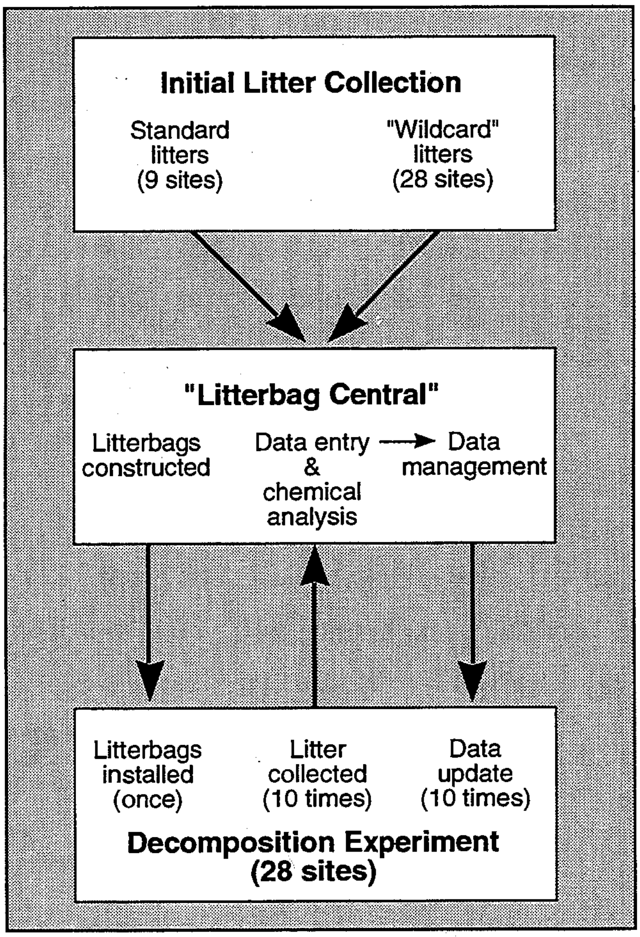
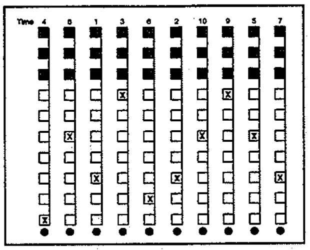


Figure 3. Flow of information and materials in the Long-Term Intersite Decomposition Experiment Team (LIDET) project.

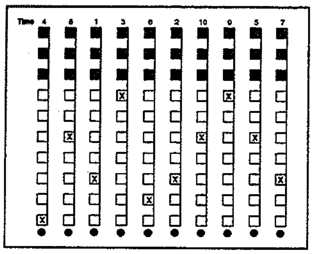
*The abiotic decomposition index reflects the annual potential rate of decomposition as controlled by the combined effects of moisture and temperature.



SPECIES USED IN LIDET PROJECT

Species	Common Name	Litter Type	Site-Source
Abies concolor	White fir	Leaves	6
Abies lasiocarpa	Subalpine fir	Leaves	13
Acer saccharum	Sugar maple	Leaves	19
Ammophia breviligulata	Beach grass	Leaves	21
Andropogon gerardii	Big blue stem	Leaves	14
Schizachyrium scoparium	Little blue stem	Leaves	15
Betula lutea	Yellow birch	Leaves	20
Boutloua eriopoda	Black gramma	Leaves	9
Boutloua gracilis	Blue gramma	Leaves	11
Ceanothus greggii		Leaves	7
Cornus nuttallii	Pacific dogwood	Leaves	5
Drypetes glauca		Leaves, roots	24
Fagus grandifolia	Beech	Leaves	19
Gonystylus bancanus	Ramin	Dowel	5
Gymnanthes lucida		Leaves	25
Kobresia myosuroides		Leaves	12
Larrea tridentata	Creosote bush	Leaves	10
Liriodendron tulipifera	Yellow-poplar	Leaves	18
Myrica cerifer	Wax myrtle	Leaves	21
Pinus elliottii	Slash pine	Leaves, roots	23
Pinus resinosa	Red pine	Leaves, roots	20
Pinus strobus	Eastern white pine	Leaves	16
Populus tremuloides	Aspen	Leaves	2
Pseudotsuga menziesii	Douglas-fir	Leaves	4
Quercus prinus	Chestnut oak	Leaves	18
Spartina alternifolia	Salt water cordgrass	Leaves	22
Thuja plicata	Western redcedar	Leaves	5
Triticum aestivum	Wheat	Leaves	17
Vochysia ferragenea		Leaves	27

Table II. Species used in the Long-Term Intersite Decomposition Experiment Team (LIDET) project. See Table I for the key number identifying litter sources.



roots, each site received wooden dowels so that decomposition rates of wood above and below ground could be compared.

The litter and fine roots used as standards were collected from nine of the sites for redistribution to all 28 sites. Collections of the standard litters were under the direction of the individual site collaborators, as were collections of wildcard samples. The wildcard species are an example of a creative solution to the conflicts that can arise between individual and group demands. At first, all the site representatives wished to have a species—or, in some cases, five or six species—from their site included in the standard set of litters to be sent to all sites. However, a 28-species, 28-site experiment was unworkable. As an alternative, we decided that one species from each site would be included, but that it would be sampled at only one of the 28 sites at each sampling time. Since the location of this litter at each sample time was selected at random, this became known as the "wildcard species." The results from the wildcard species verify

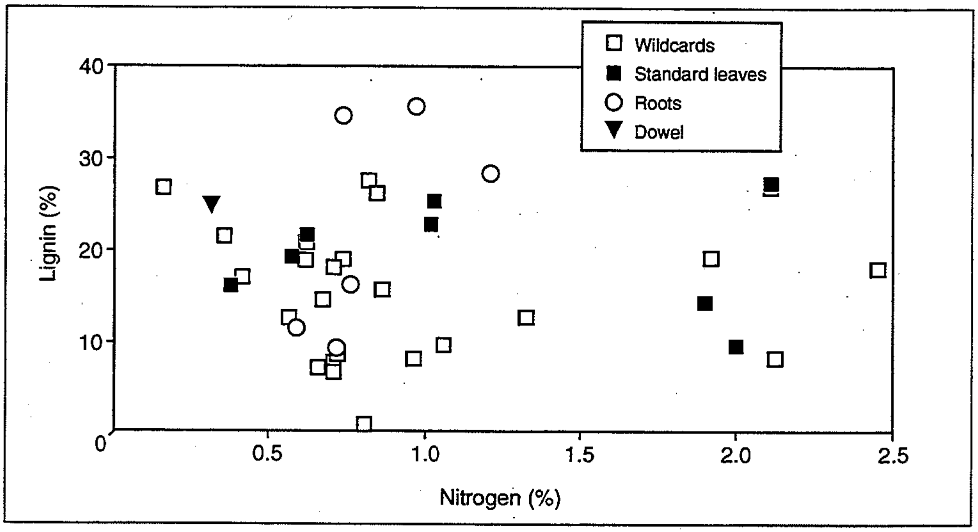
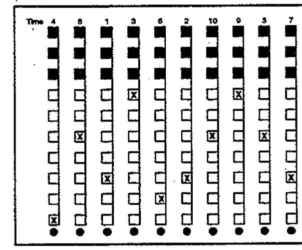


Figure 4. Initial lignin and nitrogen concentrations of leaf and fine roots being used in the long-term leaf and fine root litter experiments.

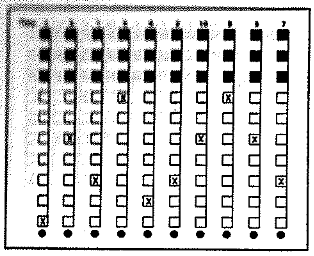


those from the standard species and tests for interactions between substrate quality and decomposer biota. Some of the wild-card species may decompose faster or slower than the standard species, indicating a preference for or avoidance of certain litter types. Thus, a useful compromise also improved the science.

The leaf litter was usually collected directly from senescent leaves or as freshly fallen litter. Fine roots (<2 mm diameter) were collected by excavating surface roots and washing. After the litter had been collected and air-dried, it was shipped to Oregon State University. There the litterbags were filled, sorted, and sent to each of the 28 sites (Figure 5). All bags were 20-by-20 cm and filled with 10 g of leaves or 5 g of fine roots. Leaf litterbags were made of two materials: a 1-mm nylon mesh top and a dacron cloth bottom. The cloth bottom, although not usually used in short-term litterbag studies, was used in our study to catch the fine particulate matter created by extensive, long-term decomposition. The fine-root litterbags were made completely of dacron cloth. The litter added to the bags was air-dried; subsamples were taken for measurement of the initial moisture content and estimation of the initial oven-dry weight. Dowels were placed so that half of each dowel was above ground and half was below. Dowels were 1 cm in diameter, 60 cm long, and composed of *Gonystylus bancanus*, a non-decay-resistant tropical tree species. Samples were placed in the field in 1990 and 1991 during the autumn stage of phenology at each site.

Collaborators at the individual sites were responsible for collecting, oven-drying, weighing, and sending samples for chemical analysis, data entry, and long-term storage

Samples are to be retrieved each year for 10 years, with four replicates for each species, site, and time. Exceptions to this include the tropical and subtropical sites (Barro Colorado Island, Guanica State Forest, La Selva Biological Station, and Monte Verde) where samples will be collected at three- to six-month intervals. Collaborators at the individual sites were responsible for



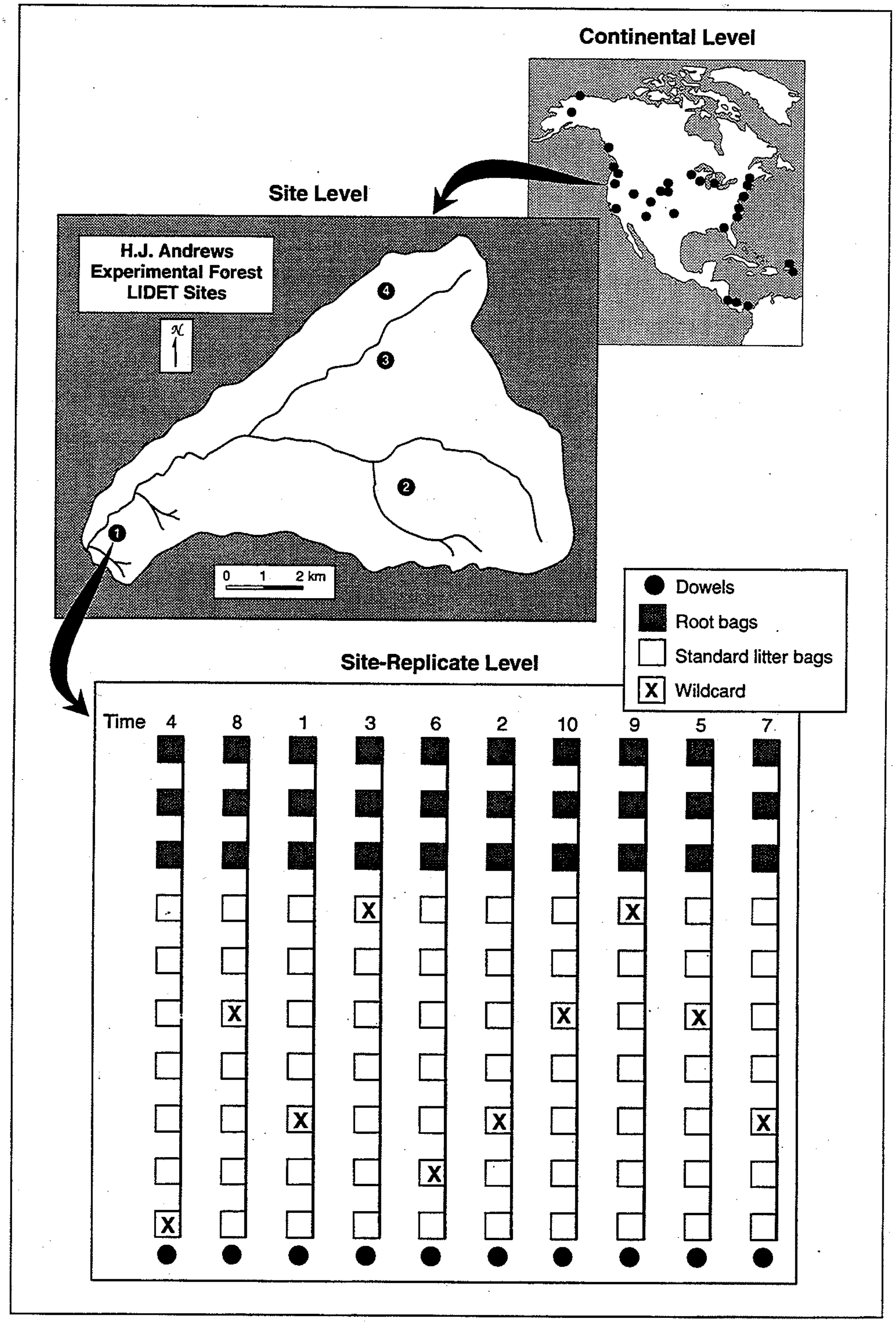
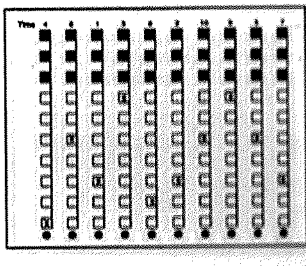


Figure 5. Geographical distribution of samples at continental, example site, and site-replicate levels.

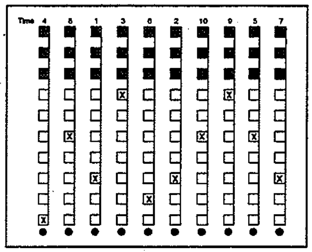


collecting, oven-drying, weighing, and sending samples to Oregon State University for chemical analysis, data entry, and long-term storage. Detailed instructions were sent to all the participants to insure methods as uniform as possible.

Total nitrogen, lignin, and cellulose in samples from each species, site, and time will be analyzed by near-infrared reflectance (NIR) spectroscopy (McClellan et al. 1991, Wessman et al. 1988a). This nondestructive sampling method is based on reflectance in the 700- to 2500-nm region of the spectrum. This method there was has potential for use in measuring litter quality over a large area from earth orbit (Wessman et al. 1988b). Determination of chemical composition by NIR is based on calibration against microKjeldahl digestion for nitrogen and proximate analysis of carbon fractions (McClaugherty et al. 1985, Ryan et al. 1990). As these are only a few of the potential chemical analyses that could be performed, samples will be stored in vials labeled with the species site, and date of the sample. In order to increase the likelihood that these samples will be analyzed for other parameters in the future, a computer-accessible catalog will be maintained.

Although many decomposition models have performed well for limited conditions, the question remains of whether or not they can predict long-term dynamics over a wide range of macroclimates and litter qualities. The field experiments described above present an excellent data base to assess such models. In LIDET, we are examining four process models (CENTURY, GEM, GENDEC, and DOCMOD) that represent a range of structures and assumptions. CENTURY, for example, is a general ecosystem model that simulates plant production, soil organic matter dynamics, and nutrient cycling for grasslands, crops, and forest systems on a monthly time-step (Parton et al. 1987, 1989). In con-

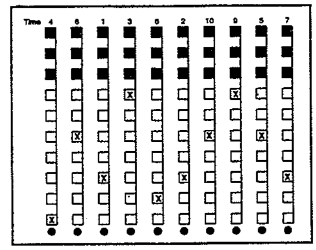
In LIDET, we are examining four process models that represent a range of structures and assumptions



trast, GENDEC is solely a decomposition model developed to examine the interactions between buried litter, decomposer organisms, and C and N pools in the northern Chihuahuan Desert on a daily time-step (Moorhead and Reynolds, 1991). Like CENTURY, GEM (Generic Ecosystem Model) is a process-based, biogeochemical model with a monthly time step (Rastetter et al. 1991). It differs, however, in that detrital pools are aggregated into extractives, cellulose, lignin, and humus pools regardless of the original source, whereas CENTURY has above- and below-ground non-woody and woody pools. As the predictions of these models are independent of the field data, the tests will reveal which structures and assumptions are most general and therefore applicable to broader-scale questions.

The tests will reveal which structures and assumptions are most general and therefore applicable to broader-scale questions

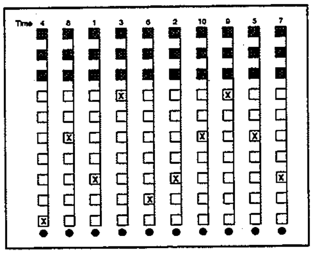
In 1995, we began the fifth year of litterbag collections in the project. Site representatives have received the first two years of data and are comparing LIDET results to past and current decomposition experiments at their sites. The modeling subgroup is predicting first-year decomposition rates and nitrogen dynamics of a low and a high quality litter at four sites representing the environmental extremes for the first two years of the study. Finally, we are about to begin analysis of the entire data set for the first four years of the study.



CONCLUSIONS

Answering the challenges of global change research requires an understanding of ecosystem behavior over greater temporal and spatial scales than have been examined in the past. Several solutions to this problem are possible. Synthesis of past results from individual fine-scale studies is critical, but uneven geographic distributions, study durations, and methodological incompatibilities all limit the scientific value of the outcome. An alternative is designing group or team experiments, such as LIDET, that can be carried out simultaneously at many sites. In addition to standardizing methods and predetermining spatial and temporal limits, this approach benefits the individual sites involved by placing the results from individual sites in a larger context, allowing general access to novel analytical methods (e.g., NIR), and creating a greater sense of participation in research on global change.

Team experiments that can be carried out simultaneously at many sites may help us to understand ecosystem behavior over greater temporal and spatial scales



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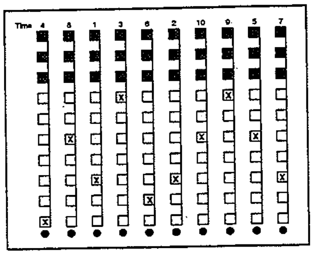

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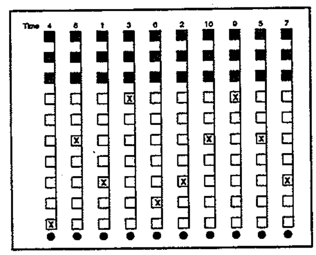

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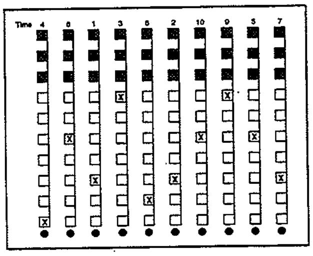

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U.S. LTER Network Office
University of Washington
Box 352100
Seattle, WA 98195-2100
USA

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PH: 206-543-4853
FAX: 206-685-7295
E-mail: *Office@LTERnet.edu*

LTER

U.S. LTER Network Office
University of Washington
College of Forest Resources
Box 352100
Seattle, WA 98195-2100
USA

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