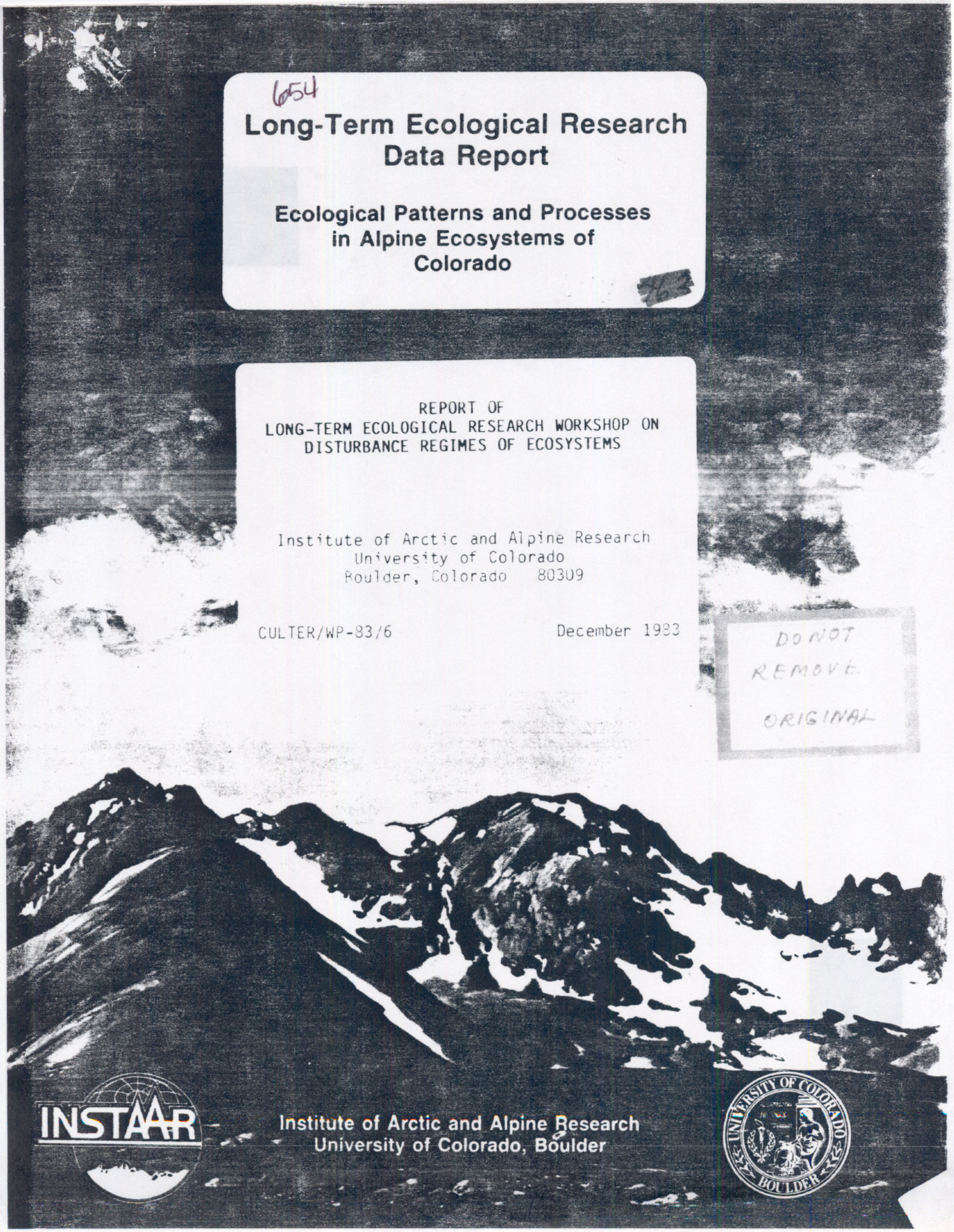

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Long-Term Ecological Research Data Report

Ecological Patterns and Processes in Alpine Ecosystems of Colorado

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REPORT OF
LONG-TERM ECOLOGICAL RESEARCH WORKSHOP ON
DISTURBANCE REGIMES OF ECOSYSTEMS

Institute of Arctic and Alpine Research
University of Colorado
Boulder, Colorado 80309

CULTER/WP-83/6 December 1983

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Report of
Long-Term Ecological Research Workshop On
Disturbance Regimes of Ecosystems

Mountain Research Station

Institute of Arctic and Alpine Research

University of Colorado

April 29-30, 1983

Nel Caine and Fred Swanson

Co-organizers, Co-editors of report

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SUMMARY

This report summarizes discussions conducted at the LTER Workshop on Disturbance Regimes held at the Mountain Research Station of the University of Colorado on April 29-30, 1983. Discussions centered on four themes:

Definition of Disturbance. This topic lead to spirited discussion, but no simple consensus. Whether or not an environmental change is called a disturbance depends on the parameter of ecosystem response under consideration and the frequency and predictability of environmental change in relation to life history characteristics of the organisms involved.

Disturbance Regimes at Individual LTER Sites. Participants from each of the nine sites represented reviewed environmental perturbations at their sites on time scales ranging from 10^{-2} to 10^{8} years. In several cases spatial dimensions of disturbances were also considered on scales ranging from 10^{-4} to 10^{15} m^2. Response variables included geomorphic features, vegetation, and communities of aquatic organisms.

Comparison among Sites. Comparison of disturbance effects is occurring among several LTER sites based mainly on themes dealing with experimental manipulations by burning and other mechanisms. Other themes for intersite comparisons discussed at the workshop include those based on paleoecology, dendrochronology, climatic fluctuations, experimental manipulations, successional patterns, terrestrial-aquatic interactions, magnitude-frequency analysis, and a variety of anthropic influences. Several of these topics offer excellent opportunities for future comparative efforts among groups of sites.

Administrative and Study Design Considerations. Logistical and funding factors affect the ability of LTER groups to capitalize on research opportunities presented by major disturbances. An approach used at least at one site is an experimental design that can yield useful results without a major disturbance, but occurrence of such an event will permit another set of hypotheses to be addressed. Another site has prepared to respond to disturbances by practicing mobilizing the people and equipment necessary for studying effects of unpredicted chemical spills. Budgetary contingencies should be considered at the levels of individual sites, the Intersite Coordination Committee, and NSF. The issue has not arisen yet, but with 11 sites in the program, each experiencing a variety of disturbances, major events of 25+ year return period are likely to occur within the network of sites every few years.

Discussions at the workshop set the stage for a variety of intersite comparisons of disturbance regimes and effects.

INTRODUCTION

This report is a summary of the discussions conducted at the LTER Workshop on Disturbance Regimes held at the Mountain Research Station of the University of Colorado on April 29 and 30, 1983. Scientists from eight LTER sites in the U.S. and the La Selva forest site in Costa Rica participated in the workshop (Table 1). Most of the participants wrote sections of the report which have been compiled with little editing in accord with the overall workshop objective of getting ideas "out on the table" for discussion.

At the outset, the workshop had four objectives:

1. To initiate communication among LTER sites on the problem of defining and sampling disturbance regimes.
2. To develop strategies for future information exchange.
3. To develop strategies for intersite comparisons.
4. To search for common conceptual and administrative approaches to the study of disturbance.

By bringing together scientists from a variety of sites and enabling them to interact, the workshop achieved these objectives on the informal level which facilitates further exchanges between researchers and sites. In order to make progress on any of these objectives, it was necessary to begin by scoping out the disturbance characteristics of each site and what past, on-going, and potential research activities exist. The progress of the workshop, summarized in this report, is not intended as a comprehensive review of disturbance ecology; it is clearly biased by the experience of workshop participants and by the sites on which they are working.

The report consists of four sections. It commences with an attempt to define disturbance and disturbance regime in a way which might be useful to the wide variety of LTER sites and studies. A second section reviews disturbance regimes on the LTER sites. The main part of the report is a discussion of common elements and common approaches that are being used or could be used in the study of disturbance on the LTER sites. Finally, the report concludes with some suggestions for further work of an inter-site nature concerning disturbance in LTER studies.

Table 1. Participants at LTER Workshop on Disturbance Regions Mountain Research Station, University of Colorado, April 28-30, 1983.

Nel Caine	Niwot Ridge/Green Lakes Valley
Julie Denslow	La Selva
Tom Frost	Northern Lakes
Jeroen Gerritsen	Okefenokee National Wildlife Refuge
David Gross	Illinois and Upper Mississippi Rivers
Jim King	Illinois and Upper Mississippi Rivers
Vera Komarkova	Niwot Ridge/Green Lakes Valley
Bill Laycock	Central Plains Experimental Range
Ron Neilson	Jornado Experimental Range
Al Swain	Northern Lakes
Fred Swanson	H. J. Andrews Experimental Forest
John Tester	Cedar Creek National History Area
Patrick Webber	Niwot Ridge/Green Lakes Valley

DEFINITION OF DISTURBANCE REGIME

Representatives of each site brought to the workshop a summary of the disturbance regime of their site (Appendix I). These summary tables were organized by frequency of disturbance events in time scales ranging from 10^{-2} to 10^{8} years.

Most participants identified as "disturbances" those episodic, perhaps catastrophic, events with return periods of decades to centuries. In these cases there can be death of individuals and/or creation of new opportunities for establishment. More frequent, regular events may be part of the day-to-day, season-to-season workings of the ecosystem. Physiological responses of organisms are tuned to the occurrence of events on this time scale, and the physical triggers for biological change are not considered in the "destructive" sense of disturbance. Very long-term changes at the scale of 10^{3}-10^{4} years involve whole shifts in ecosystem position on the landscape and are usually examined by paleoecological methods. Ecologists may view such changes not so much as working within an ecosystem, but more as causing shifts of ecosystem locations on the landscape.

On some scales disturbance events are relatively simple to define. The eruption of a volcano and concomitant wholesale destruction of aboveground biota is easily identified as a disturbance. Landslides and earthquakes are also routinely characterized as exogeneous. Fire is another large magnitude event which is usually classed as a disturbance. However, fires can vary in their impact, in some cases wiping out all of the organisms in an area but in other instances affecting only some portion of the biota. Fires cannot be simply defined as exogeneous, because they are the result of climatic conditions, an initiating event, and the fuel produced by the vegetation itself (White 1979). Vegetation differs in its flammability and fire frequency and fuel loading may be closely related. Thus, fire magnitude and frequency is controlled in large part by endogeneous factors.

In some ecosystems events which open space or cause major shifts in species abundance occur on smaller spatial scales than volcanic eruptions, landslides, and fires. Systems such as rain forests and coral reefs experience formation of small patches by collapse of one or a few individuals or colonies of species (Connell 1978). Gap formation by tree fall in rain forests and the subsequent growth of different species in the opening may be the primary mechanism by which shifts occur in canopy species. Such tree falls are not necessarily associated with a major windstorm and seem to be primarily a function of the biota itself--a partially endogeneous event.

Similarly, events with a high frequency may have a major impact on species composition in some ecosystems. The annual turnover of freshwater lakes causes major changes in water chemistry and consequently in phytoplankton and zooplankton populations. Seasonal succession in the plankton is analogous to the changes that occur in some terrestrial communities after an event such as a fire. However, the timescale is completely different. A terrestrial analog would be a system dominated by annuals where community composition at any time would be determined by timing of intraannual climatic events.

Species introductions which cause large scale changes in ecosystems are distinctly biological disturbances. Some introductions cause the loss of one species from an ecosystem (e.g. Dutch Elm Disease); others trigger radical shifts in the assemblage of species in an ecosystem [e.g. Peacock Bass in Gatun Lake, Panama (Zaret and Paine 1973)]. Yet other species introductions, which have a relatively minor impact, may not be recognized as an ecosystem-level disturbance.

Some disturbances are not pulse events but affect an ecosystem over a protracted period. Drought for example, may kill organisms directly or might have indirect effects, such as altering physiology and increasing susceptibility to predation, disease, or fire.

Different species within an ecosystem may be primarily affected by events which vary in frequency and spatial impact. In a forest where annual plants respond to a yearly cycle, species composition may respond to fires with a frequency of fifty years. Fish usually live more than one year and respond only indirectly to the major seasonal shifts in other aquatic communities. Ecosystems, therefore, contain groups of species which are responding to a variety of events that are nested within each other in their impact and return frequency. At one extreme, some organisms respond to diel fluctuations. Individuals of other species persist through daily and annual events but are affected by rarer, more dramatic events.

It is also important to note that some disturbances change the impact or frequency of others. Drought, for example, may increase the severity and frequency of fire. Shifts in climate appear to affect the elevation of tree line in a complex manner with a lag response, because adult trees may persist under conditions that are much less than optimal for their growth. However, seedling establishment may not occur under conditions that permit suboptimal growth of adults. If a fire or landslide removes adults from an area after a climate shift, reestablishment in an area may not lead to the same type of community that was removed.

Table 2 lists events on two scales, representing a range of situations that may be considered as disturbances. On the high magnitude extremes of each scale there are events which would be considered universally as ecosystem level disturbances (e.g. a volcanic eruption). Similarly, low magnitude events would not be defined as disturbances. Problems arise in defining a disturbance between these extremes, i.e. within the matrix of possibilities in Table 2. An ecologist who works in a forest where a major fire occurs every 100 to 200 years would not consider an occasional tree fall as an important ecosystem level disturbance. One working in a rain forest, however, would list gap formation due to tree fall as of primary importance. A major question lies in considering how widespread an event must be in its impact before it is recognized as an ecosystem level disturbance rather than as part of some normal suite of events occurring in an ecosystem. A related question is the frequency and predictability of an event.

As illustrated in Table 2, it is possible to consider disturbance as any event or set of events, other than self-generated senescence, that leads to the demise of an organism. However, such an inclusive definition of disturbances provides little basis for comparing disturbance regimes between ecosystems.

Table 2. Examples of disturbances arrayed by (1) biological level of effects on organisms and species and (2) spatial scale described in units of organism size; but which could also be shown in direct physical units (cm^2, m^2, etc.).

Biological Level of Effect	Spatial Scale			
	sub-organism	1 organism	1-^{2} organisms	10^2+ organisms
Physiology	light flecks, leaves	wind stress	water table fluctuations	drought
damage to part of an organism	branch fall	leaf cutters	tent caterpillars	gypsy moths
mortality of an individual organism		lightning strike	tree fall, gap formation	
removal of a species		fungal attack	sprucebud worm	Dutch Elm Disease
removal of some subset of the organisms in an area			gopher mound formation	turbidity in a lake
removal of the biota from an area			bottom ice formation	fire, volcanic eruptions

Tom Frost suggested some simplifying divisions within the range of events in Table 2 that provide a perspective on disturbances that can be considered at an ecosystem level. There are two perspectives from which to consider events that remove organisms from an area. First, disturbances lead to the mortality of organisms. On the other hand, the same disturbances create opportunities for establishment or growth of other individual organisms. Thus, space can be opened literally (e.g. in gap formation) or in a biological sense (e.g. winterkill events in lakes selectively removing some fish species and releasing others from competition and predation). The space opening approach avoids problems involving events that remove part of an organism without killing it; a branch falling from a tree may open substantial space without the death of the tree itself. A space-opening perspective also eliminates some problems in the distinctions between biological and physical events. Patch formation, whether due to branch fall or through the activities of leaf cutters, leads to the same physical opening of space through two different mechanisms.

Accepting that "disturbances are space opening events", it is necessary to consider:

1. a measure of the size of space that is opened,
2. the frequency of an event that opens space,
3. the time required to open a space,
4. the rate at which open spaces are closed,
5. the group of organisms (grouped on trophic or physiognomic level) which should be examined.

As a practical consideration, it is useful to focus on actual physical space opening events for cross-ecosystem comparisons. For physical occurrences it is possible to describe a number of different events that open space and lump them on a scale of the extent in square meters of their effect. Having identified events on a spatial scale it is possible to determine their frequency.

Identifying a time scale of a disturbance and the ecosystem response to it is a critical consideration, though one that must, for practical purposes, be somewhat arbitrary. A drought may occur for several years before it has an impact on the composition of the main structural components of an ecosystem. Also the consequences of a drought may vary depending upon the occurrence of other events such as fires or pest outbreaks. This raises the further complication of the need to consider interactions among successive disturbances of the same or different types. Focusing on events which act relatively quickly, e.g. treefall rather than drought, may facilitate comparisons between ecosystems.

Finally, space-opening events may only be defined for particular groups within the biota of an ecosystem. The same event may have radically different effects on different subgroups within the biota (e.g. shrub versus canopy species in forests). The uppermost stratum of producers, such as the canopy in forest ecosystems, is a useful level for cross-ecosystem comparisons.

From this perspective, an ecosystem level disturbance can be defined as an event which opens some area in an ecosystem with a definable recurrence. A space opening event alters the rate of slower biological processes (growth, competition, senescence).

DISTURBANCE REGIMES AT INDIVIDUAL LTER SITES

To begin the discussions about disturbances in ecosystems, LTER site representatives briefly described the characteristics of their site and presented tables summarizing types of disturbance events and their geomorphic and ecological effects on a broad range of time scales (Appendix 1). Spatial scales of disturbances were included for some sites and these showed a positive correlation between time and space dimensions (Fig. 1). On log-log coordinates, this plot is very similar to that of organism size and generation time (Bonner 1965: Fig. 2).

These tables are very useful in identifying common conditions across many sites and distinctive characteristics of individual and small groups of sites. Common to many sites are a set of exogenous influences including diel and annual temperature and precipitation patterns, infrequent droughts and floods, climatic change on time scales of the Holocene and Pleistocene. Fire is a significant factor at half a dozen sites, windthrow gaps at three, and sea level change at two. Four sites were glaciated and all sites experienced a marked environmental change at the start of the Holocene, which is frequently thought to set the age of the ecosystem at a site.

These disturbances appear to have a range of degrees to which they are exogenous (White 1979). Climate change at the scale of glacial and interglacial periods is a phenomenon operating on the same real-time basis at all sites. Fire frequency, on the other hand, may respond to climate change (Swain 1978), but also strongly reflects endogenous factors such as fuel loading and flamability, so we observe differences in fire frequency between sites.

Many of the disturbance regime tables describe human influences. Anthropic disturbances include (1) chronic, pervasive types, e.g. acid rain (Cedar Creek and others) and persistent grazing; (2) "one-shot", site-specific events, e.g. logging (Cedar Creek), brief period of heavy grazing (Jornada), plowing (Shortgrass Prairie); (3) periodic phenomena, e.g. logging (H. J. Andrews), slash-and-burn agriculture (LaSelva), turbidity due to barge traffic (Illinois River); (4) random introduction of exotic compounds, e.g. chemical spills (Illinois River); (5) reduction of natural disturbance, e.g. damming to reduce peak water flows and maximize low water volumes (Illinois River, Okefenokee), elimination of buffalo (Konza), fire suppression (Coweeta, H. J. Andrews, etc.), engineering controls of channel positions (Illinois River). Most of the imposed, anthropic disturbance regimes are substantially different from the natural disturbance regime in terms of type, frequency, intensity, and areal extent. A site such as the H. J. Andrews Forest and adjacent forest lands managed for timber production probably comes closest to having a managed disturbance regime (clearcutting and burning on 100 yr rotation) that mimics the natural, yet even there the two are quite different. All sites have some degree of anthropic alteration of disturbance regime, though it may be as subtle as fire suppression over a period as yet much shorter than the natural fire rotation period.

Figure 1. Disturbance frequency and area relationship, data points from Niwot (O), Jornada (X), Cedar Creek (Δ).

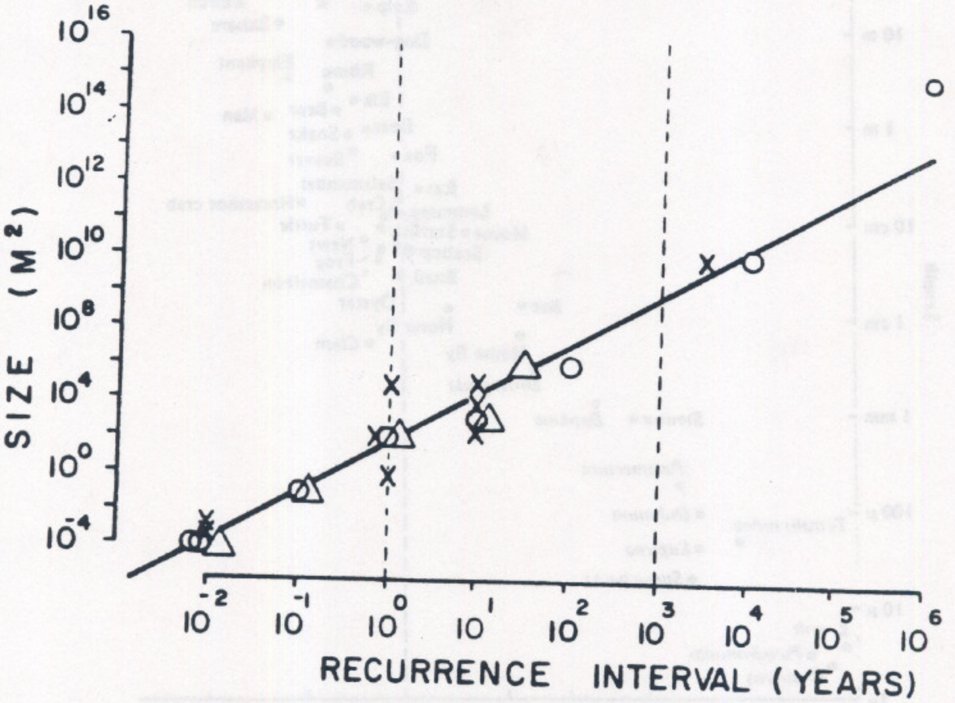
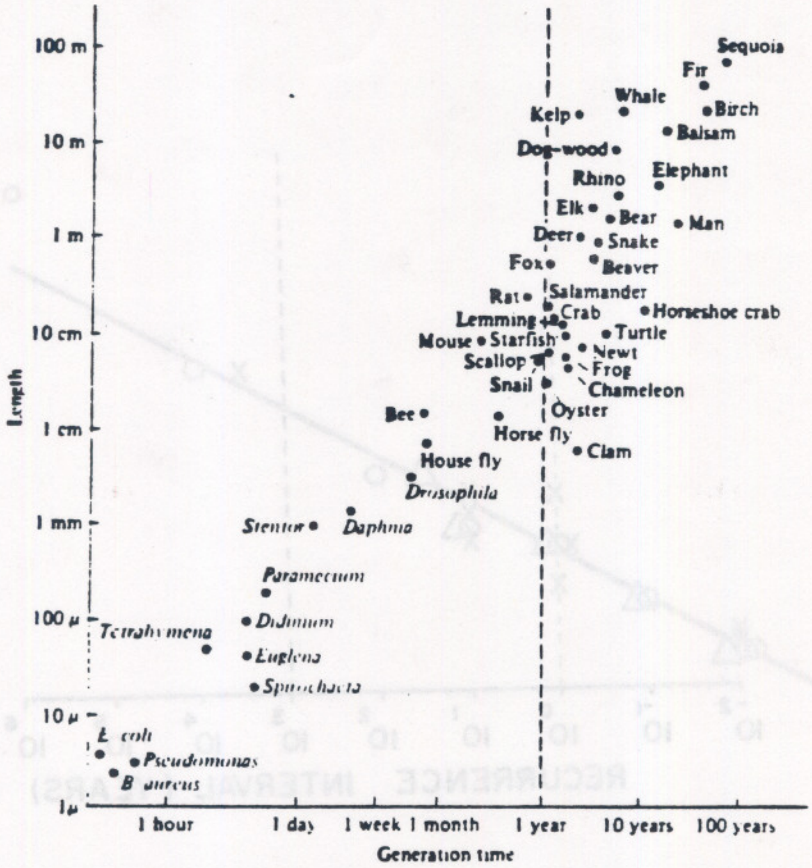


Figure 2. Relationship between organism size (length) and generation time (from Bonner 1965).



COMPARISON OF DISTURBANCE REGIMES AMONG LTER SITES

The relative importance of different disturbances within individual sites or across groups of sites depends on the magnitude of exogenous driving factors and the response characteristics of the ecosystem. Consequently when workshop participants listed primary and secondary natural disturbances for sites represented there emerged a broad range of types and frequencies of major disturbances dominated by precipitation extremes, fire, and wind (Table 3, Appendix I). This in part reflects the tremendous diversity of ecosystems represented (Table 4). Human influences are even more varied in type and frequency, ranging from current activity of scientists to logging and grazing nearly a century ago.

Also listed are estimated life expectencies of dominant species. This reflects some discussion, limited by time constraints, of a possible correlation between this parameter and frequency of primary natural disturbances. (Pat Webber pursued some related ideas further in Figures 1 and 2.)

A listing of probable periods during which the ecosystems have persisted as roughly the same type reveals a marked convergence at about 10,000 years. Landform change caused by deglaciation, associated outwash, and changes in sea level and the establishment of an interglacial climate appear to have set the stage for development of the modern ecosystem at most LTER sites.

Paleoecological Studies as a Basis for Intersite Comparisons

Studies of the past flora and fauna provide the primary means of assessing the impacts of contemporary environmental disturbance. Changes in the physical environment are quickly manifest in the biotic community and in the steadily accumulating fossil record. Palynological studies are perhaps the primary method of determining paleoecological history and most applicable for studies of climatic perturbations. Fossil pollen records provide a regional history of species change on the order of hundreds to thousands of years. Studies of shorter duration (tens to hundreds of years) environmental fluctuations that affect tree growth, but not species replacement, are frequently addressed by dendrochronology, the study of tree-rings. For time scales shorter than 100 years, the historic or instrument record provides a direct measure of disturbance. These records can usually be used to provide a check on paleoecological records. Stratigraphic correlations are useful in understanding cycles of river alluviation, glacial events and major geologic phenomena.

As each LTER site has experienced environmental perturbations in the past, each should make an attempt to understand its own Quaternary history. Events large enough to alter entire ecosystems are climate induced and such events will continue to occur in the future as critical climatic thresholds are crossed and species compositions altered. To this end, workshops on individual aspects of ecosystem disturbance discussed in this workshop would be productive. They might best be organized as the fossil record is organized, chronologically and taxonomically. Chronological evidence divides easily into four

Table 3--Disturbance characteristics of LTER sites represented at workshops

	Disturbance				
	Natural				
	Primary	Secondary	Human	Life Expectancy of Long-lived Individuals of the Dominant Species	Period of Ecosystem at site (yr)
Illinois River	Precip-flood (50-100 yr)	Sedimentation	Agriculture	5d aquatic 100 yr aquatic plants	15,000 (glaciation)
Wisconsin Lakes	Turnover (1 yr)	Ice (1yr)	Logging (one-shot, 80-90 yr ago)	5-10d plankton 3-20 yr fish	10,000 (glaciation)
Wisconsin Forest	Fire (100 yr)	Wind	Logging (one-shot, 80-90 yr ago)	100-300 yr	10,000 (glaciation)
Cedar Creek Savanah	Fire (10 yr)	Drought	Agriculture (one-shot) Logging (one-shot)	100 yr	10,000 (glaciation)
Jornada Desert	Wet-dry periods (10-50 yr)	Climate change (10^2-10^4 yr)	Grazing (late 1800's to early 1900's)	100 yr (?) (creosote bush)	10,000
Shortgrass Prairie	Drought (50 yr)	High intensity precipitation	Plowing (1+ yr)	100 yr (blue grama)	10,000 (glacial outwash)
Niwot Ridge Alpine	Big summer storms (100 yr)	Heavy snow years (30-50 yr)	Scientists, recreationists	10-100's yr	10,000 (glaciation)
Okefenokee Swamp	Hydrol. extremes (50+ yr)	Fire	Logging (one-shot)	5-10d aquatic 600 yr cypress	6,000
LaSelva Forest	Windgaps (100 yr)	Flooding	Slash-and-burn agriculture	200 yr?	?
H. J. Andrews Forest	Fire (200+ yr)	Major storms (50+ yr)	Logging (80-120 yr)	800 yr	10,000 (?)

Table 4--Types of ecosystems represented by LTER sites where research is underway (X) or there is a potential for research (P)

	Aquatic		Terrestrial	
	Standing	Flowing	Grass	Forest
Illinois River	X	X		P (flood plain)
Wisconsin Lakes	X	P		P
Cedar Creek Savanah	P	P	X	X
Jornada Desert	P (playa)		X (desert shrub)	
Shortgrass Prairie			X	
Niwot Ridge Alpine	P	X	X (tundra)	P
Okefenokee Swamp	X (swamp)	X	X (marsh)	
LaSelva Forest		P		X
Coweeta Forest		X		X
H. J. Andrews Forest		X		X
Konza Prairie		X	X	P
North Inlet Estuary		X	X (marsh)	P

categories: the instrument record (< 100 years), the dendrochronological record (< 200 to 1000 years), the pollen record (< 2000 years), and the geological and pollen record (> 2000 years). Within these chronological categories, the effects of environmental disturbance and change in taxonomic groups can be assessed.

Detailed pollen and charcoal records are planned for the Northern Lakes site to extend the fire history record based on tree rings back for at least 1000 years. Similar studies underway at the H. J. Andrews Forest may provide a point for comparison between these two conifer forest types with substantially different fire return periods.

Dendrochronological Studies as a Basis for Intersite Comparison

Tree ring chronologies provide accurate records of environmental disturbances (e.g., logging, fire, and climate variations) on time-scales of one year to centuries. At least four LTER sites are using or are planning to use dendrochronology as part of their research programs. Preliminary fire-scar chronologies are available from H. J. Andrews and Northern Lakes sites. In one or two years, when these records are complete, investigators from these two sites expect to compare fire chronologies and possibly maps showing the relationship of topography and fire boundaries. Similar results from other areas such as the Boundary Water Canoe Area (Heinselman 1973) and Mt. Rainier National Park (Hemstrom and Franklin 1982) may also be included in this analysis. Tree-ring studies are planned for the floodplains of the Illinois and Mississippi Rivers to reconstruct past flood histories. Tree-ring studies also underway at Niwot Ridge will aid in determination of recent migrations of tree line.

Climate Considerations in Intersite Comparisons

Disturbances with a return frequency of less than 100 years and particularly those with a frequency of less than 20 years can be analyzed directly from the meteorological and biological records. However, return frequencies defined on this time scale are highly variable, e.g. an order of magnitude of change in fire frequency in Wisconsin forests from the "Little Ice Age" to the present (A. M. Swain, personal communication). The frequency of these relatively high frequency events appears to be, in itself, a function of whether the globe is in a long-term (centuries) warming or cooling trend. This is primarily because upper air flow patterns tend to be more meridional and resonant during global cooling trends (Dzerdzeevskij, 1968; Reitan, 1979, Reiter, 1979).

Although each LTER site is sensitive to its own particular suite of disturbances, e.g. fire, drought, wind, etc., these can usually be related to some specific extreme variation from the average meteorological regime. In recent years meteorologists from around the globe have been coordinating efforts to understand the causes of these unusual meteorological disturbances (Hecht and Imbrie, 1979). One of the primary results of these studies is that major climatic fluctuations observed at any point on the globe are usually one manifestation of the global shift in the atmospheric fluid dynamics (Angell and Korshover, 1978b; Kanamitsu and Krishnamurti, 1978; Namias, 1980).

One of the most highly documented examples of such a climatic variation is the weather regime over the North American continent during the years 1975 through 1978 (Angell and Korshover, 1978a; Diaz and Quayle, 1978; Namias, 1978; Namias, 1979; Paegle *et al.* 1979). The winters of 1975-1976 and 1976-1977 were characterized by extreme drought in the southwest, while the winter of 1976-1977 was characterized by extreme cold and above average snowfall over the eastern half of the United States. The subsequent winter of 1977-1978 was extremely wet across most of the continent. These anomalies corresponded to a shift in the upper air long-wave pattern from mostly zonal to mostly meridional. In turn, the atmospheric shifts are related to sea-surface temperature anomalies which produced a persistent El Nino (Namias, 1978). El Nino (the failure of the Anchovy fishery off the west coast of South America) is typically associated with the "Southern Oscillation". However, these anomalies were also related to a global climatic "pulse" as demonstrated by the largest observed expansion (4% above average) and displacement of the northern circumpolar vortex (Angell and Korshover, 1978a). Variations in sea surface temperatures and the circumpolar vortex have also been implicated in record-setting weather patterns for the same years in the Mediterranean Region (Perry, 1981). Also, the topography of the main thermocline of the northwestern Sargasso Sea with attendant shifts in the gulf stream have been described for this period (Leetmaa, 1977).

The particular events described above likely had some effect on all LTER sites, through drought, flood, prolonged cold, heat or some other manifestation of these global circulation anomalies. In reconstructing climatic variation since 1602, Fritts *et al.* (1979) singled out the winter of 1976-1977 as one among several useful signals in the pattern of climatic variation. The average frequency of "1976-1977" winters was 0.178 yr^{-1} for the 377 year period, but ranged from 0.574 yr^{-1} during 1615-1655 to 0.0 yr^{-1} during 1667-1720 (Fritts *et al*, 1979). Fire frequency also varied with climatic change during the "Little Ice Age" (A. M. Swain, personal communication) as a result of a shifting community composition and possibly lightning frequency (Schaefer, 1957). Virtually all of the major disturbance types affecting the LTER sites can or have been related to upper atmospheric dynamics (e.g. Starrett, 1949; Schaefer, 1957). Unusual weather, i.e., disturbance generating weather, typically appears to be related to global resonance of a strongly meridional polar jet stream (Kanamitsu and Krishnamurti, 1978; Tung and Lindzen, 1979a,b; Tung, 1979; Namias, 1980). It is no coincidence that the Big Thompson (1976) and Rapid City (1972) flash floods occurred in two such years (Maddox *et al.*, 1978) and that the Rapid City flood coincided with the peak of the Sahelian drought (Kanamitsu and Krishnamurti, 1978). Most of these citations contain numerous comparisons between specific "kinds of weather" years and shifts in their frequency during and since the "Little Ice Age". Clark, *et al* (1975) have demonstrated that "growth of conifers in western North America and the distribution of albacore tuna...along the west coast...are linked by large scale atmospheric flow patterns..." They continue "the success of the calibration of tree rings with albacore catch indicates the possibility of relating tree-ring variations to any type of biological variations which are affected by large scale climatic fluctuations." This conclusion bears obvious pertinence to the possibility of intersite synchroneity of disturbance regimes. It should be pointed out that large scale synchronous changes in the biota can, in turn, affect the global climatic regime (Shukla and Mintz, 1982).

Meteorologists have been actively searching for causes of climatic change. Although these are acknowledged to be multiple and varied, one school of thought is concerned with astronomical controls of incident solar radiation, e.g. Broecker (1966). One recent study delineates a complex 79 year cycle which appears to account for major climatic pulses going back to the 6th millennium B.C. (Landscheidt, 1981). The last pronounced pulse occurred in the decades following 1811. The next predicted (and larger) pulse should occur in 1990.

If large climatic pulses produce synchronous disturbances on a global scale, the LTER program is positioned temporaly to test that proposition and to investigate the nature of various atmosphere-biosphere feedback processes.

To this end, two kinds of studies could be undertaken. The first would simply be to ascertain the degree of interconnectedness, i.e., "teleconnection", between sites. Perhaps the easiest way to accomplish this would be to have each site construct a 3-D graph and corresponding contour map of their entire climatic record. A computer program for accomplishing this is available from R.P.N. The pattern of events both within and between years is easily discerned at a glance, which sould make intersite comparison relatively simple. The Las Cruces, NM record is a sensitive indicator of climatic patterns from New Zealand and Australia to South Africa and all of North America (Bryson and Murray, 1977); Miles, 1978; Tyson, 1980; Brinkman, 1981; Diaz, 1981; Diaz and Fulbright, 1981; Grant, 1981; Horel and Wallace, 1981; Walsh and Richman, 1981; Budyko, 1982; Balling and Lawson, 1982; Kelly <u>et al</u>., 1982; McGuirk, 1982; Neilson and Wullstein, 1983) and is enclosed as an example representative of the Jornada site. The Jornada site is a particularly sensitive indicator of global climatic and biotic patterns since it is situated at the southern end of the Rocky Mountains, a major feature controlling global circulation patterns (Namias and Cayan, 1981; Wallace and Gutzler, 1981; Douglas <u>et al</u>., 1982). Contour maps of precipitation and temperature are most useful in themselves (Figs. 3 and 4). However, a contour map of a running "Walter Climadiagram" (Fig. 5, a composite of temperature and precipitation) (Walter 1979) has proven to be sensitive in delineating periods of relative drought and flood and the temporal characteristics of these events. This is useful in defining "kinds of time" in the sense of Westoby (1979/80).

Once the pattern of climatic events has been discerned, the second investigational phase should be undertaken. This would involve the delineation of all important life history characteristics of all major species, such as, reproductive requirements (and hindrances), dispersal requirements, age of first reproduction, length of reproductive period, etc. (see Cattelino <u>et al</u>., 1979; Westoby, 1979/80). Animal ecologists have developed a strong literature on the theory of life histories which should be directly transferrable to plants if appropriate analogies can be made (Willson, 1972a, b, 1973a, b). In plants, seedling establishment is often considered to be one of the most sensitive periods in the life span of an individual (Ibid). Two modes of "progeny" production might be considered analogous to zoological "progeny" in the sense of altricial (true seedlings) or precocial (suckers, etc.). Each requires different amounts and "kinds of time" (parental care in aminals, "environmental care" in plants). These characteristics can be overlain on the record of climatic "pattern" providing power regarding community establishment, maintenance and sensitivity to specific climatic anomalies.

Figure 3. Contour map of Las Cruces precipitation graphed by month and year. Each year is graphed against 15 months (last October to next December). Contours at 10 mm intervals indicate annual and interannual variability (or continuity) of precipitation. Gaps in the graph indicate missing data.

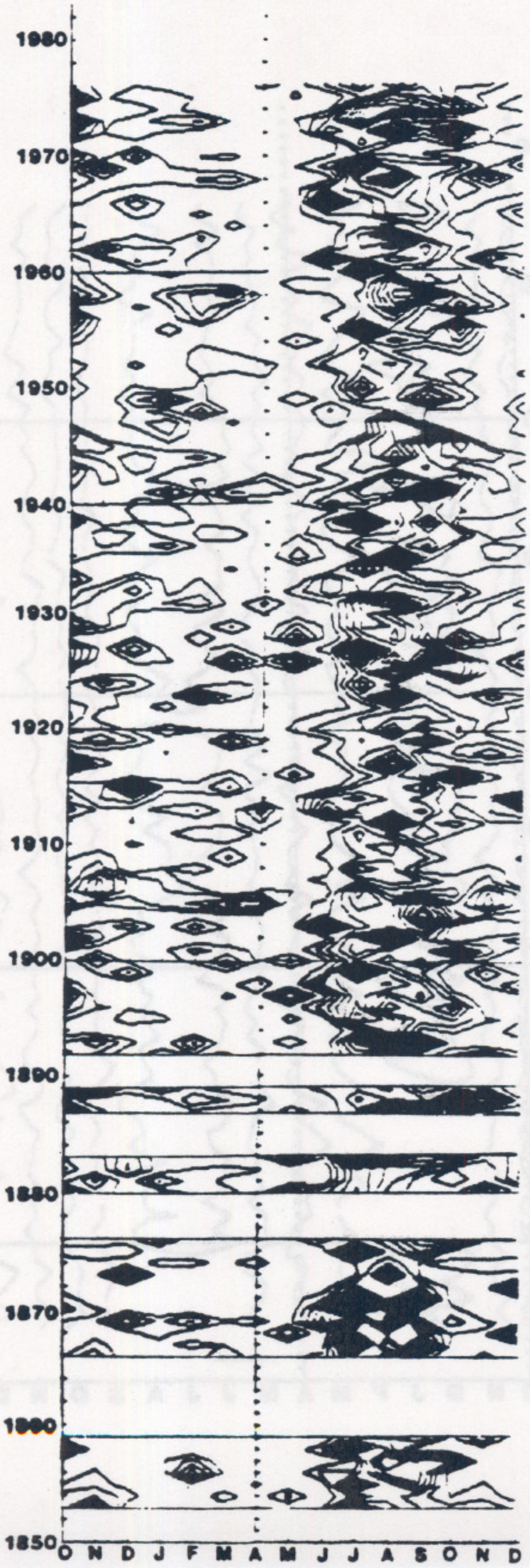


Figure 4. Contour map of Las Cruces average monthly temperature, graphed as in Figure 3. Contours are at 5°C intervals.

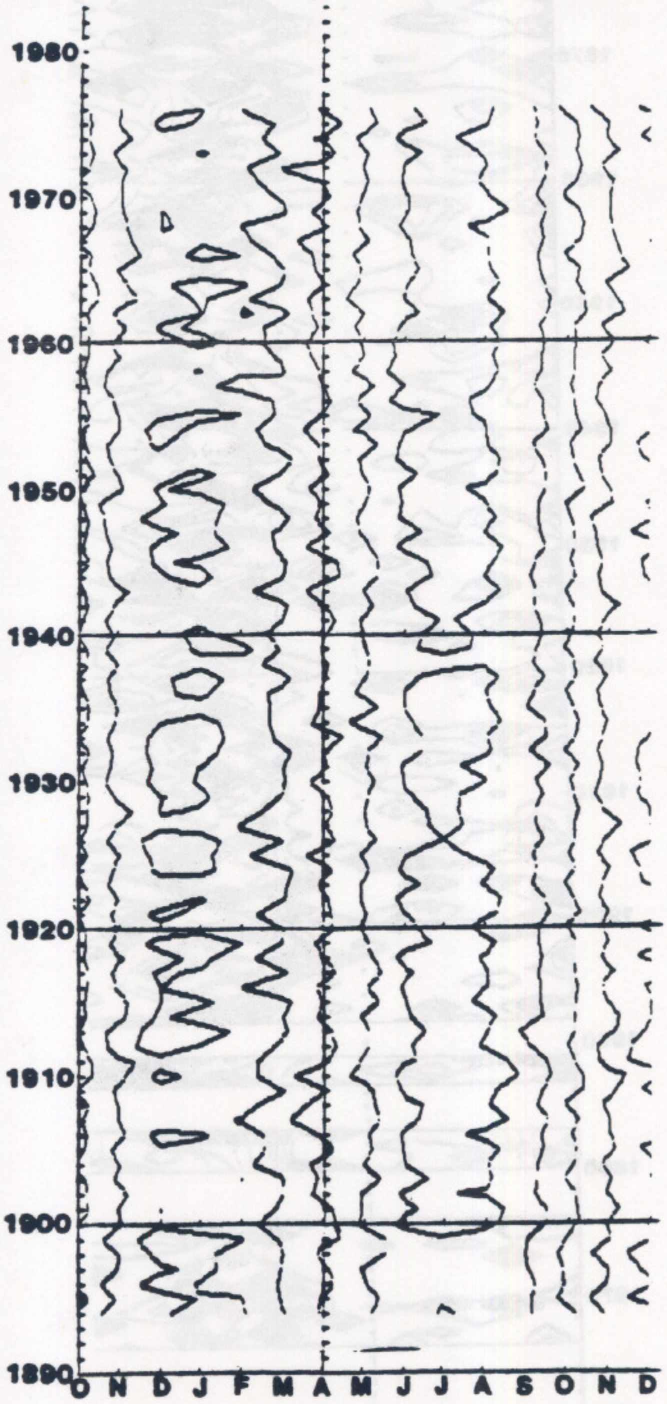
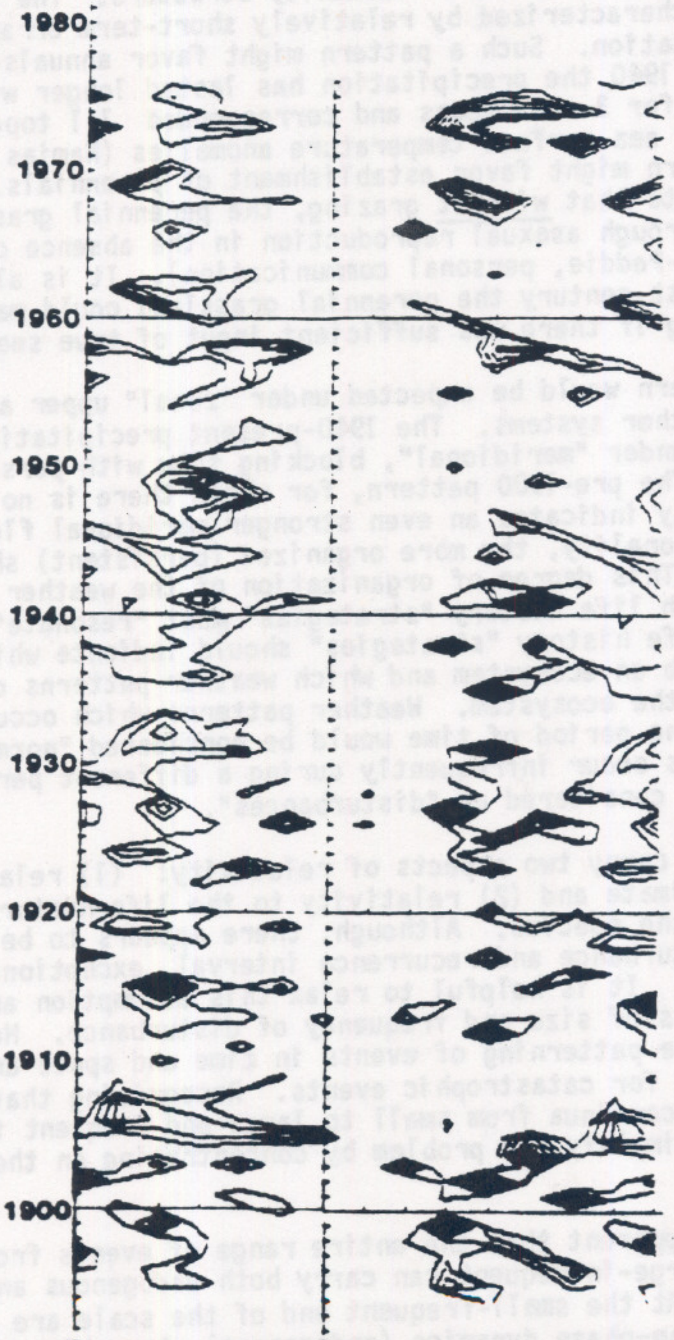


Figure 5. Contour map of "effective precipitation" (Walter 1979), graphed as in Figure 3. A "running Walter Climadiagram" was created by algebraically relating the Las Cruces precipitation and temperature monthly values as in a typical "Walter Climadiagram", i.e. 2T(C) - P(mm). Only those periods when the precipitation exceeded the temperature curve are graphed in this figure. Blank regions are, therefore, drought periods. The topology of the figure (and Figures 3 and 4) is the major feature of interest. Therefore, any drought index could have been used and would have produced the same topology. Contour intervals are at 10 units.



For example, (the following discussion is from Neilson, in preparation) in the southwest deserts, at least three winter droughts of duration 5 to 7 years occurred between 1850 and 1900. No such events have occurred since 1900. This climatic pattern (which included summer rain) should have favored the establishment of warm-season species, i.e., C4 perennial grassland. However, the current century's increase in winter precipitation would favor establishment of cool-season species, i.e., C3 perennial shrubs. The sequestering of soil nitrogen by cool-season species would hinder the establishment of warm-season species even in the presence of summer rain. Thus, a subtle change in climate represents a disturbance (ultimate cause?!). The result was a highly sensitized ecosystem, allowing the "disturbance" (proximate cause ?!) of overgrazing to produce a large-scale shift in community structure. The climate from 1900 to 1940 was characterized by relatively short-term erratic (in time) pulses of precipitation. Such a pattern might favor annuals or biennials. Since 1940 the precipitation has lasted longer within a season, persisted for 3 to 5 years and corresponded 1:1 topologically with north Pacific sea surface temperature anomalies (Namias and Cayan, 1981). This pattern might favor establishment of perennials. There is evidence to indicate that without grazing, the perennial grassland can maintain itself through asexual reproduction in the absence of sexual reproduction (Dick-Peddie, personal communication). It is also possible that during the last century the perennial grassland could maintain itself with grazing if there was sufficient input of true seedlings.

The 1900-1940 pattern would be expected under "zonal" upper air flow with rapidly moving weather systems. The 1940-present precipitation pattern would be expected under "meridional", blocking flow with persistent weather systems. The pre-1900 pattern, for which there is no modern analogue, presumably indicates an even stronger meridional flow. The stronger the meridionality, the more organized (persistent) should be the weather patterns. This degree of organization of the weather should be a key feature to which life history "strategies" must "resonate" to be successful. The life history "strategies" should indicate which weather patterns can disturb an ecosystem and which weather patterns can change without disturbing the ecosystem. Weather patterns which occur frequently during one period of time would be considered "normal". But, if the same patterns occur infrequently during a different period of time, they would be considered as "disturbances".

Disturbance regimes carry two aspects of relativity: (1) relativity to the "background" climate and (2) relativity to the life history characteristics of the species. Although, there appears to be a relation between size of disturbance and recurrence interval, exceptions to this generality do occur. It is helpful to relax this assumption and list all possible combinations of size and frequency of disturbance. However, let us first consider the patterning of events in time and space and reserve the word disturbance for catastrophic events. Recognizing that size and frequency represent continua from small to large and frequent to infrequent, we can simplify the problem by concentrating on the extremes, Table 5.

From Table 5 it is apparent that the entire range of events from small-frequent to large-infrequent can carry both endogenous and exogenous factors. At the small-frequent end of the scale are single tree senescence in gap-phase dynamics (endogenous), tree blow-down (exogenous) or lake turnover. At the other extreme are large-infrequent events, such as major epidemics, e.g. spruce budworm or the evolution of man (endogenous), or they could be hurricanes, volcanoes, etc. (exogenous). It should be remembered that large epidemics may be the "proximate" event, while a change in the weather might be the "ultimate" casual event. Although all scales carry endogenous and exogenous factors, there appears to be a gradient of increasing importance of exogenous factors with increasing spatial scale. The range of events can be classified as to spatial influence, again on two extremes, local (community, population, deme) to ecosystem or landscape (inter-ecosystem). In Table 5 all frequent events, large or small, have been classified as chronic at local and ecosystem scales and represent background events. Small-infrequent events, such as local flood, landslides (infrequent gap dynamics) or local predator or competitor incursion (e.g. starfish invading mussels) are acute events at the local scale and may be classified as local disturbance, but are still viewed as background at the ecosystem scale. Large-infrequent events are classified as disturbance at all scales.

The temporal relationship of these four "boundary" categories of events in schematically portrayed in Figure 6. Arrows (Fig. 6) indicate times when events at one scale might enhance (up arrow) or diminish (down arrow) events occurring at other scales. If the curves can be based on some common denominator such as fire, flood, etc., they should be summable. The sum of these curves (Fig. 6) would represent the "apparent" sequence of events and disturbances. Thus, a variety of waves, pulsating through the environment, occassionally interact, sometimes cancelling each other, producing environmental ameliorations, other times resonating and producing extreme events, i.e., disturbances. Examples of this are manifest in the Las Cruces precipitation graph (Fig. 3). In August, 1945 an extreme event was apparently triggered by the resonance of the natural summer precipitation peak and a moving precipitation wave with a periodicity of ca. 1.07 yrs. There are many similar examples in Fig. 3. This is precisely the mechanism hypothesized by Namias (1978) for the unusual winter of 1976-77, and is being considered as a general phenomenon producing dynamics of wather regimes (Rheinhold and Pierrehumbert, 1982).

It should be remembered that infrequent events can become frequent events and vice-versa as a function of very large scale (global) climatic shifts. A shift in climatic regime would represent a "large-infrequent" event and would in itself be a major disturbance by changing the frequencies of the smaller scale events (i.e., the character of the "background"). Examination of Fig. 6 and the preceding logic imply that the topologic nature of the various frequency functions is repeated at different scales. This suggests (as does the climate literature) that frequency functions of events are recursive and that such a theoretical approach might offer a means of simplifying a complex, apparently chaotic, sequence of events and "disturbances". Apparently the physics controlling high-frequency oscillations (days to weeks) are the same as those factors which control lower frequency oscillations (30-40 years) (Polowchak and Panofsky 1968, van Loon and Williams 1976a, b, Douglas et al. 1982, Reinhold and Pierrehumbert 1982) and can presumably be extended to longer time periods (centuries to millenia) (Bryson and Murray 1977, Kelly et al. 1982).

Table 5. Event types, source, spatial influence and examples, for four space/time scales of disturbance.

Event type	Source	Spatial Influence		Example
		Local	Ecosystem	
Small-frequent	endogenous (senescence)	chronic	chronic	gap-phase dynamics
	exogenous (weather)	(background)	(background)	
Small-infrequent	endogenous (sp. shift)	acute	chronic	predator incursion
	exogenous (weather)	(disturbance)	(background)	local flood
Large-frequent	endogenous (seasonal cycles)	chronic	chronic	nutrient dynamics
	exogenous (weather)	(background)	(background)	cyclones, drought
Large-infrequent	endogenous (epidemics)	acute	acute	demography of man
	exogenous (weather)	(disturbance)	(disturbance)	extreme weather

Both the low resolution topologic analysis of weather (Neilson and Wullstein 1983) and, particularly, the high resolution analysis of weather (Neilson (1983) and Figs. 3, 4, and 5) delineate in detail with a resolution from 1 month to decades virtually every climatic shift and both local and global patterns of events that have been described from the modern record. These include shifts in global climatic regime around 1900, 1940, 1951, and 1956 with attendant shifts in drought/flood frequencies as well as a 1:1 topologic match of winter precipitation at Las Cruces, NM with north Pacific sea surface temperature anomalies.

The schematic diagram in Figure 6 is a gross oversimplification of the frequencies of events. However, the literature is replete with detailed descriptions of frequencies of events and shifts in such frequencies with temporal wavelength scales of distinct events ranging from days to months, the annual cycle, a potential 1.07 year cycle (Fig. 3), 2 to 7 yr cycles, 1/2 to 5 decadal cycles, 1 to several century cycles, and glacial-interglacial cycles.

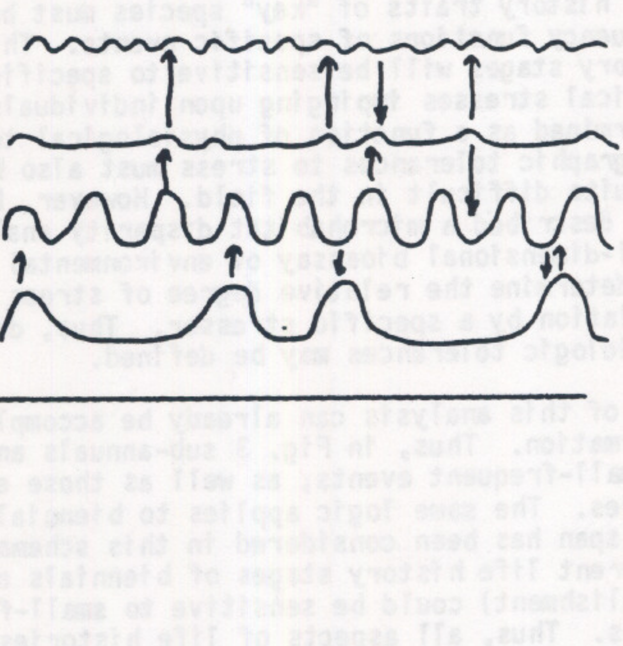
The delineation of event sequences in this manner will describe "disturbances" relative to background kinds of events. Once "disturbances" have been defined on a purely physical basis the next question is one of relativity to the biota. For this purpose, crucial life history traits of "key" species must be matched against the specific frequency functions of specific events. This will determine which life history stages will be sensitive to specific event sequences. Thus, the critical stresses impinging upon individuals of a given species can be determined as a function of physiological tolerances. However, demographic tolerances to stress must also be determined. This usually is quite difficult in the field. However, Neilson and Wullstein (1983) have described a microhabitat disparity analysis, which is a multi-dimensional bioassay of environmental heterogeneity. This method can determine the relative degree of stress impinging on a species' population by a specific stressor. Thus, demographic as well as physiologic tolerances may be defined.

Much of this analysis can already be accomplished from extant information. Thus, in Fig. 3 sub-annuals and annuals would be sensitive to small-frequent events, as well as those events affecting longer lived species. The same logic applies to biennials and perennials. Only total life span has been considered in this schematic example. However, different life history stages of biennials and perennials (e.g. seedling establishment) could be sensitive to small-frequent or infrequent events. Thus, all aspects of life histories, particularly reproduction, must be examined to determine species sensitivities to specific types of events and shifts in frequencies of those events.

Experimental Manipulations by Burning as a Basis for Intersite Comparison

A cooperative reseach project involving effects of controlled burning is underway between Konza LTER site in Kansas and the Cedar Creek LTER site in Minnesota. Tall grass prairie constitutes the principle biome type at Konza and is an important component at Cedar Creek. Maintenance of the prairie at Cedar Creek in the face of invasion by deciduous forest species is largely a result of repeated fires. At Konza, burning is an important management tool and constitutes an integral part of the manipulation of study sites.

Figure 6. Schematic representation of temporal pattern of event types and examples of organisms with sensitive life history characteristics. Under "Sensitive Organisms", only the longest lived organisms have been listed. Shorter lived organisms are also presumed to be affected. Up arrows indicate positive (resonant) interactions. Down arrows indicate negative (ameliorative) interactions.

Event Type	Sensitive Organisms	Schematic Representation of Event Type in Time
Small-frequent	sub-annuals, annuals	
Small-infrequent	biennials, perennials	
Large-frequent	perennials	
Large-infrequent	perennials	

As a result of a visit by six Minnesota LTER scientists to Konza in September, 1982, a cooperative burning experiment has been implemented at Cedar Creek. Sixteen plots, each 8 m on a side, have been laid out in a 25-year old abandoned field. Composition and abundance of plant species will be determined by clipping in summer 1983. Soil nutrients and organic matter will also be measured. In spring 1984 burning will be initiated in a design using 4 replications. In each replication, one 8 m^2 plot will serve as a control, one will be burned every year, one will be burned every other year and one will be burned every fourth year. This burning pattern corresponds to the experimental design being used at Konza.

Because many plant species characteristic of tall grass prairie are present at both Konza and Cedar Creek, we anticipate that measurements of primary production and possibly of grazing by insects and pocket gophers may provide interesting comparative data. While climatic regimes and soils are quite different, intensive monitoring of these parameters at both sites should enable us to determine effects of these factors with reference to the burning experiments.

Experimental Manipulations by Clearcutting as a Basis for Intersite Comparison

Comparable studies of hydrology, nutrient cycling, and erosion in small forest watersheds have been underway at Coweeta and H. J. Andrews for many years. Experimental removal of forest vegetation from small watersheds was accomplished at both sites in the mid-1970's. LTER provides a very useful and appropriate medium for developing published comparisons between these two sites and results from Hubbard Brook where similar experiments were carried out earlier.

Terrestrial - Aquatic Interactions as a Basis for Intersite Comparison

Many terrestrial-aquatic interactions are driven by runoff and groundwater flow from land to water, hence disturbances to aquatic systems caused or mediated by terrestrial systems largely involve changes in energy and nutrient input to the aquatic system. Terrestrial ecosystems influence aquatic systems by shading, litterfall as a source of nutrients, and structural effects of live and dead organic matter. Natural disturbances to aquatic systems are primarily the result of climatic variation, i.e. floods and droughts, and changes in terrestrial ecosystems adjacent to waterbodies. Floods can cause increased nutrient and sediment loading from runoff, and droughts can cause changes in nutrient dynamics, decomposition processes, and the areal extent of terrestrial vs aquatic systems, especially in wetland ecosystems. Anthropic disturbances can include almost any human activity in a watershed resulting in alteration of aquatic systems: logging, construction, agricultural activities, watershed modification (damming or channelization), and municipal or industrial waste disposal.

LTER sites with aquatic systems represent a tremendous range of conditions in terms of (1) lotic to lentic characteristics, (2) size of waterbody, (3) type and timing of fluctuations of water volume, quality, and state (solid-liquid), and (4) stature, composition, and disturbance regime of adjacent terrestrial vegetation. Hence there is a broad range of types and degrees of coupling between terrestrial and aquatic systems. Low levels of coupling, for example, may occur at Northern Lakes where most lakes are fed by subsurface flow whereas small streams flowing through forests (Coweeta, H. J. Andrews, Konza) are strongly influenced by terrestrial systems. At some sites terrestrial and aquatic systems are difficult to distinguish and ecotones are very transient at seasonal and even daily time scales (Okefenokee, North Inlet, mountain stream sites).

This theme of comparisons based on terrestrial-aquatic interactions seems to be worthy of consideration across all LTER sites with aquatic systems. The theme was pursued in a more narrow sense at a LTER workshop on streams and rivers held in for July, 1983, at Konza and small groups of sites are beginning to explore intersite comparison on specific topics such as the role and dynamics of woody debris in streams (subalpine forests near Niwot Ridge, H. J. Andrews, Illinois River, Konza).

Ecosystem Recovery after Disturbance as a Basis for Intersite Comparison

LTER sites may be compared on the basis of parameters characterising ecosystem response to and recovery from disturbance; for example, on the basis of resistance (ability to remain unaffected by disturbance) and resilience (ability to recover to a more or less persistent state). Resistance may be measured as the damage (compression, partial removal, organism death) caused to an ecosystem by a standard partial disturbance, e.g. single pass of a standard vehicle. Resilience may be measured by the rate and direction of recovery from a standard partial or total disturbance, e.g. removal of a certain percentage of the phytomass or removal of all phytomass and of the surface soil layer. The degree of complexity of successional pathways after total disturbance is an important indicator of resilience; communities limited to early successional stages may inhibit the return of the original ecosystems. More detailed comparisons may determine the role of various growth forms in the recovery of principal communities or the point of entry of the dominants of undisturbed communities into the successional sequence. Key life history characteristics of the primary species in relation to environmental dynamics (Cattelino et al. 1979) provide insight into the mechanisms of succession (see discussion under Climate Considerations in Intersite Comparisons).

After an initial, usually exogenous disturbance, a relatively rapid, short-term period of community response takes place. This process of "succession" operates like a control system, driving populations and related variables toward environmentally determined limits which physically cannot be exceeded (Gutierres and Fey 1980), i.e., toward the beginning of the following "climax" period during which the now mature community undergoes long-term changes at a slow rate. This slow community change is controlled by low intensity, slow disturbances, either exogenous, e.g. climatic change, or endogenous, and it includes both small cyclical variations and slow directional changes (Komarkova, in press).

Magnitude and Frequency Considerations in Intersite Comparison

Figure 1 illustrates, from LTER sites, the long-accepted principle that the magnitude and frequency of disturbing events in ecology are inversely related, i.e. that more catastrophic events occur less frequently (Wolman and Miller 1960) where magnitude is here defined as area effected. This empirical observation is important in long-term research and provides a common rationale for programs such as LTER: the need to sample better the frequency and spatial, e.g. patch size, distributions of stresses which produce change in ecosystems, e.g. Brunsden and Thornes 1979.

The scales of measurement used in estimating both magnitude and frequency are usually defined conventionally, as they are in Figure 1 where m^2 and years are used. These units are readily understood but they may not be the best in a cross-ecosystem comparison. In such a comparison, it may be preferable to scale both the spatial and temporal dimensions by the characteristics of the systems involved, for example to the life-span and size of the dominant species within the system. Thus, we might suggest that the impact of the seasonal weather cycle on plankton populations in lakes is equivalent to that of the 100 year flood on the affected human population (Fig. 2).

Two other problems arise from the classic model of magnitude and frequency in disturbance regimes defined by Figure 1. Both have been widely recognized. The first arises from the lack of independence among disturbing stresses acting on an ecosystem. At one level, this involves compound factors which contribute to a single disturbance or serial events which make the identification of simple cause-effect mechanisms difficult. At a broader scale, it may be defined in continent-wide ecological (of different form) responses to climatic anomalies (of different type,e.g. drought) anamolously high precipitation on widely separated LTER sites. The second problem is more local and arises from the recognition that 'disturbance' is a response within the ecosystem. The response to a given stress varies between ecosystems, and between different components of the same system. This variation in response has been treated by defining thresholds at which responses are initiated within a magnitude and frequency framework: the transient behavior of Brunsden and Thornes (1979). The identification of such transient or critical conditions remains important in empirical research on simple systems (Caine 1980) and will prove more difficult in more complex systems.

In LTER, a definition of different disturbance regimes in the classical context of magnitude and frequency analysis, e.g. Figure 1, gives a useful, simple means of inter-site comparison. However, it should not be allowed to mask the wide contrasts in ecosystem components and responses involved. We have no reason to believe that the 100 year event at different sites should correspond in any way, except that of relative frequency.

A more rigorous analysis of magnitude-frequency relations could be made using the scheme proposed by Wolman and Miller (1960). With this approach one could analyze, for example, (1) the relative amount of stand opening of various sizes and frequencies of occurrence by an individual disturbance mechanism, e.g. treethrow landslides, fire, (2) the relative amount of stand opening by different disturbance types at a particular site, and (3) the relative amount of disturbance by one or more mechanisms between sites. Unfortunately, at the present time few sites have data available to accomplish (1), and no two sites have data for a common disturbance mechanism so approaches (2) and (3) cannot be tested yet.

Anthropic Influences as a Basis for Intersite Comparison

As discussed in the section Disturbance Regimes at Individual LTER sites influences of man fall in a variety of classes:

1. Chronic, pervasive, e.g. acid rain, persistent grazing
2. "One-shot" treatments followed by abandonment, e.g. logging, brief period of heavy grazing or plowing
3. Periodic, e.g. logging, slash-and-burn agriculture
4. Introduction of exotic compounds, e.g. chemical spills
5. Introduction of exotic species
6. Reduction or elimination of natural disturbance factors, e.g. elimination of buffalo, fire suppression, minimizing peak streamflow and maximizing lowflows.

Some of these anthropic influences on disturbance regimes are the subjects of experimental manipulation designed to examine the effects of either mimiced natural disturbances (e.g. fire) or clearly unnatural disturbances (e.g. plowing, clearcutting). Intersite comparisons based on controlled experiments are probably the most fruitful approach to comparing anthropic influences on disturbance regimes. The plethora of anthropic influences and types of ecosystems and their natural disturbance regimes present such a complicated set of factors that it would be difficult to arrive at meaningful comparisons of anthropic influences beyond those achieved through experimentation.

ADMINISTRATIVE AND STUDY DESIGN CONSIDERATIONS FOR INCORPORATING STUDY OF DISTURBANCES IN LTER

The time scale of research that may ultimately be available under the LTER program presents special opportunities and challenges, both in research design and administration. Some of the use of long-term aspects of LTER involves observing system response to imposed disturbances such as burning. However there has been little emphasis on designing monitoring programs and experiments to capitalize on infrequent major natural disturbances.

One difficulty is to set up a research program that will yield results of value whether or not a major disturbance occurs during a 5 to 10 year study period. The land-water interaction component of LTER research at the H. J. Andrews Forest is an example of an effort to do this. Aquatic habitat and communities are described in relation to controls of adjacent terrestrial vegetation on food resources and channel structure in manipulated study reaches and in a chronosequence of natural and managed stands. Land-water interactions can be examined as a function of stage of stand development, including the dynamics of each system, such as treefall into streams that may alter habitat and retention of food resources. These studies can be conducted successfully in the absence of major floods. If such an event does occur, however, additional questions can be addressed, such as how do riparian-stream systems in various stages of vegetation development, i.e. degree of riparian vegetation control of aquatic ecosystems, respond to major floods.

Logistical and funding problems also confront scientists who wish to study major natural ecosystem disturbances. Logistical difficulties include having personnel, equipment, access, and a communication network available for prompt response. The Illinois River LTER group has set an interesting example for others concerned about this problem. Anticipating that chemical spills will be a major disturbance in the Illinois and Mississippi Rivers, they have held a trial run at rapidly mobilizing a research effort to study effects of unexpected spills.

Funding of responses to unanticipated disturbances is a thorny issue, because it is difficult to budget for such contingencies. Three levels of contigency budgeting are possible: (1) at individual sites, (2) across the LTER program as a whole, perhaps within the intersite coordination committee, (3) at NSF. At present the LTER program appears to rely on flexibility at individual sites with the possibility of emergency, supplemental funds from NSF. The issue has not arisen yet, but with 11 sites in the program, each experiencing a variety of disturbances, major events of 25+ year return periods are likely to occur within the network of sites every few years.

We request that the Intersite Coordination Committee consider this issue.

CONCLUSIONS

This workshop initiated contact among scientists in LTER who are concerned with disturbance regimes and surfaced common thoughts and concerns about a variety of topics. These contacts should be fostered on a network-wide level, because studies of disturbance are central to LTER and they explicitly recognize man's influence on ecosystem dynamics.

We suggest that future work involving cooperative efforts be more narrowly defined. Of the many possibile themes for narrower consideration of ecosystem disturbances, three are suggested here:

1. By ecosystem type, e.g. disturbance regimes in forest ecosystems, in grassland area, etc.

2. By topic, e.g. Holocene disturbance history, disturbance propagation through the interaction of terrestrial and aquatic systems.

3. By disturbance type, the example of fire ecology is an obvious one. Other examples include the evaluation of disturbance due to hydrologic management, climatic change, timber harvest, recreation and even scientific research itself.

Results of this workshop suggest that time and spatial scales in disturbance ecology might be tied together in a unified theory involving landscape scale factors (recurrence interval, size of disturbance) and organism scale factors (lifespan, physiognomy, dispersion rate).

Finally, we point to the need for LTER to respond to adventitious disturbance on and near the network sites. Disturbance in some systems is rare and, to a degree, partially unpredictable. Important events which are not predictable on the time scale of budgeting of funds and other resources, but such natural events are likely on at least one site during each 3 to 5 year increment of LTER program life. It is important that each site and the network be able to take advantage of these 'catastrophes' as they occur.

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APPENDIX I

Disturbance Regimes Affecting LTER Sites

These tables were compiled as preparatory work for the workshop.

Overview of Geomorphic and Vegetative Temporal Variation, Cascade Mountains, Oregon

Time Scale (yr)	Ecosystem Perturbation	Geomorphic Response to Perturbation	Record of Geomorphic Response	Vegetative Response to Perturbation	Record of Vegetative Response	Stream Response (Physical)
10^{-2}	Precip-Discharge Events		Direct observation			Fluctuation of fine debris storage
$10^0 - 10^1$	Annual water budget, large storms	"Base Flow" erosion by non-catastrophic processes	Direct observation	Physiologic response of individual plants	Direct observation	Fluctuation of fine debris storage Input of coarse debris
10^2	Major disturbance of vegetation: e.g. fire, very large storm, insect attack, etc.	Periods of accel. erosion slide scars, stream channel impacts	1.Synthesis based on direct observation over various veg. and land use cond. 2.Record in natural catchments, e.g. lakes 3.Historical records	Secondary succession (plant) catchments,	1.Direct observation 2.Synthesis of stand age and type distrib. 3.Record in natural-torrents e.g. lakes. 4.Historical records	Fluctuation of coarse + Total debris storage and bed stability, sun light, nutrients hydrology debris
$10^3 - 10^4$	Climatic change glaciation	Intermediate Scale landforms, e.g. terraces, fans moraines	Analysis of landforms (e.g. volume of alluvial fans)	Primary succession (soil + plant) Migration Macro-evolution	1.Pollen analysis 2.Vegetation on dated landforms	Aggradation-degradation Substantial downcutting thru bedrock
10^6	Episodic volcanism	Gross morphology of major drainages, Volcanic landforms	Analysis of landforms e.g. volume of erosion below dated land surface	Succession (soil) Migration Macroevolution	Fossil record Downcutting	Aggradation-degradation, substantial downcutting thru bedrock
10^8		Physiographic province as a whole	Possible if shed debris collected in depositional basin	Macroevolution	Fossil record	

Exogenous events affecting the Okefenokee ecosystem.

Frequency (years)	Event	Effects
10^0	Annual hydrologic variation	Physiological response of plants; annual faunal dynamics
10^1	Dry years	Minor fires; successional dynamics
10^2	Severe droughts, major storms	Major fires; 2° succession; creation of lakes, prairies
$10^3 - 10^4$	Climatic and sea level changes	1° succession: lake, swamp or woodland; barrier island formation
$10^5 - 10^6$	Uplift, subsidence	Drainage patterns; gross morphology
?	Human hydrologic disturbance: canals, boat trails, dams, channelization	Drainage pattern; 2° successional dynamics; nutrient dynamics; fire recurrence
?	Human vegetation disturbance: logging	2° successional dynamics

DISTURBANCE REGIMES: EXAMPLES FROM THE ILLINOIS RIVERS LTER SITE

Frequency	Event	Geomorphic Variation	Vegetation Reponses
10^{-3}	Passage of tow boats	Sediment resuspension	Probably a slow decrease in aquatic vegetation
10^{-2}	Diurnal solar cycle	None	None
10^{-1} & 10^{0}	Annual spring flooding	Water over floodplain, sedimentation	Minimal because vegetation is in equilibrium with this cycle
10^{1}	Major floods, chemical spills, etc.	Water over levees inundating "uplands"	Kills vegetation & resets succession to earlier stages; chemical spills may cause long-term destruction of vegetation
10^{2}	Dam and leeve construction, intensive agriculture	Increases in water area and depth, destruction of natural backwater lakes, decreases in annual flooding, increases sedimentation rates	Kills upland vegetation in impoundments, kills, relocates and changes species composition of aquatic vegetation, destroys natural floodplain forests
10^{3} to 10^{4}	Interstadial climatic warming	Slow erosion but speeding up with any vegetation change	Establishment of prairie and shifts in forest composition
10^{4}	Glaciation	Erosion of valleys, alteration of landscape, displacement of river systems	Complete alteration of vegetation, establishment of new biotic proveniences

DISTURBANCE REGIMES: EXAMPLES FROM THE ALPINE SYSTEMS OF THE COLORADO FRONT RANGE

Recurrence Interval	Event	Geomorphic Variation	Vegetation Impact	Space Scale
10^{-2} yr	Diurnal Frost Cycles	Needle Ice Disturbance	Seedling Disturbance	10^{-4} m^2
10^{-1}	Summer Thunderstorms	Splash Erosion Surface Flow	Soil Erosion	10^{-1}
10^{0}	Annual Frost/ Runoff Cycles	Solifluction, Creep	Micro-environments Burial	10^{2}
10^{1}	Catastrophic Storms/Avalanche Low Snow Year Fires	Debris Flows, Fluvial Erosion, Large Rockfalls	Destruction & Burial Timberline lowering	10^{3}
10^{2}	Climatic Fluctuations	'Neoglacial' Events, Snowbank Expansion, Exp./ Contraction of Sediment source Areas	Community Shifts, Colonisation of new Substrates	10^{6}
10^{4}	Glacial/ Interglacial	Glacial removal. Large-scale mountain slope instability	Widespread elevation Shifts. 'Clean Slate'	10^{10}
10^{6}	Tectonics	Mountain relief development		10^{15}

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DISTURBANCE REGIMES: EXAMPLES FROM THE JORNADA DESERT LTER

Recurrence Interval	Event	Geomorphic Variation	Vegetation Impact	Space Scale
10^1 yr	Frost Cycles	Needle Ice Reduce Soil Compaction	Seedling Disturbance Establishment Increase Infiltration	10^{-4} m^2
10^{-1}	Summer Thunderstorms	Splash Erosion Surface Flow	Soil Erosion Establishment process Filling of some playas Filling of stock tanks	10^{-1}
10^0	Runoff Cycles	Transport fine Particle Deposition base piedmonts	Low Slope Fine deposition	10^2
10^1	Catastrophic Storms	Debris Flows, Fluvial Erosion, Large Rockfalls	Water Channel Changes, destruction of arroyo edge vegetation, playa filling	10^3
10^1-10^2	Climatic Fluctuations	Drought or increased rainfall; increased or decreased temperature	Community Shifts, Colonisation of new Substrates	10^6
10^2	Hard Freeze	Needle Ice Frost Heaving* Reduce Compaction Increase Infiltration Erosion Reduction Hilling	Death of above ground parts of some shrub species	10^{-4}

NATURAL DISTURBANCES TO RAIN FOREST ECOSYSTEMS

Event	**Geomorphic Variation**	**Vegetation Impact**	**Spatial Scale**	**Temporal Scale**
Rain Storms	Splash erosion	Seedling Disturbance	10^{-4} m^2	10^{-2} years
Leaf Cutter Ants	Soil exposure and turnover	Seedling Disturbance Defoliation	10^2 m^2	1-10 yr
Treefalls	Soil exposure Nutrient flush?	Fall of canopy trees, Germination and establishment of seedlings	10^2-10^3 m^2	10^2
Landslides	Soil erosion, rock falls	Local distruction of vegetation including seed bank	10^4 m^2	10-10^2
Volcanism	Ash, lava	General destruction	10^5	10^2-10^3
Tectonics	Mountain development		10^{15}	10^6

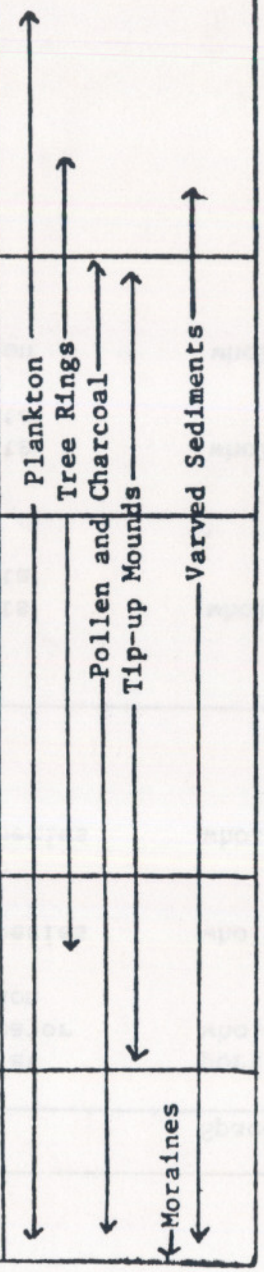
Disturbance Regimes - North Temperate Lakes Site - LTER

(T. Frost - University of Wisconsin)

Recurrence Interval	Event	Physical-Chemical Impact	Biotic Impact	Space Scale
		EXOGENOUS EVENTS		
$10^{-1}-10^{0}$	lake turnover	major nutrient pulses & possible shifts in oxygen regime	internal shifts and cascading effects on phytoplankton and zooplankton	whole lake
10^{0}	ice cover	changes in dissolved gases, nutrients and light	shifts in phytoplankton and zooplankton, resting stage formation	whole lake
10^{0}	spring runoff	pulses in nutrients & acidity	changes in species composition	portion of or whole lake
$10^{0}-10^{1}$	winterkill (oxygen depletion associated with ice cover)	loss of oxygen	mortality of many organisms, especially fish	whole lake (some refugia occur)
$10^{1}-10^{2}$	biogenic meromixis	depletion of nutrients and oxygen	overall shift in lake metabolism	whole lake
$10^{1}-10^{2}$	major discharge effects from inflow streams or overland flow	influx of nutrients and shift in light due to turbidity	varied changes in species composition	portion of or whole lake
$10^{1}-10^{2}$	watershed coupled events (e.g. fire, windstorm, landslide)	influx of nutrients and turbidity	changes in species composition	portion of or whole lake

Recurrence Internal	Event	Physical-Chemical Impact	Biotic Impact	Space Scale
$10'-10^2$	drought and high water effects	change in physical structure of lakes and nutrient regimes	changes in habitat availability - major effects on benthon	portion of or whole lake
10^3-10^4	climate and glacial effects	major changes in lake basin	major loss of species	whole lake
? 10^5	volcanism and tectonic activities	major changes in lake basin	major loss of species	whole lake
		BIOLOGICAL EVENTS		
$10'-10^2$	major year class successes or failures for components of the biota (e.g. fish)	possible shifts in internal nutrient cycling	cascading effects through the biota	whole lake
$10'-10^3$	species introductions	possible shifts in internal cycling	cascading effects through the biota	whole lake
	anthropogenic pulse introductions of materials (e.g. nutrients, toxic substances)	varied effects in lake chemistry	varied effects on the biota	whole lake

Recurrence Interval	Disturbance events	Vegetation Response	Proxy Records of past Disturbances
10^{-2} - 10^{0}yrs	Precipitation Cloud Cover Temperature Cycles (Daily and Yearly) Slight changes in Timing and Duration	Individual Plant Responses Reduced production of Biomass Delayed Flowering Times and Duration Reduced Pollen Dispersal and Fruiting Reduced Germination and Seedling Establishment	
10^{0} - 10^{1}	Heavy Thunderstorms Late Spring Frosts Late Summer Frosts Drought (Minor - lasting a few weeks to a month)	Lightning Damage Soil Erosion Damage to Flowers, Fruit, and Leaves Reduced Productivity and Seedling Establishment	
10^{1} - 10^{2}	Large Wind Storms Fires Insect Infestations and Other Diseases Severe Droughts Unusually Wet, Warm or Cold Periods Logging and Agricultural Clearance	Secondary Succession Initiated Soil Erosion from Up-rooted Trees Sensitive or Nonresistant Species are Killed - Changed Species Dominance Introduced Species	
10^{2} - 10^{3}	Fires (Change in Frequency) Climatic Change (e.g., Little Ice Age)	Changes in Species Dominance	
10^{3} - 10^{4}	Climatic Change (Major)	Plant Migrations - New Assemblages of Species Primary Succession After Glaciation	



Events affecting ecosystems at the Cedar Creek Natural History Area in east-central Minnesota.

Event Frequency (yrs)	Event	Area (m2)	Geomorphic Variation	Vegetation Variation
10^{-2}	Daily temperature change (a)	10^{-4}	Frost action	Seedling disturbance
	Precipitation (a)	$10^3 - 10^4$	Soil erosion	Seedling disturbance
10^0	Seasonal temperature change (a)	10^5		Seasonal change
	Fire (b)	10^7	Soil erosion	Destruction, secondary succession
	Pocket gopher activity	10^0	Soil surface disturbance	Seedling establishment
$10^0 - 10^2$	Abandonment of agricultural land (c)	$10^2 - 10^4$	Soil surface disturbance	Secondary succession
	Extreme storms (rain, ice, wind) (a)	$10^2 - 10^4$	Flooding, erosion	Destruction, secondary succession
	Drought	10^5	Erosion (wind)	Physiological response, death
	Early/late frost (a)	10^3		Physiological response, death
	Acid rain	$10^3 - 10^4$	Leaching	Physiological response
	Fire (b)	10^2	Soil erosion	Destruction, secondary succession
	Atmospheric CO_2	10^{10}		Physiological response
$10^3 - 10^4$	Climate change (d)	10^{10}		Primary succession
	Glaciation (d)	10^{10}	Land form	Primary succession

DATABASE SOURCE

(a) CCNHA weather station

(b) Fire history known since 1940; controlled burns on 12 sites at intervals from 1 to 7 years since 1964.

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(c) Field history known since 1940; planned abandonment of designated areas since 1973.

(d) Paleoecological data from pollen analysis.

Recurrence Interval	Event	General Effect on Site	Vegetation Impact
Yearly	Strong winds Soil erosion	Short-distance transport of soil particles from bare areas to within vegetation clumps. Transport of plants & litter.	Little impact except in drought periods (see below). Causes some hummocking of vegetation over long periods of time.
Yearly (6-7 out of 10 yrs)	Strong winds Snow re-distribution	Transport of snow from exposed sites to leeward of vegetation clumps, in gullies, leeward slopes, etc.	Most upland areas may receive little or no effective winter precipitation and soil is dry in spring. Areas of large snow accumulation receive extra soil moisture.
3-6 yrs	High-intensity summer thunder storms	Overland flow and some soil erosion on slopes, especially on certain parent materials. Flood flow in intermittent streams sometimes expanding to cover floodplain sites.	Vegetation on floodplain or overflow sites may receive a large amount of water. This periodic phenomenon may be important to persistance of some plants.
3-6 yrs	High-intensity hail and wind.	Same as above	Hail can damage shrubs. May break and spread pricklypear through rooting of broken pads.
20 yrs	Moderate drought for 3-6 consecutive years	Increase in effects of wind erosion and soil particle transport. Increase in water erosion during high intensity storms.	Reduction in production of above-ground biomass and thinning of number of tillers of blue grama. Increase in pricklypear cactus if prolonged. Small composition shifts, including increase in annual forbs, decrease in cool-season grasses.
20 yrs.	Above-average precipitation for 3-6 yrs.	Possibly some slight increase in soil movement due to water erosion. Probably minimal.	Increase in above-ground biomass production. Increase in tillering of blue grama. Reduction in pricklypear if wet period is prolonged. Small composition shifts, including increase in cool-season perennial species.
5-20 yrs (10-40?)	Fire (Pre-European man)	Not enough fuel to carry fire long distances in many years. Wind erosion of ash and soil from burned areas during first winter if burned late in growing season, fall or winter. Some shifts of soil nutrients.	Little direct effect on vegetation. Antelope and bison probably ate pricklypear in burned areas because spines were burned off by the fire. This periodic heavy use of pricklypear may have kept amounts relatively low. Temporary decrease in small shrubs.
25-50 yrs	Heavy infestations of insects (grasshoppers, range caterpillars, etc.)	Not much effect on site. Possible slight increase in wind and water erosion if heavy infestations occurred for several consecutive years.	Heavy defoliation of plants. Not much impact unless repeated yearly infestations or followed by drought.
50-60 yrs (1885-6) (1948-9)	Severe winters	Severe cold, heavy snow, drifting, over prolonged periods during the winter. Extremely hard on large ungulates due to stress and lack of food. Native ungulates (bison, antelope) probably better adapted than domestic livestock.	Impact on vegetation would largely be favorable due to increased moisture after snow melt.
100-? yrs	Heavy white grub infestations	Areas of bare soil or covered with annuals due to death of blue grama. Soil erosion (wind) after blue grama crowns deteriorate.	Blue grama killed in small patches or large/(1-2 ha) areas. Secondary succession is very slow. This may result in "patchiness" in shortgrass areas.
100-300 yrs	Severe drought (<?% avg precip. for 3-6 consec. yrs)	Initially, wind erosion from natural bare and disturbed areas. Cover gradually decreases and wind erosion accelerates. Soil from eroded areas covers healthy vegetation and causes death.	Little or no above-ground production for 2 or more years. Death of plants, increase in bare ground. Cactus survives and may shelter remnants of other species. Slow recovery due to slow rate of secondary succession.
10^2-10^3 yrs	Long periods of much above-avg. precipitation	Re-distribution of material, cutting, deposition. Landscape shaping.	Community shifts.
10^4 yrs	Glaciation-large amounts of water during melting	Outwash from Rocky Mountains. Cutting of material previously laid down.	Community shifts. Primary succession on new substrates.
MAN-MADE DISTURBANCES			
	Plowing	Depletion of organic matter in soil. Nutrient cycles disrupted. Increase in wind erosion, water erosion. Wind erosion severe in drought years.	Secondary succession following plowing is very slow. In less than 15" precipitation, blue grama may require 50-300+ years to return to the community.
	Restriction of fire	Some soil stabilization.	Lack of interaction of fire with ungulates may have [illegible] increase in pricklypear. Some other minor shifts in [illegible]sition may have occurred.
	Grazing by domestic animals	Most grazing much like that of bison and other native ungulates. Prolonged, extremely heavy grazing probably has changed vegetation composition and increased bare soil and wind erosion from limited areas.	Large herds of bison grazed areas very heavily and vegetation evolved under heavy grazing. Thus there probably is little effect of domestic livestock on much of the area.