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Addendum to proposal BSR-8514329 to the

National Science Foundation

for

LONG-TERM ECOLOGICAL RESEARCH IN THE COLORADO ALPINE

Name and Address of Institution:	The Regents University of Colorado Campus Box B-3 Boulder, Colorado 80309
Desired Starting Date:	January 1, 1986
Amount Requested:	$1,825,000
Time Period for Contract:	January 1, 1986 - December 31, 1990
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ADDENDUM

Long-Term Ecological Research in the Colorado Alpine

This addendum modifies the proposal BSR-8514329 submitted to the National Science Foundation in April 1985 for Phase II of the University of Colorado Long-Term Ecological Research (LTER) program. The addendum incorporates changes discussed at the recent site visit (August 8 and 9, 1985) and addresses the research issues identified by Dr. James C. Callahan, Associate Program Director of Ecosystem Studies, in a letter (August 22, 1985) that followed the site visit. It also provides a revised and annotated budget that reflects substantive changes from the original proposal.

I. Aquatic and Wetland Studies

The proposed aquatic program was too ambitious for the level of available funding and did not take into account the logistic problems associated with reservoir manipulation in the lower Green Lakes Valley. In order to be more realistic, we will focus our aquatic effort on two integrated studies within the upper Green Lakes Valley (2.1 km^2 catchment to Green Lake 4). One study will involve the wetlands system between Green Lake 5 and Green Lake 4 drains into the inlet stream of the latter. The other study will involve Green Lake 4 itself. We will continue to maintain a small number of key data sets on aquatic subsystems elsewhere in the valley.

1. Wetland and Riparian. We propose to study a microcatchment containing extensive wetlands. It is a well-defined 2-ha area that contains wetland communities and habitats representative of those on the floor of the upper valley. Precautionary measures to protect the catchment from investigator disturbance will be taken using a series of walkways and piers in sensitive areas. No manipulated experiments are planned for this catchment. The study will be conducted in two phases: (1) Basic mapping of attributes such as topography, vegetation, composition and production, animal populations, soils, sediments, and water chemistry will be made in 1986 and 1987. In this first phase, the catchment will be instrumented for water flow, chemistry, and temperature, and seasonal fluxes of all major materials (N, P, C, sediment, and major ions) through it will be estimated. Feeding habitats and food-web interrelations will be semi-
in this first phase in order to identify key organisms which represent trophic

structure (see section IV). All data will be recorded within a system of spatial coordinates and stored in a Geographic Information System (GIS). Analysis of this GIS will allow for habitat analysis for key organisms and provide the basis for assessing any changes as they occur. (2) Selected measurements will be continued in the intensively studied catchment in phase 2 (1988, 1989, and 1990), when the main objective of the study will be a series of manipulations to test system resistence and resilience within equivalent habitats outside of the catchment. The GIS will then serve as a basis for predicting the effects of change on the microcatchment. Manipulations will include increasing and decreasing water levels and the addition of nutrients. We are particularly interested in understanding the dynamics of the late-summer greening of small ponds and streams. This greening may be controlled variously by water temperature and flow rates, and by increased nutrient availability. We hypothesize that this fall greening may be the principal source of high quality food for the stream and lake communities which otherwise are limited to low quality particulate matter.

2. Green Lake 4. We will continue to monitor the volume and quality of water influxes through Green Lake 4. A map-based survey of many biotic and abiotic attributes will be made for Green Lake 4. This survey will not begin until 1988 and will, because of the nature of the lake, include data gathered in the three spatial dimensions. Water temperature, oxygen, chemistry, sediments; light penetration, plankton and periphyton populations; and substrate types would be recorded. A special emphasis will be made to study seasonal fluctuations of these attributes and especially recruitment and death of zooplankton. Trophic structure will also be investigated. The resulting geographic data base will again be incorporated into a GIS and used to identify important components, which can be monitored in the future and which might be the basis of *in situ* microcosm manipulation and lead to the testing of resistance and resilience hypotheses. For example, Green Lake 4 is fishless and the effect of predation by brook trout on trophic structure could be examined with appropriate *in situ* cages.

II. Subsurface Hydrologic Studies.

Hydrologic records are important to our research since water is an important transporting medium. Estimates of material flux are derived as the product of concentration (e.g., in solution) and volume flux of water. Our work to date has emphasized surface water exchanges, which tend to dominate in summer, and concern has been raised that we have not addressed subsurface flows in the same detail. We address this concern over subsurface flows under three headings.

1. Hydrologic tightness of upper Green Lakes valley.

We do not plan to test in detail for leaks through the dividing ridges around Green Lakes valley. The upper catchment is defined by sharp bedrock ridges of unaltered granites with almost no surficial cover. No detailed joint-structural surveys of these materials are available nor are they planned as part of LTER. Empirical surveys and drilling, which would be required to estimate the potential for hydrologic leakage into or out of the basin, would be uneconomic. We should point out that joint and fracture opening at shallow depth on the valley floor, e.g., near Green Lake 5, has been a relaxation response to deglacial unloading. Nothing equivalent to this is evident on the drainage divides, which were not glaciated during the late Pleistocene. We assume losses through the dividing ridges to be very small.

2. Leakage through the valley-floor deposits. We do intend to estimate the volumes of flows through the surficial cover adjacent to the gauging stations at Green Lake 4 and the Martinelli Snowdrift. This can be done by installing access wells in networks of three or more each at both sites. During the flow season, water levels in the wells will be monitored to define the piezometric surface. Saturated hydraulic conductivities can be estimated at the same wells by pump and slug tests. From the resulting data, groundwater flow directions and velocities will be derived through Darcy's Law and converted into saturated zone discharges by factoring in the depth of the surficial debris.

Validation of these results will be sought through dye tracing and dilution studies based on the same well networks. The same dilution approach will also be used in estimating leakage along bedrock fissures at the Green Lake 5 microcatchment.

3. Soil Moisture and Drainage. Unsaturated soil water fluxes and volumes will only be estimated for detailed study sites near the Saddle and in the Martinelli snowdrift. (In wet sites, flows can be defined from access wells by the Darcy model, above.) Since use of neutron probes in the source of a municipal

water supply may cause problems, we plan on using soil moisture blocks and tensiometers (the latter only in summer) to define moisture contents and gradients. At some sites (as per our original plans), we will measure subsurface flow interception by traps which will also provide samples of water in transit, as compared to that stored in soil interstices.

4. Phasing of these jobs. Simple groundwater access wells at two sites (Green Lake 4) and Martinelli) will be installed in summer 1986. At the time of installation, testing for permeability will be conducted. Thereafter, these wells will be surveyed for water levels on a weekly interval during summers and will also be available for water sampling and tracer studies.

Installation of soil moisture sensors and tensiometers will be phased with construction of interflow traps during 1986 and 1987. Full use of these, allowing for disturbance effects, will probably not be possible until 1988.

III. Coupling of Upland and Valley Studies.

The spatial separation of our two study areas and the logistics of travelling between them causes problems in integrating them as a single study of alpine ecosystems. There are two levels at which we propose to address this problem: conceptually and pragmatically.

1. At the conceptual level, our studies should be linked by a basis in common approaches and models. Thus, we will be concerned with material exchanges and storages in a set of drainage catchments on a variety of spatial scales which are, at least conceptually, nested. Three procedures will be used to formalize this:

(a) The geosystem model of French (1985) will continue to be developed. By its hierarchical nature, this is well suited to the variety of spatial scales being studied and will aid much in integration.

(b) The development of Geographic Information System (GIS), again on a variety of geographic scales, should provide an integrating framework within which studies are to be set. Further, it will allow us to synthesize models of materials fluxes in the fashion of Burns and Tonkin (1982) and Caine (1979) in a more quantitative and rigorous manner than was done by those authors.

(c) The common objective of our studies of trophic structure will be to define food webs in a number of alpine systems (Section IV). This will provide a conceptual similarity for those research topics which it involves.

2. Empirically, the coupling of our work on upland and valley-floor systems will be forced by four characteristics:

(a) We intend to study similar communities, by the same procedures, in both areas.

(b) We plan to emphasize the same materials in our studies of fluxes in both areas. This supports the common objective of evaluating system resistance and resilience by defining these properties with respect to a common currency, for example, water, C, N, and P.

(c) We intend to evaluate the spatial homogeneity of an input common to both systems: atmospheric deposition. This involves biotic (pollen, insects, plant debris) and abiotic (dust) materials as well as those dissolved in precipitation and which are important to both terrestrial and aquatic systems in the Colorado alpine.

(d) Some of the sites of our study will be nested hierarchically within a system that is intermediate between upland and valley floor, e.g., the Martinelli snowdrift.

Finally, we have reduced considerably the number of projects and investigators for the second phase of our study. This, too, should increase the opportunities for integrating these parts.

IV. Integration of Trophic Component Studies

Core research area 2 of LTER calls for the study of spatial and temporal distribution of selected populations which represent trophic structure. The geosystem model (French 1985) provides a first integration of these studies in terms of productivity, phenology level, and population structure. Further integration of trophic studies will be forced by focusing on (1) change of state (phenological patterns resulting from variability of weather and resulting changes in feeding relationships) and (2) food web interactions.

1. Phenology. An ecosystem-wide phenological study was initiated as a cross-subproject theme during Phase I. Species were selected to represent major trophic levels as follows: primary producers - 10 species; insect herbivores - two grasshopper species; insectivores - two bird species; and mammalian herbivores - two species. Studies of carnivores were not undertaken as individuals are too rare to make the effort worthwhile. However, opportunistic observations will continue to be made. Simultaneous data collection for each trophic level provided the first within-ecosystem published record of phenophase diagrams (Halfpenny et al., 1984a, 1984b). These diagrams show the timing of biological events during the growing season and their relationship to driving variables such as insolation and precipitation. Initial modeling efforts have defined phenological relationships with temperature which will be useful in predicting organismal changes caused by temperature anomalies, including possible warming effects of greenhouse gases. Additional models will be developed to predict the relationships between the timing of biological events at different trophic levels.

The phenological data sets are sensitive indicators of climate change and represent important baseline and yearly indicators of weather and related phenomena such as food availability. During Phase II, we will continue to collect key data sets as part of the archiving of the long-term data base. A manuscript detailing work to date is now in progress for submission to American Scientist early in Phase II. There were, however, many more data collected than could be analyzed under the CULTER budget, and a proposal will be submitted to NSF to allow for complete reduction of the data base and subsequent mathematical modeling on appropriate time scales. This portion of the phenology study will have to wait for additional funding.

2. Food Web interactions. Studies of food web interactions will consist of three stages: summarization of existing data, selection of key species, and field studies to supply information where it is deemed necessary to fill existing gaps. During stage one, existing papers and CULTER data sets will be analyzed to develop producer-consumer interaction matrices. From these matrices, conceptual food-web models will be developed for aquatic and terrestrial systems as heuristic tools to identify important gaps.

Two food chains, the bistort-gopher and the vegetation-pika chains, were identified and studied during Phase I. Bistorts were selected because of their circumpolar distribution, identifiable life history strategy, history of study, and because they represent a major component in the diet of gophers--the gopher representing a keystone species in the alpine. Expanded studies, during Phase II, will explore the spatial and temporal interactions within the bistort-gopher food chain. The dynamics of the pika population and the relationship to primary productivity were also analyzed. Pikas appear to remove substantial amounts of primary production each season and their densities clearly reflect the timing of vegetation greenup (Golian, 1985). A manuscript of this work is in preparation for submission to Journal of Mammalogy. Pika populations will be monitored at the peak of the growing season during Phase II.

A third chain, the graminoid-deer and elk chain, has been selected for Phase II research. This chain will be particularly important for the studies in the Martinelli and lower basins, where grazing ungulates represent important movers of ecosystem materials. Additional chains may be identified by the stage one process of food-web analysis.

Phase II field studies will quantify relationships within the gopher and elk chains mentioned above, especially in terms of nutrient movements between habitats and interactions at the population biology level. Surveys of ungulate herds and habitat usage will be added. Habitat usage and plant-animal interactions will be analyzed on the GIS system at spatial and temporal levels to determine their role in landscape formation. Continued field studies will elucidate other food-web interactions at a qualitative level.

V. Belowground Dynamics

The importance of the belowground component of the tundra ecosystem is well recognized (Webber, 1977; Webber and May, 1977). However, our original proposal called for no special program to focus on this other than to monitor fluxes of materials and biomass in response to the resistance and resilience experiments. The reviewers saw this as a serious omission and have recommended studies of the belowground processes relating to primary production, nutrient dynamics and controls, and organic matter accumulation and removal. We are prepared to review this omission during 1986 by contracting to Dr. Robert Woodmansee, Colorado State University, to guide us in making a current state-of-knowledge assessment, to develop initial conceptual models of the belowground alpine system, and to plan an appropriate research strategy. Dr. Woodmansee would lead a week-long workshop to be preceeded by the state-of-knowledge assessment. Sufficient funds have been identified in the budget for this belowground assessment and for the ensuing research program. This cooperation between LTER sites should lead to comparative studies of belowground systems between the Central Plains Experimental Range LTER site and CULTER and we would endeavor to expand this intersite activity to at least the grassland sites of the LTER network.

VI. Evaluation of a Catastrophic Disturbance

The central theme (resistance and resilience in alpine ecosystems) of our proposed research is clearly germane to disturbance studies, which have also been important in our Phase I research. Resistance is intuitively related to a threshold concept of catastrophic disturbance, whereas resilience relates to the speed of system recovery. The historical record from the Colorado alpine already provides a system-wide context within which disturbance regimes will be considered. Traditionally, this record has been interpreted in terms of climatic variation and responses to climatic change on a relatively large time-and-space scale (10^6 m^2 and 10^3 yr: Table 1). On even larger scales, glacial fluctuations affecting entire alpine valleys define the physical landscape and represent a shock from which system recovery continues. At smaller scales, a variety of physical catastrophes are possible: rockfall, debris flow, channel breakout, large snow avalanches, summer drought, etc. We will continue to evaluate these disturbances opportunistically as they occur within the Indian Peaks region of the Front Range with the view to revising the estimates of Table 1.

Setting transient events in a temporal context will be done on the basis of available instrumental and proxy records, as Payton and Brendecke (1985) have done for flood-producing events. Other studies that have attempted to estimate disturbance events and their significance in landform development in our study area are those of Harbor (1984) and Caine (1985) and these will be continued.

Using these data to define the nature of experimental manipulations is subject to great uncertainty but can be done in a qualitative way. Experiments involving gopher disturbance, trampling, and snowcover modification should all be set in the context of basic probability statements of their actual occurrence. The "natural" experiments involving recovery from past disturbance initiated during Phase I will continue to be monitored during Phase II. These will provide the equivalent of a recovery-period which, with estimates of disturbance probabilities, will provide a semi-quantitative evaluation of the importance of disturbance events on different parts of the alpine system.

VII. Publications

The University of Colorado Long-Term Ecological Research program acknowledges the importance of disseminating of research results and CULTER personnel are firmly committed to publishing their results in the open, refereed literature. Our plan for the next five years stresses the importance of synthesis articles. These synthesis articles are designed to bring together the work of our interdisciplinary team. In addition, each principal investigator is committed to the publication of one major article per year in the refereed literature. In accordance with the perceptions of the reviewers and NSF personnel, few articles will be submitted to Arctic and Alpine Research and most will go to other major journals in the field of ecology and other specialized fields.

Listed below are the synthesis articles which CULTER personnel, as a group, are committed to produce during the first two years of Phase II. These articles represent the culmination of the first phase of LTER and our current state of knowledge about alpine ecosystems. Further synthesis articles will be produced in the last three years of Phase II. The exact nature and direction of these articles will be determined by the first two years of our research on landscape ecology and materials movement.

1. "The Colorado alpine landscape: A geosystem model (Lead Author - French) for submission to Ecological Modeling. This article will be an expansion and specific application of the general geosystem model developed as part of the conceptualization of the Phase II proposal. The model will not be a complete ecosystem model but will serve to increase our understanding of the alpine system.

2. "Niwot Ridge: A continental, mid-latitude alpine ecosystem" (Editor - Halfpenny) for publication in book form. This book will present the state of knowledge on our alpine ecosystem and will be structured around the Geosystem Model.

3. "An Evaluation of tundra paradigms" (Author - Webber) for submission to the Annual Review of Ecology and Systematics. The article will examine the accepted paradigms about the structure and function of tundra organisms and systems. It takes the view that tundra has no unique individual characteristics that are not found in other biomes.

4. "Variability in alpine ecosystems "Author - Caine) for submission to Ecology. The concepts of scale-independent self-similarity and the procedures of geostatistics and serial analysis offer a framework for the examination of spatial and temporal variability in ecologic data. If the results are truly useful they should give a basis for extrapoltion and prediction, for estimating site representativeness and for model construction.

5. "Persistence and nutrient cycling in LTER sites" (Lead Author - Webber) for submission to Ecology. This paper will report on the findings of the planned intersite activity which will examine the relationships between the response of ecosystems to disturbance as a function of their nutrient cycling characteristics.

6. "Oral History of Niwot Ridge" (Lead Author - Ingraham) for preparation as an INSTAAR Occasional Paper. This will be a report on the proposed workshop

where "old-timers" will be brought to the Mountain Research Station to explain and record their views of the the scientific history of Niwot Ridge and the functioning of alpine ecosystems.

7. "Alpine tundra ecosystem phenology: Patterns, processes, and predictions" (Lead Author - Halfpenny) for submission to American Scientist. (See section IV).

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