

PROGRESS REPORT

Introduction

This progress report is for the period February 1990 - July 1991 for the Central Plains Experimental Range Long Term Ecological Research project at Colorado State University. Our previous report was included with our 1990 renewal proposal.

Significant Accomplishments

Pattern and control of primary production

Aboveground Production

Aboveground net primary production has been measured at four sites since 1983. Uplands ungrazed since 1969 are 27% less productive than grazed uplands (Fig. 1). Annual differences between the grazing treatments range from +3 to -61%, but the differences show no relationship to annual precipitation. Grazed lowlands are 41% more productive than grazed uplands. The range in annual differences between topographic positions (26 to 55%) is less than between grazing treatments, but again there is no relationship with annual precipitation. Additional ANPP work (long-term grazing by defoliation by water interactions) is described in the grazing section and results from our ^{14}C experiment are described below.

Belowground Net Primary Production

Large plots were labeled with ^{14}C in 1985 to assess short-term patterns of carbon allocation and the long-term process of herbivory, death, decomposition, and to compare estimates of net aboveground, crown, and root primary production using ^{14}C dilution, ^{14}C turnover, and traditional harvest methods (Milchunas and Lauenroth 1991). Exudation was 17% of plant ^{14}C after stabilization of labile pools. Turnover estimates for leaves, crowns, and roots by ^{14}C turnover were 3, 5, and 8 years, respectively, yielding estimates of belowground production that were much lower than previously thought. Harvest-peak-crop underestimated ANPP by only 16% compared with estimates by ^{14}C turnover, but estimates of root and crown production by summation of positive increments in biomass were up to 160 and 353% greater than by turnover. In contrast to reliable estimates by ^{14}C turnover, ^{14}C dilution estimates of root production were anomalous. The anomalous estimates were attributed to nonuniform labeling of tissue age classes resulting in differential decomposition/herbivory of ^{14}C . ^{12}C through time, as well as movement and loss of labile ^{14}C through the first growing season.

Spatial and temporal distribution of populations chosen to represent trophic structure

Population dynamics of *B. gracilis*

In 1989 we initiated a field study to evaluate the population dynamics of *B. gracilis*. We selected ten locations to represent the variability in soil texture and grazing intensity at the CPER. At each site, seed production, storage in the seed bank, and seedling establishment data were collected in 1989 and 1990. Seed production data were collected on an individual plant basis for 96 plants at each site, and included the number, weight and height of flowering culms, numbers of inflorescences and viable seeds, and plant basal area and biomass. Grazing was important in mediating the effects of soil texture on seed production. Different relationships were found for grazed and ungrazed locations between seed production and number of flowering culms on a per plant basis, and between seed production and clay content on a square meter basis (Fig. 2). Density of viable seeds per plant was linearly related to density of flowering culms per plant, although the slope for ungrazed sites was larger than that for grazed sites (Fig. 2a). For both grazed and ungrazed sites, density of viable seeds (no./m²) was negatively related to clay content of the soil. A seed budget was developed for each site by comparing seed production in the fall of 1989, seed storage in the soil in April, 1990, and seedling establishment in June, 1990. Plans for 1991 include establishment of permanent plots for demographic analyses, and a study to evaluate the mortality of individual *B. gracilis* plants as a result of death of all or part of a plant.

Pattern and control of organic matter accumulation and of inorganic inputs and movements of nutrients

Landscape-scale ¹⁵N Experiment

The objective of this experiment is to evaluate the controls over the distribution of nitrogen into pools of soil organic matter of various turnover times. The final ¹⁵N was applied in the spring of 1989 and initial samples were taken in the fall of 1989. Because of the expense involved in analyzing these samples and the long-term nature of the experiment, we are not finished with the analysis of the initial sampling. We will re-sample the plots at three or four year intervals for the next 20 to 30 years.

N Uptake by Grasses and Shrubs

Plots containing both grass (*B. gracilis*) and shrub (*Atriplex canescens*) plants were labeled with ¹⁵N injected at four depths in the soil profile (5, 25, 45, and 65 cm), and plots containing grasses from around which shrubs were killed or shrubs from around which grasses were killed two years prior to labeling were injected with ¹⁵N at 5 and 65 cm in the soil profile. Shrubs exploited nitrogen where ever it was located, but grasses were relatively more constrained to exploiting surface pools (Fig. 3). Shrubs tended to affect grasses, but grasses had little effect on shrubs. No difference in internal recycling

abilities of the two life-forms was observed, and soil nitrogen concentrations did not differ under versus between shrubs.

Patterns and frequency of disturbance to the site

Long-Term Grazing

Previous work on the grazing treatments that were established in 1939 showed that heavily grazed shortgrass steppe was more similar to disturbed sites (Milchunas et al. 1989, 1990), had little effect on crown or root biomass (Milchunas and Lauenroth 1989), and was more susceptible to invasion, but had lower ANPP and soil nutrients compared with ungrazed treatments (Milchunas et al. submitted). Even with lower ANPP, equal compensation to current grazing was observed. An experiment was designed to examine how long-term grazing interacts with current defoliation and soil water availability. ANPP increased with defoliation in a year of average precipitation in lightly grazed treatments, and had no effect in heavily grazed treatments (Fig. 4). Defoliation and/or long-term grazing treatment had no effect on ANPP in a simulated wet year. Rain use efficiency did not differ between long-term ungrazed, lightly, or heavily grazed treatments in a wet year, but was lower in the ungrazed treatment in the year of average precipitation (Fig. 5).

We are continuing to monitor the recovery of the nutrient stress sites established in 1971-77. At the time of our last report, data through 1987 suggested a relatively rapid period of recovery. An additional two years of data show a period of retrogression, suggesting long-term cyclical trends in community composition of disturbed sites (Fig. 6a). The dominant species of undisturbed shortgrass steppe (*B. gracilis*), usually considered to be very stable, appears to display both year-to-year fluctuations and long-term oscillations (Fig. 6b). We hope to relate long-term changes at the population and community level to abiotic variables after collection of a sufficiently long data set. Preliminary analyses of short-term fluctuations in response to abiotic variables suggest, for example, that current-year densities of *B. gracilis* are correlated with current and previous year's precipitation during summer (June, July, August), forbs with previous winter (Dec., Jan., Feb.) and current and previous spring (March, April, May) precipitation, whereas densities of exotic-opportunistic species are correlated with their abundance the previous year and precipitation the previous fall (Sept., Oct. Nov.).

Small-scale disturbances

We continued our study of the effects of interactions among disturbance characteristics for small disturbances (0.1 - 0.3 m- diameter) by comparing plant recovery on naturally-occurring and artificially-produced disturbances of different type, seasonality, size, and location by soil texture. This study began in 1985 and species composition data have been collected annually since that time. Although annuals were important on these disturbances initially, perennial grasses and forbs are currently important components of the vegetation on the disturbed areas. Additionally, *B. gracilis* plants have recovered on some of the disturbances, with long-term monitoring needed to

determine the length of time required for this species to dominate on these areas.

We also evaluated the effects of cattle fecal pats, the most frequently-occurring small disturbances of sufficient size (0.1-0.3 m-diameter) to kill *B. gracilis* plants, on plant mortality and recovery. The time required for pats to decompose indicates the cumulative effect of pats through time; both in terms of the probability of plant mortality and the length of time the area is disturbed before plant recovery can begin. Two years were required for most (90%) pats to decompose; slow decomposition occurred after that time (Fig. 7a). Plant recovery by *B. gracilis* on areas killed by pats occurs within two years; this species dominated plant cover on disturbed areas within three years for both types of plant communities where the study was conducted (Fig. 7b). *Buchloe dactyloides* (buffalograss) was also an important perennial grass to recover within two years after the disturbances occurred.

Synthesis and intersite activities

Grazing Impacts Over a Range of Environments

Why certain plant communities are very sensitive to grazing and others are not has generated a large volume of quantitative, site specific research and qualitative, theoretical considerations. We used quantitative techniques to analyze close to 300 grazed-ungrazed comparisons from studies conducted across 6 continents.

Average levels of consumption for shrubland sites was greater than for grassland sites, but ANPP was lower for shrublands. Grazing of areas with a shrub component is often reported to lead to the conversion of grassland to less desirable shrubland -- Why then are we grazing shrublands at a relatively greater intensity than grasslands?

Of nine potential variables, species dissimilarity of grazed vs ungrazed grasslands plus shrublands was most sensitive to ANPP, followed by evolutionary history of grazing, and consumption (intensity of grazing). Dissimilarity increased with increases in each of the three variables. The most productive sites were more susceptible to change when grazed at the same percentage removal rates, and past history of grazing was more influential than current levels of consumption (Fig. 8).

Increases in the dominant species with grazing was most likely to occur under conditions of short evolutionary history, low consumption, and low ANPP. Bunchgrasses were most negatively impacted by grazing (-43%), followed by sodgrasses (-29%), grass-like (-25%), shrubs (-16%), and forbs (+18%). The analyses support the perception of grazing as a factor in the conversion of grasslands to shrublands and perennial grasslands to annual grasslands.

Although most conditions resulted in a negative impact of grazing on ANPP, conditions of long evolutionary history, low mean high temperatures, low ANPP, and low consumption resulted in slight positive effects; the statistical models and the data support the hypothesis that herbivory may in some situations increase productivity.

Differences in root mass were not related to differences in ANPP with

grazing. Further, positive effects of grazing on root mass occurred in 61% of the cases where grazing had negative effects on ANPP. The common perception that grazing generally has negative effects on root systems is not supported, and the mostly negative effects of grazing on ANPP are offset when total plant production is considered.

Changes of root mass, soil organic matter or carbon, or soil nitrogen with grazing were not related to species dissimilarity of grazed versus ungrazed sites. The use of species based criteria in the management and assessment of rangeland condition and trend, as is the current practice on government and private lands, may lead to erroneous conclusions of the long-term ability of grazinglands to sustain productivity.

Modeling plant community dynamics

Our approach to modeling plant community dynamics has been to use a spatially-explicit individual-based gap dynamics simulation model (STEPPE) to evaluate the recovery of shortgrass communities after disturbances. Because the results of this work have indicated the importance to recovery of processes associated with recruitment, especially for *B. gracilis*, our modeling efforts have recently included a focus on understanding controls on the recruitment of *B. gracilis* seedlings, and in particular effects of weather and site conditions on recruitment and recovery.

Previous experimental studies indicated the germination and establishment of *B. gracilis* seedlings is dependent upon the occurrence of a set of conditions related to the timing in availability of soil water near the soil surface where seeds are located, and in the upper 30 cm where root growth of seedlings occurs (Briske and Wilson, 1977). Timing of precipitation and temperature, and effects of soil texture are important to the probability of these conditions occurring and resulting in seedling establishment. We used a multi-layer soil water model (SOILWAT) to evaluate the relationship between the probability of seedling establishment in given year and soil texture. Simulations were conducted in Monte Carlo fashion using a first-order Markov analysis of historical weather data from the CPER. Establishment probabilities were small (<0.1), and were linearly related to the silt and clay content of the soil (Fig. 9). These small probabilities indicate that, on average, establishment events of *B. gracilis* range from once in 12.5 years to once in >400 years.

Simulations conducted with the STEPPE model also indicated the importance of soil texture to the recovery of *B. gracilis* after disturbances of various sizes (Fig. 10). Average probabilities of seedling establishment from the SOILWAT simulations were used in STEPPE based on silt and content. Disturbances on the soil with a large silt content (silt loam) had large *B. gracilis* biomass through time compared to soils with low silt content (sandy clay loam, loamy sand). Additionally, recovery was dependent upon disturbance size, where small disturbances recover faster than large disturbances. A nonlinear relationship was found between the proportion of plots recovered by *B. gracilis* in year 500 and silt content of the soil (Fig. 11). Disturbance size was less important than soil texture in determining plant recovery.

Recently, we linked the STEPPE and SOILWAT models to allow

feedbacks between plant processes and soil water processes to affect plant recovery and soil water dynamics. The models were linked using network functions under the UNIX operating system. By contrast to previous simulations of small and intermediate-sized disturbances (2-49 m²), these simulations represented large-scale disturbances, and in particular plant recovery on abandoned agricultural fields; disturbances were represented by a transect of interactive plots where one STEPPE and one SOILWAT simulation were conducted for each plot. Spatial processes between plots were associated with the dispersal of *B. gracilis* seeds from recovered plots to nearby disturbed plots. Simulated fields on the soil with the largest silt and smallest clay contents (silt loam) had the fastest recovery of *B. gracilis* biomass through time compared to soils with large silt and clay (silt clay) or with small silt and intermediate clay (sandy clay loam). Old fields on silt loams were the only disturbances of those simulated where *B. gracilis* recovered to the end of the 42 m transect by year 200.

Shortgrass Steppe Synthesis Volume

We have begun work on the design of a book length synthesis of the research conducted by USDA and other researchers particularly those working under funding from two NSF funded programs, the International Biological Program and the LTER program. We are currently in the stage of setting a time schedule and outlining the book. We will soon move to defining individual chapters and preparing outlinings.

Data management

Our data management efforts for the past 18 months have focused on two issues; organization and expansion of our data storage capabilities, and development of tools for easy data access and analysis. Our data management over the past 2 years has slowly been migrating from a mixed UNIX/DOS environment to a predominantly UNIX environment. We still have DOS machines and many project participants that use them but our recent development efforts have been largely focusing on the UNIX environment. We continue to provide mechanisms for transferring data from the UNIX network to DOS computers so that investigators can make use of DOS based analysis and display software.

Limited storage capacity over the past years was creating data management and organization problems. Recovery of archival data required the intervention of our programmers to mount tapes and restore files to disk. Our recent acquisition of an additional 3 Gigabytes of disc storage as well as optical drives will solve our short and perhaps long-term storage problems. We plan to keep active data on the hard drives and use the optical drives for files that are used only infrequently. The active data include historical data sets which can be accessed without concern about ownership of the data.

The ability to store the majority of our data on disks has stimulated the development of software tools to facilitate access to the data without programmer intervention. We now have available a collection of data

manipulation tools that were derived from software developed for simulation modeling. These allow individuals to view the data in a graphical form and to create files containing subsets of the data to use for further analysis. The data files are accessed through servers running on the host UNIX computer. A typical client program is called LTERmenu. LTERmenu has been made available to investigators at other sites through the mechanism of anonymous ftp. LTERmenu uses a series of menus that allow investigators to select data sets to be manipulated (Fig. 12). The software is based upon the system of data file descriptions that we developed to document our data sets. LTERmenu retrieves the data file description from the server on the host computer, then uses the data description to retrieve data from the data files. Specific data items are assigned names in the data file descriptions, and these names are loaded into a menu when a data set is selected (Fig. 13). The names of data items are used to select data for plotting, or to be extracted from the data file and displayed in a tabular format (Fig. 14). The server may download the entire data file, or download only selected portions of the data. LTERmenu is a prototype for testing menus and the interprocess communication library we are developing. LTERmenu runs under the Sun Microsystems Sunview shell. We plan to make available a version that runs under OpenLook (the X windowing environment), and will attempt to provide a version that will run under DOS on PCs. Last year we distributed to the LTER data managers and other interested people a PC program and database that allowed them to retrieve entries from our local LTER bibliographic data base. Entries could be located by author, keyword, or simply by browsing through the database. The entries can be saved in either ASCII or WordPerfect formats. We are currently extending this capability to our Sun computers, and plan to make this software freely available within the next year.

Figure Titles

Figure 1. Aboveground net primary production ($\text{g}/\text{m}^2/\text{yr}$) for 1983-90 in moderately grazed lowland, midslope, and upland plant communities and uplands ungrazed since 1969.

Figure 2. (a) Relationship between density of flowering culms per plant and density of viable seeds per plant for two grazing intensities. (b) Relationship between percentage clay content and density of viable seeds per m^2 for two grazing intensities.

Figure 3. ^{15}N concentration (%) of shrubs (leaves, live stems, and roots) and grasses (leaves, crowns, and roots) when soil was labeled at either a 5, 25, 45, or 65 cm depth in the profile. Data is from plots with both life-forms growing in the same plot.

Figure 4. A) Aboveground net primary production ($\text{g}/\text{m}^2/\text{yr}$) of lowland plant communities for light and heavy grazing treatments established in 1939 that were not defoliated or defoliated at levels simulating cattle grazing and not watered in an average year of precipitation or watered to simulate a wet year. B) Rain use efficiency ($\text{g}/\text{m}^2/\text{year}/\text{mm}$) for long-term ungrazed, light, and heavy grazed lowland plant communities that received the water treatments described above.

Figure 5. Species dissimilarity (1-Whittaker's index of community association) for 1975-77 and 1982-89 and *B. gracilis* densities for 1971-72, 1975-77, and 1982-89 on control, water, nitrogen, water plus nitrogen treatments and areas disturbed by white-grub larvae. The nutrient stress treatments were applied from 1971-1975, and white-grubs killed large areas of perennial grasses in 1976. Species dissimilarities were calculated using density data, and by comparing each treatment with its respective control and controls against each other.

Figure 6. (a) Fecal pat decomposition through time for three types of pats (intact, decomposing, gone or decomposed). Results are average of 112 pats from five sites at the CPER (two *B. dactyloides*- and three *B. gracilis*- dominated communities). Study began in 1987 (year 0). (b) Recovery of *B. gracilis*, *B. dactyloides*, and total cover on sites disturbed by fecal pats in two community types (*B. gracilis*- and *B. dactyloides*-dominated) at the CPER. Pats of variable sizes (5 to 40 cm-diameter) were deposited in Year 0 (1987). Plant recovery is shown for Year 2 (1988) and Year 3 (1989).

Figure 7. Species dissimilarity of grazed versus ungrazed communities (1-Whittaker's index of community association) for grasslands and shrublands. Data is from 276 pairs of grazed-ungrazed comparisons across six continents; and models were generated by kriging and multiple stepwise regression using six other potential independent variables. Dissimilarity values of 1 indicate completely different communities and values of 0 indicate completely similar communities.

Figure 8. Average annual probability of establishment of *B. gracilis* seedlings for ten soil textures by (a) silt content (b) clay content.

Figure 9. Average simulated aboveground biomass of *B. gracilis* for 500 years for five disturbance sizes and three soil texture classes (a) silt loam (b) sandy clay loam (c) loamy sand.

Figure 10. Average proportion of plots recovered by *B. gracilis* after 500 year-simulations for five disturbance sizes as a function of silt content.

Figure 11. Average simulated aboveground biomass of *B. gracilis* on abandoned agricultural fields for three soil texture classes at four times.

Figure 12. LTERmenu allows investigators to select and view data via the Internet. The data are selected using a series of menus.

Figure 13. Names associated with the data fields are loaded from the data file description and placed into a list menu. The investigator can select data to be displayed in a table or a figure from the list menus.

Figure 14. After selecting the X and Y variables, a plot of the selected data can be displayed.

Figure 1

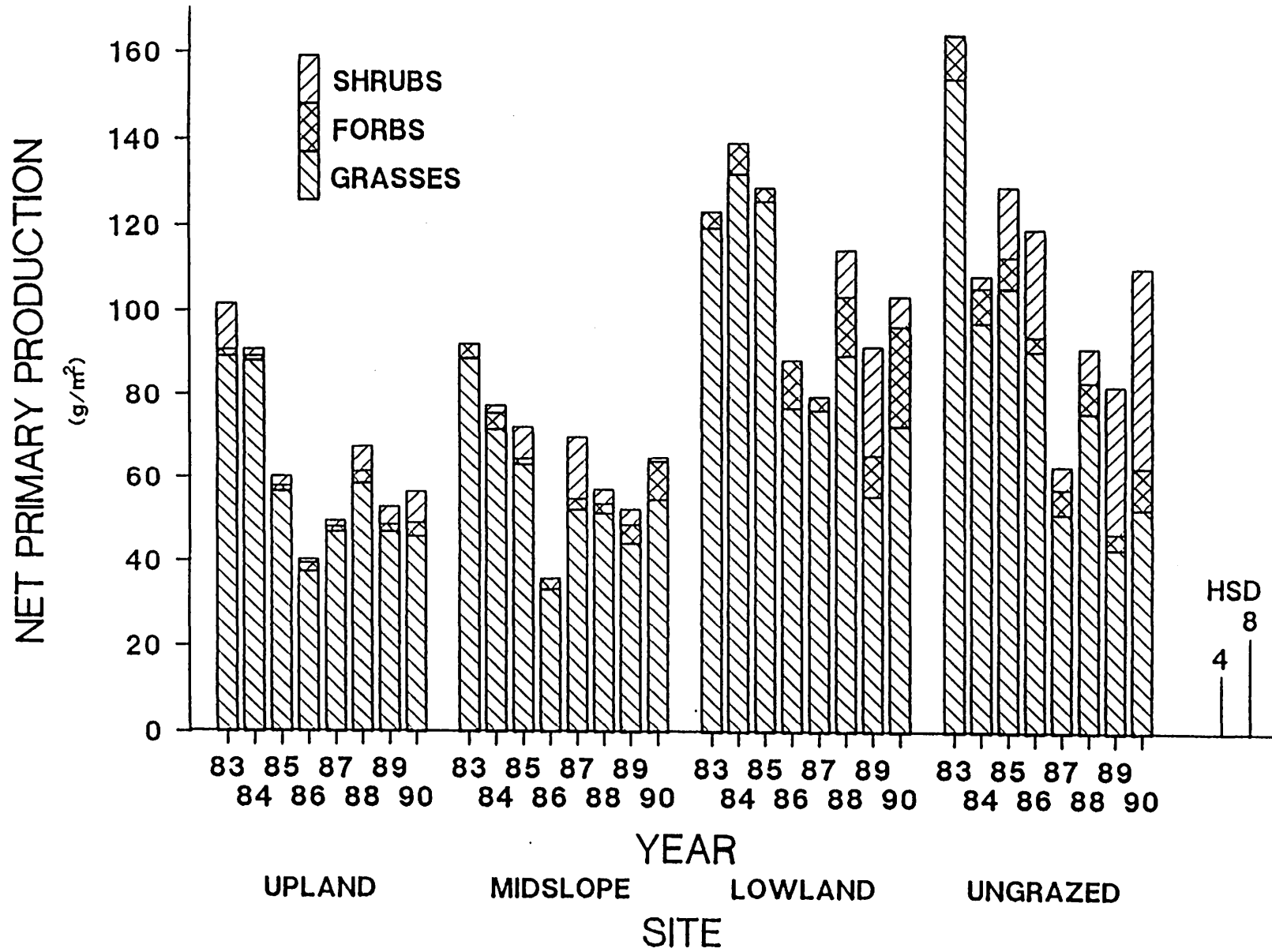


Figure 2

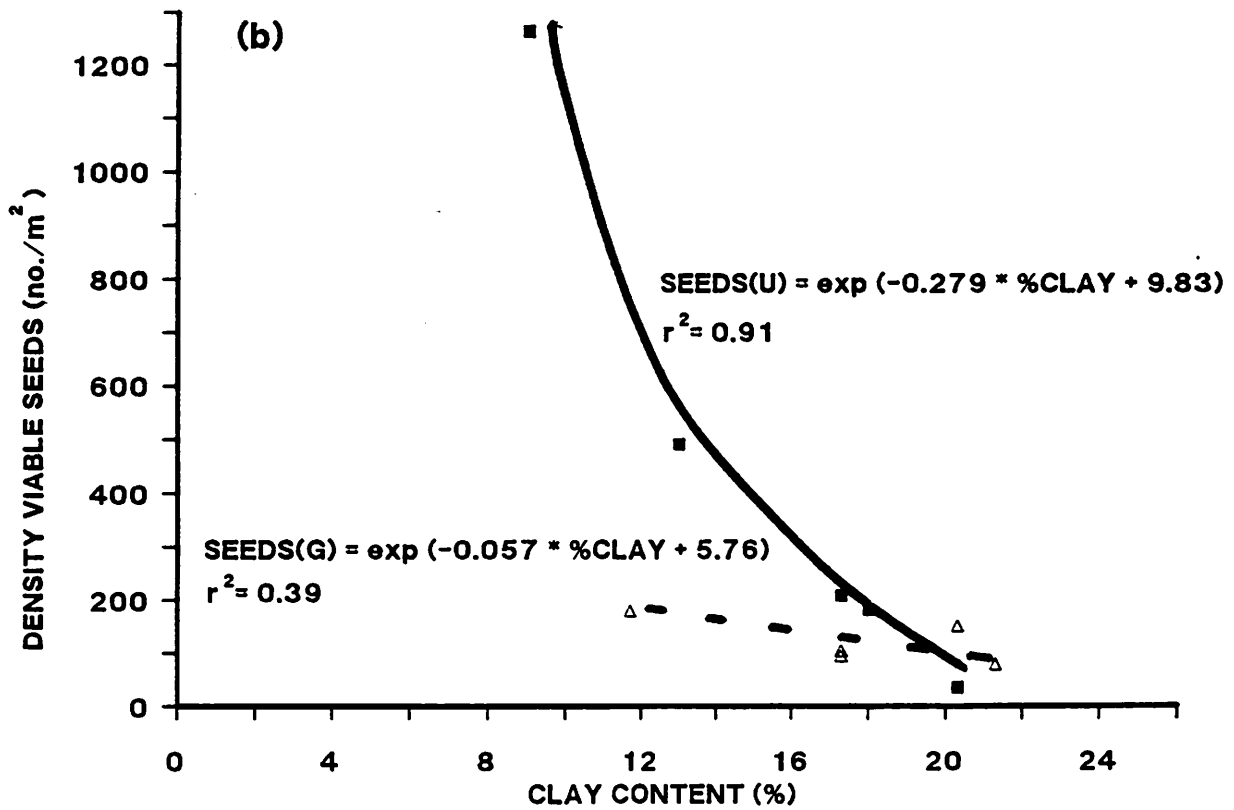
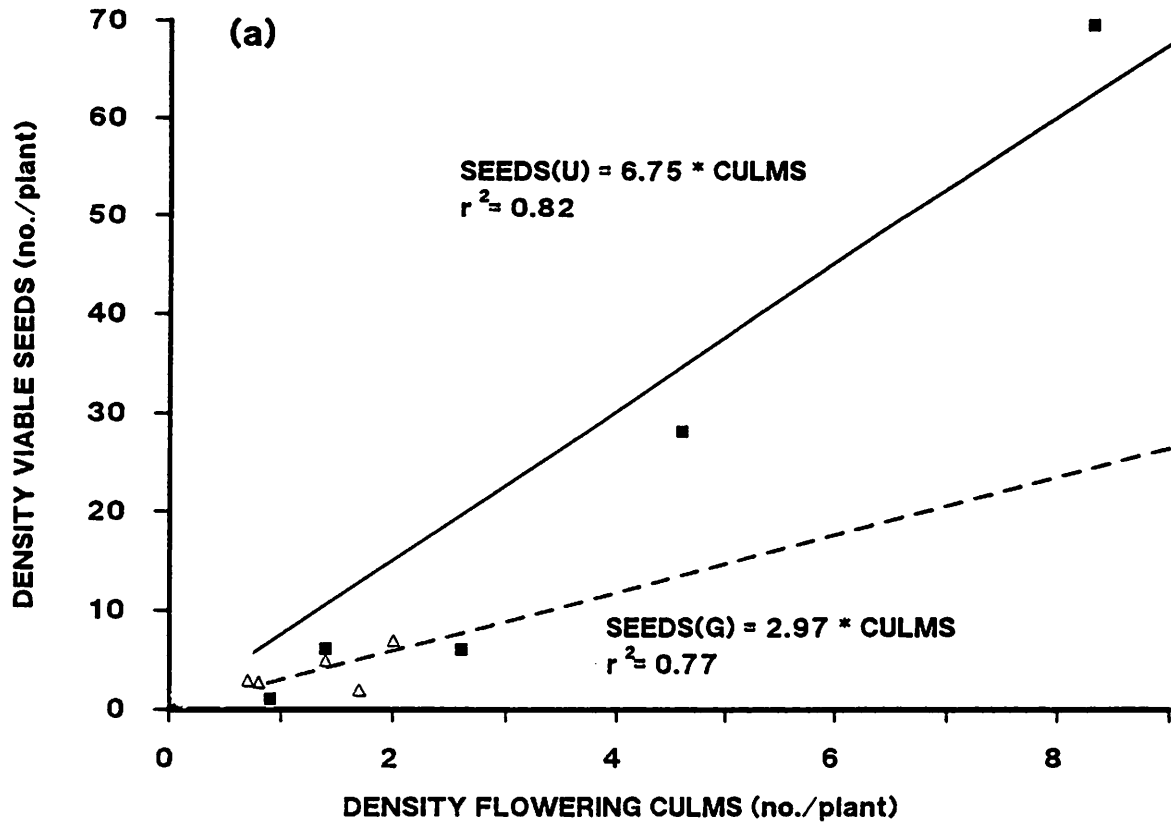


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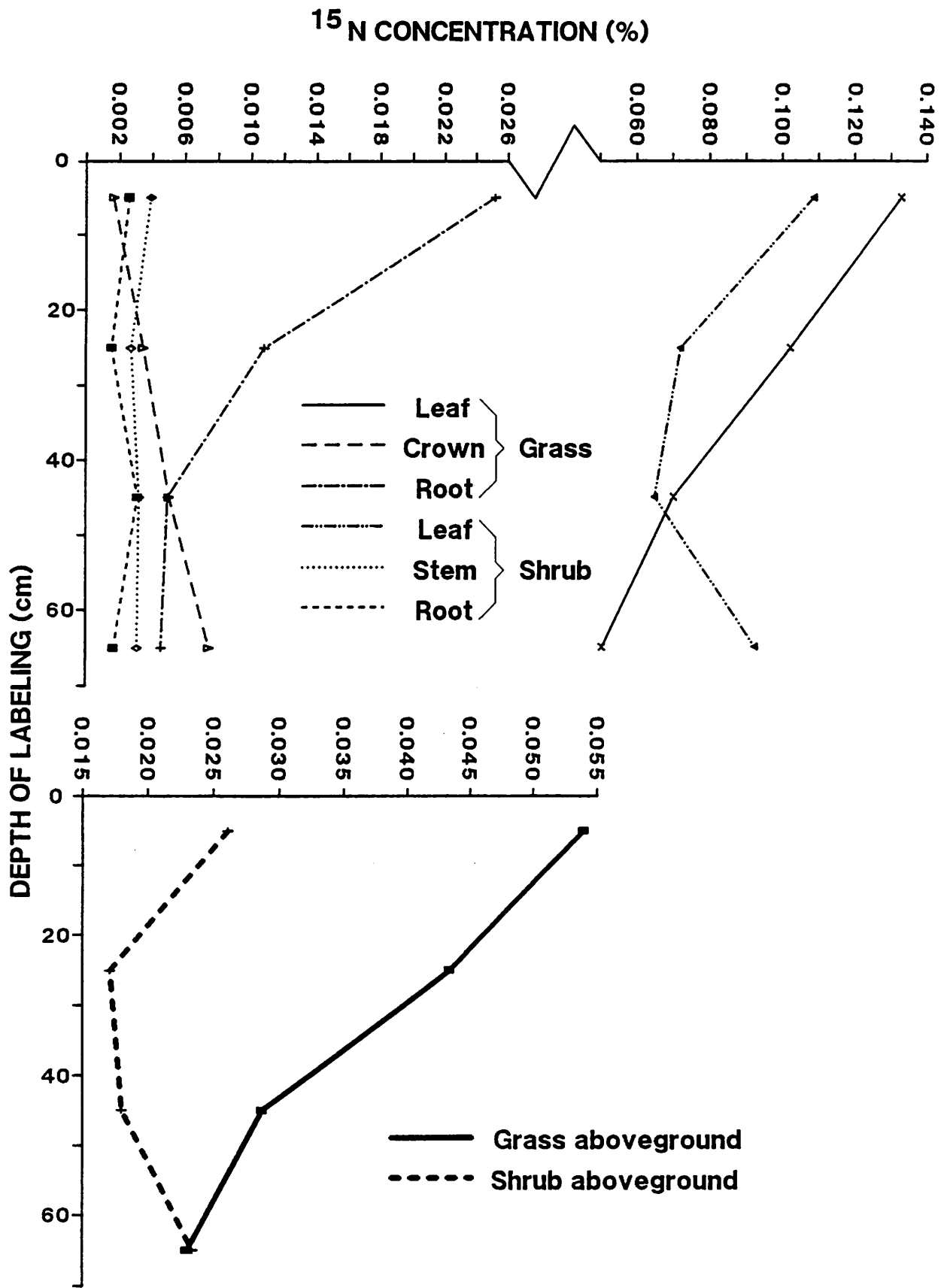


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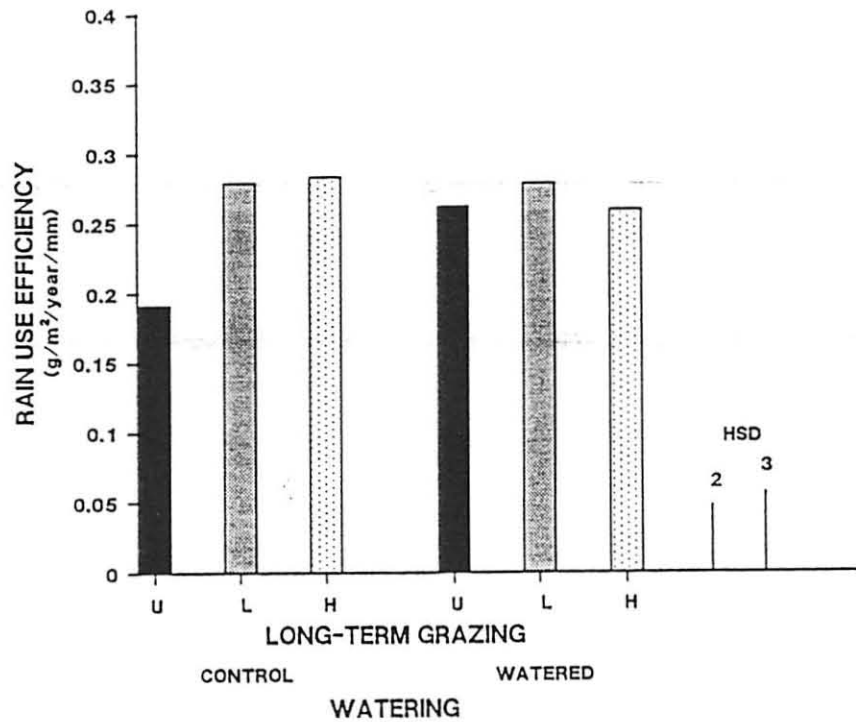
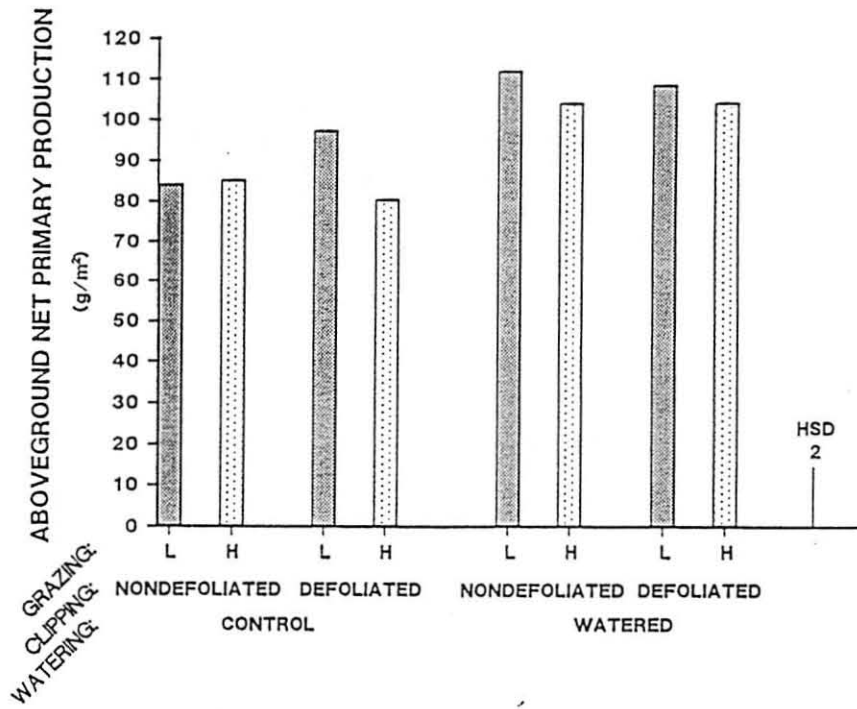


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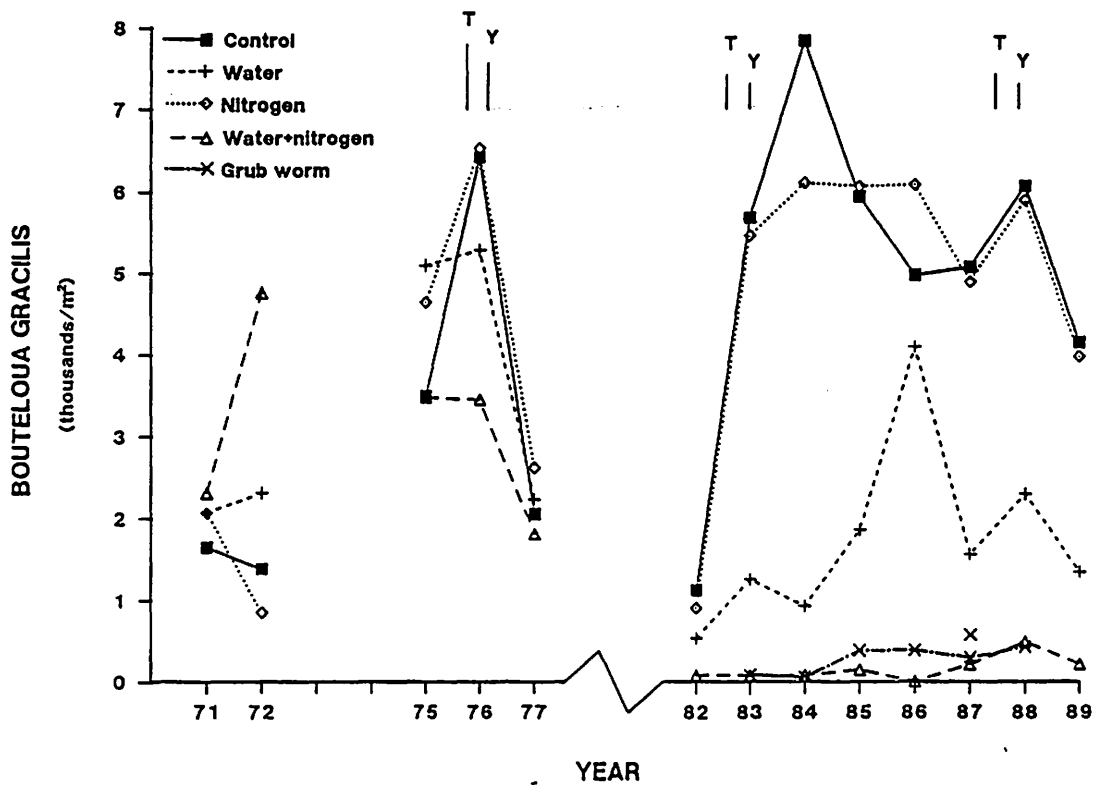
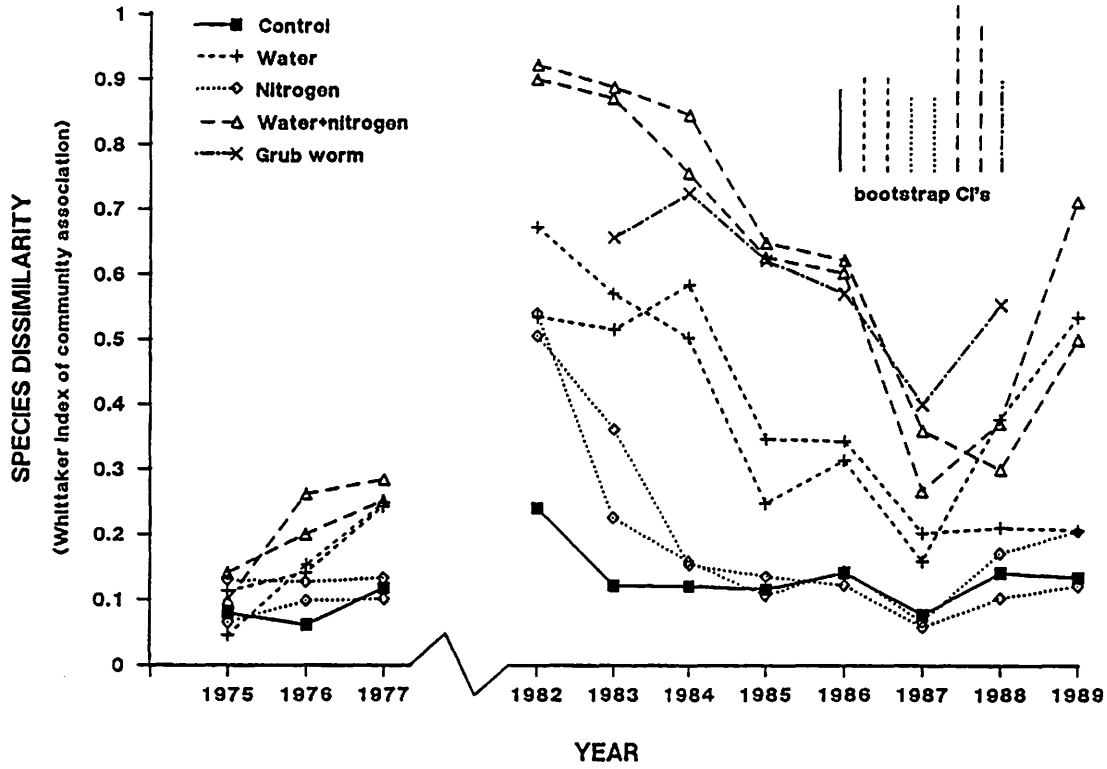
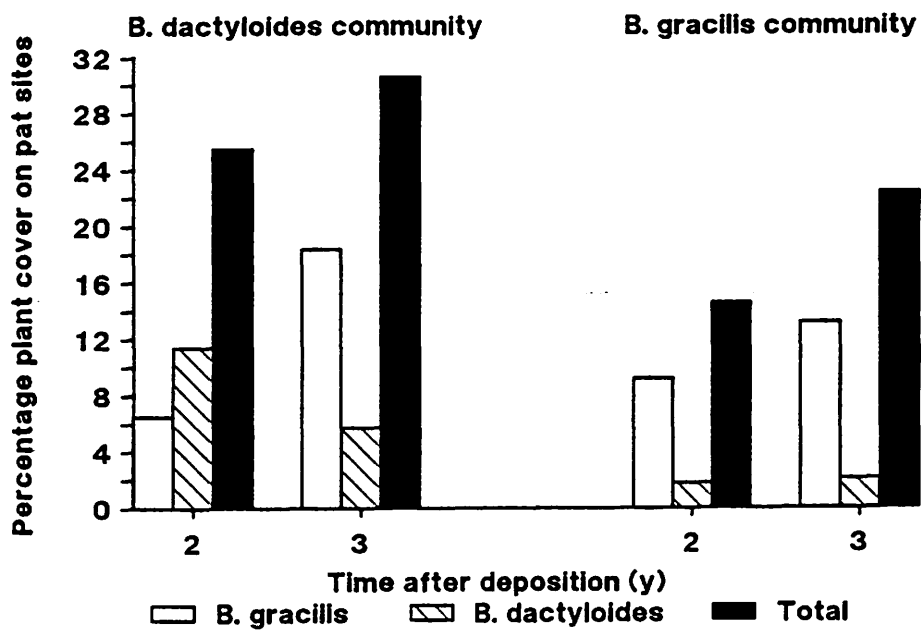
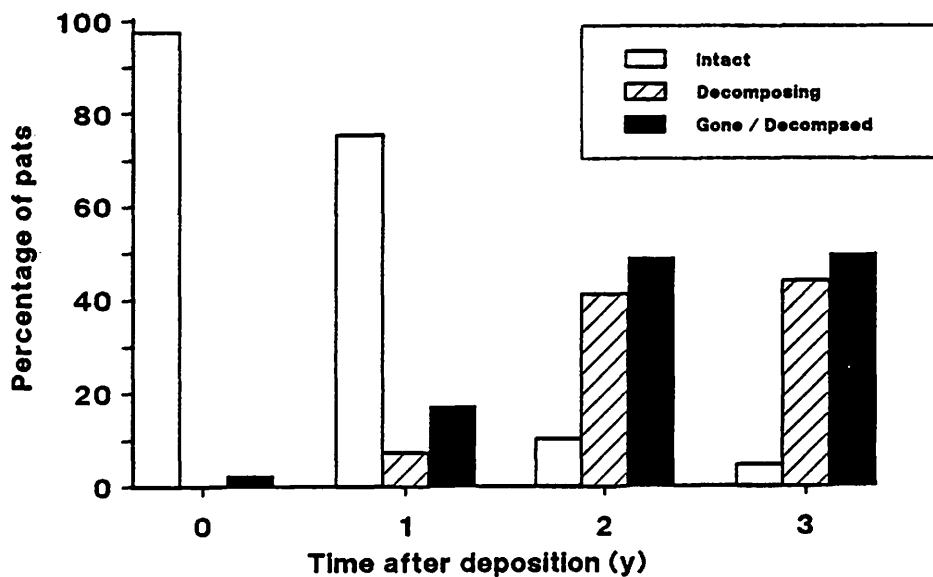


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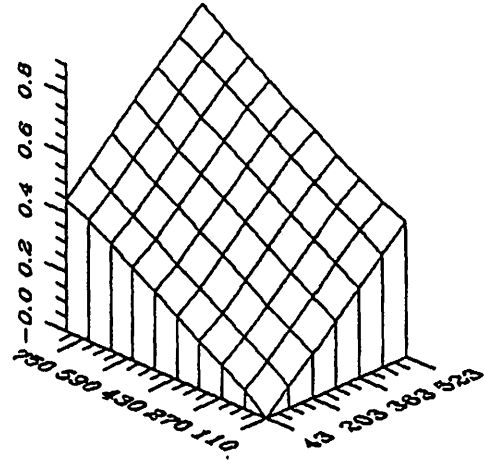
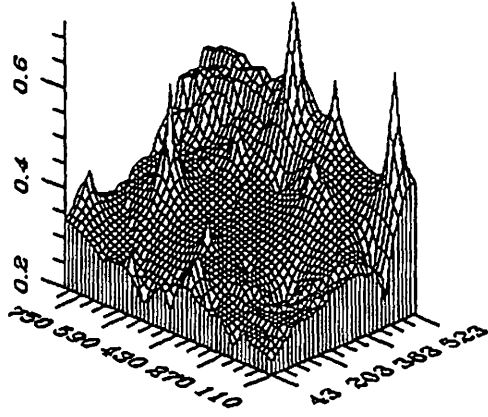


KRIEGING

STATISTICAL MODEL

Short Evolutionary History

SPECIES DISSIMILARITY



Long Evolutionary History

SPECIES DISSIMILARITY

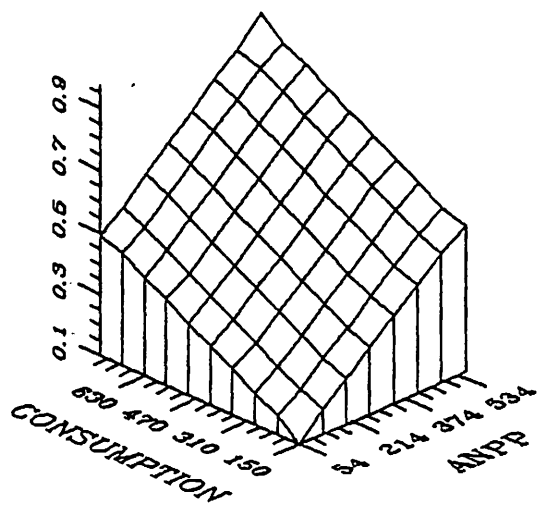
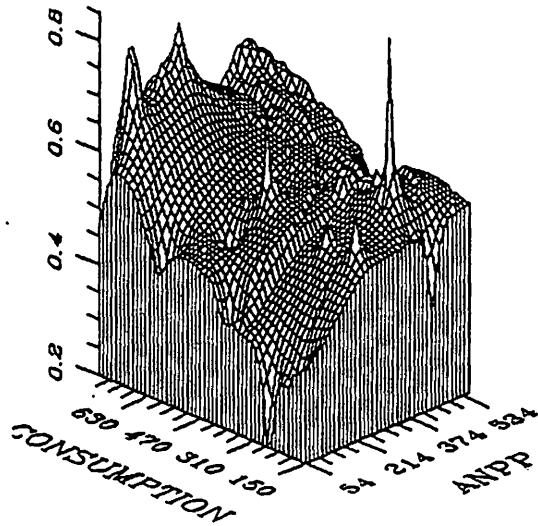


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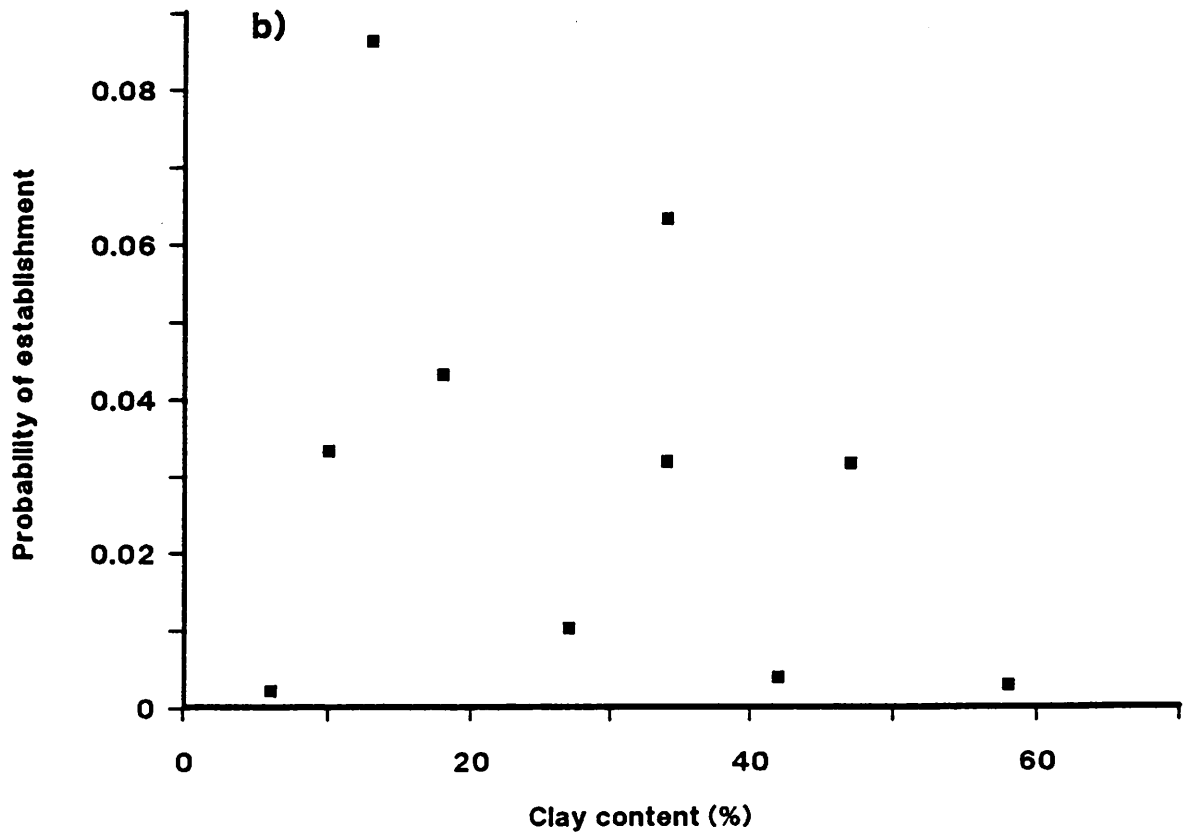
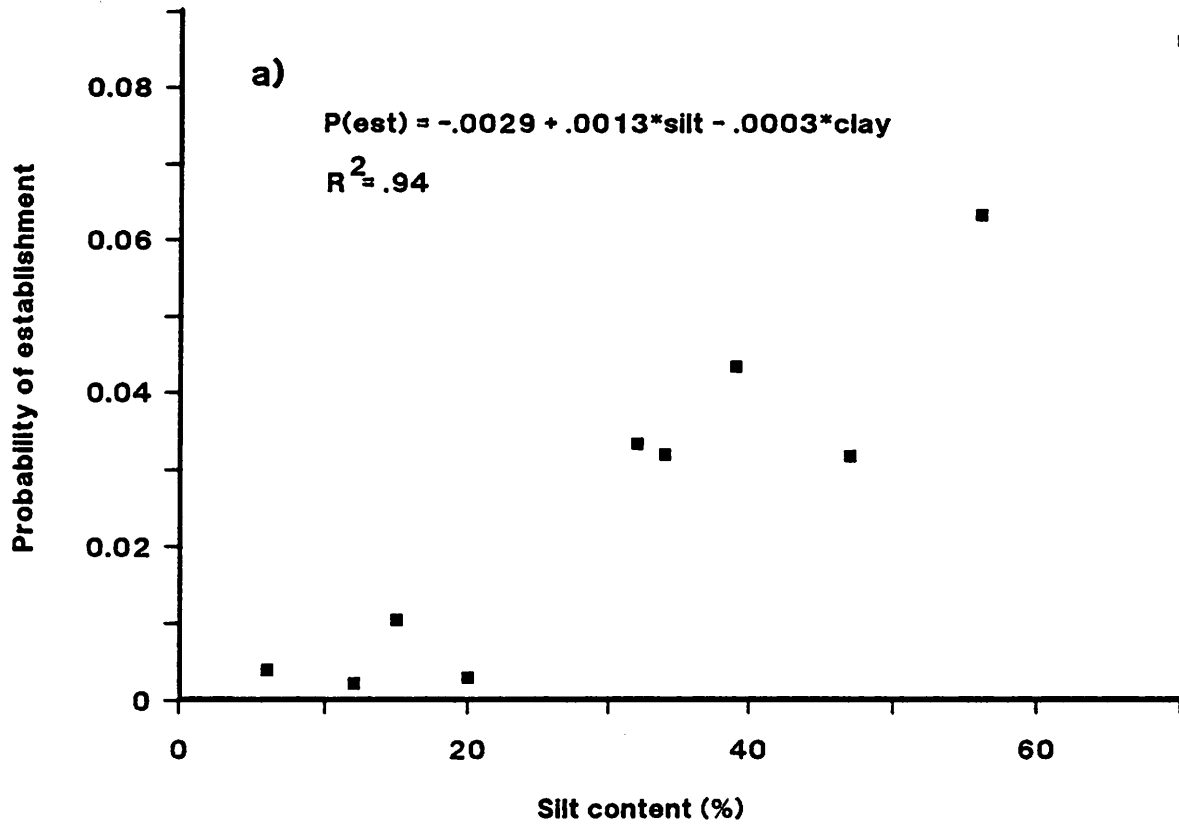


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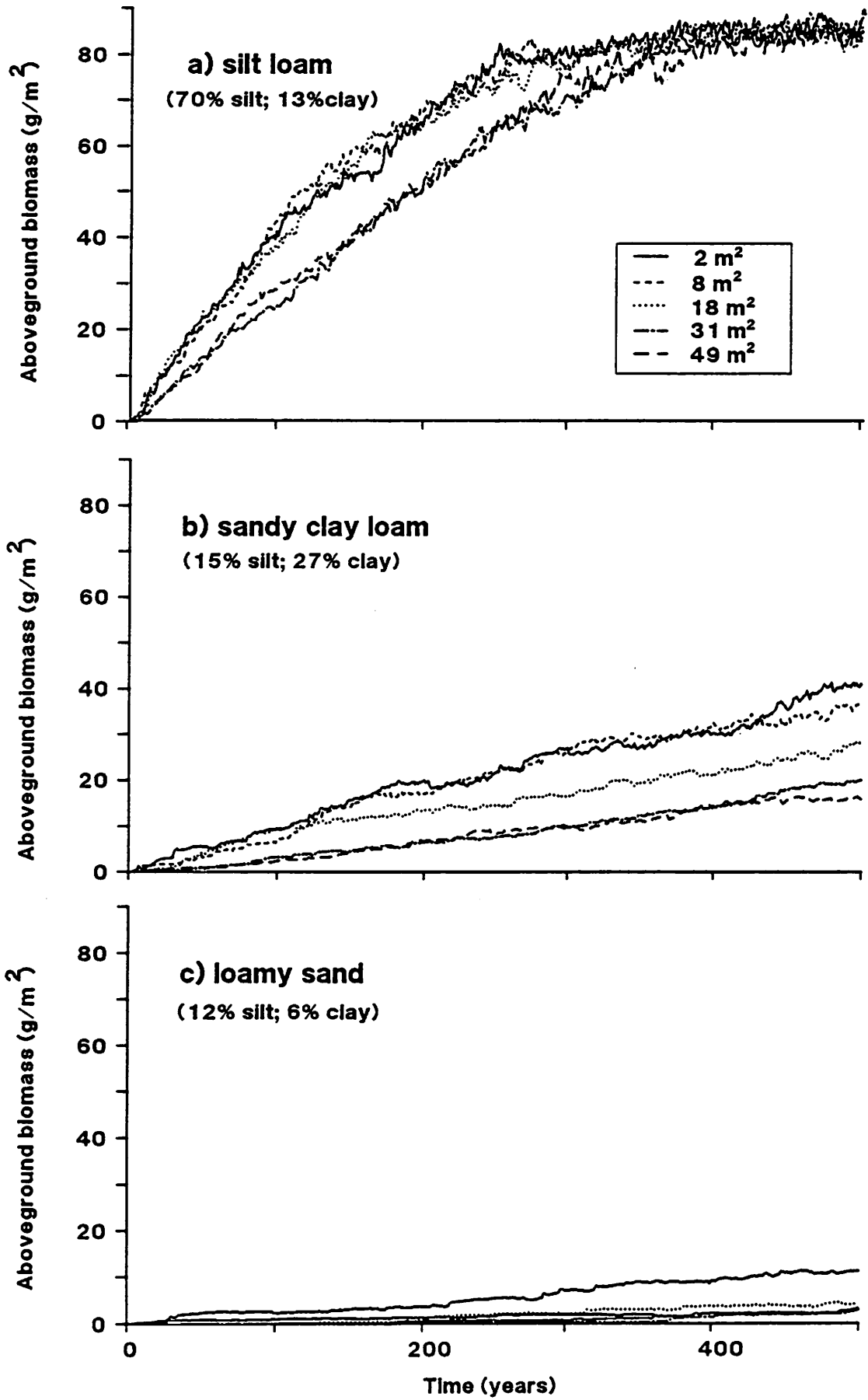


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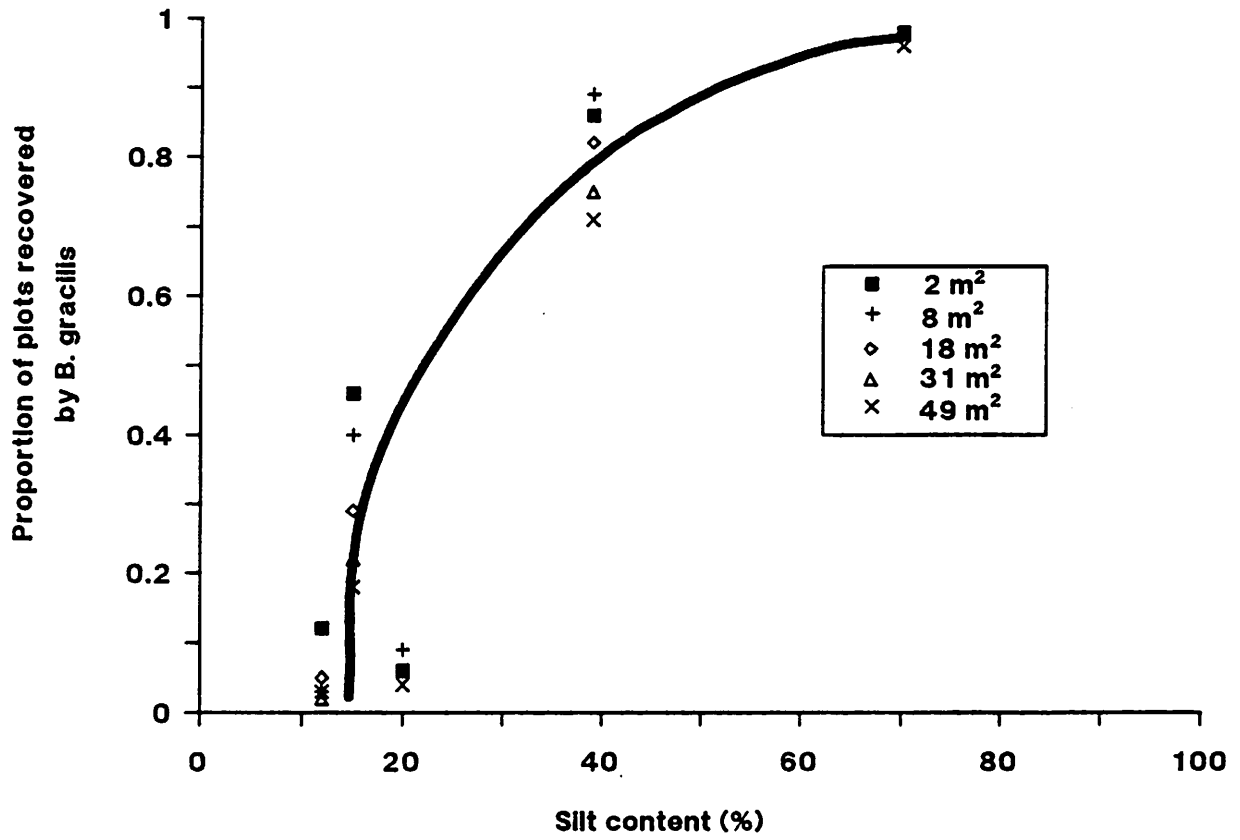
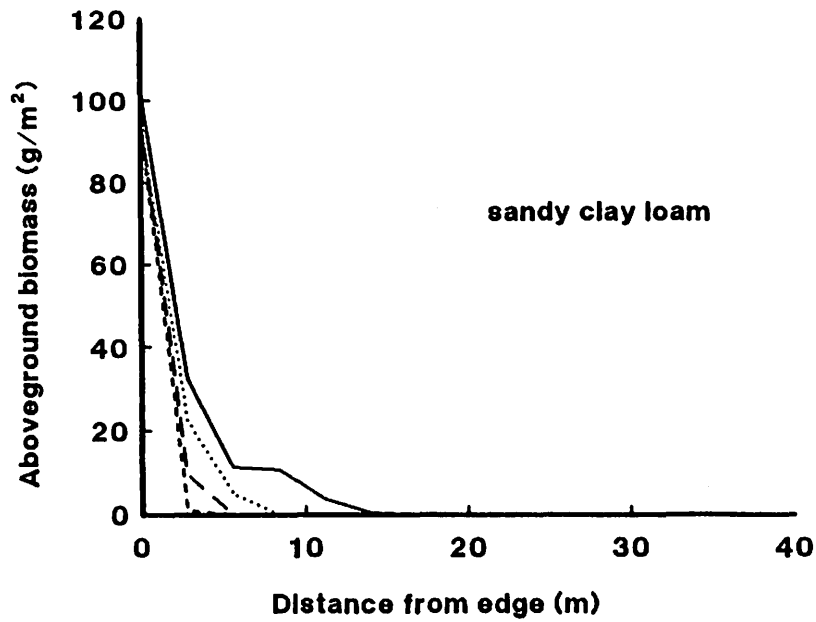
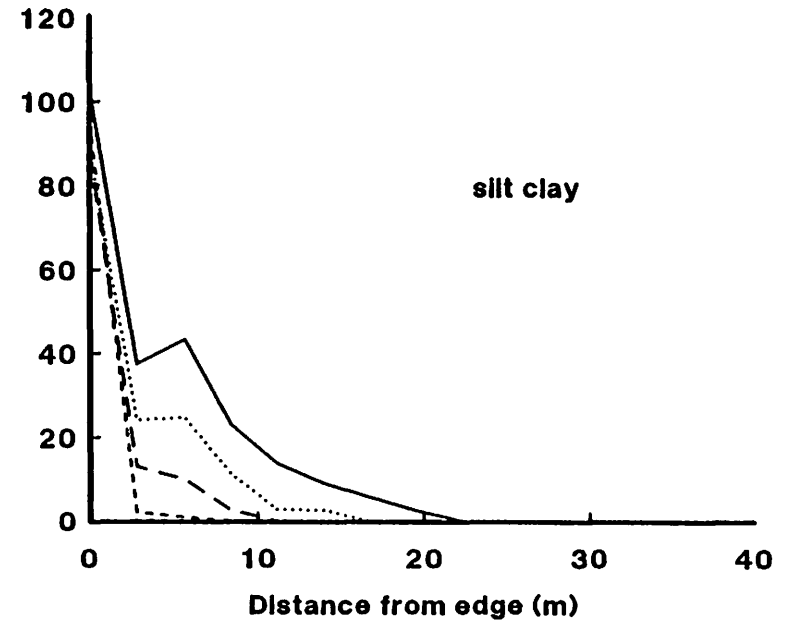
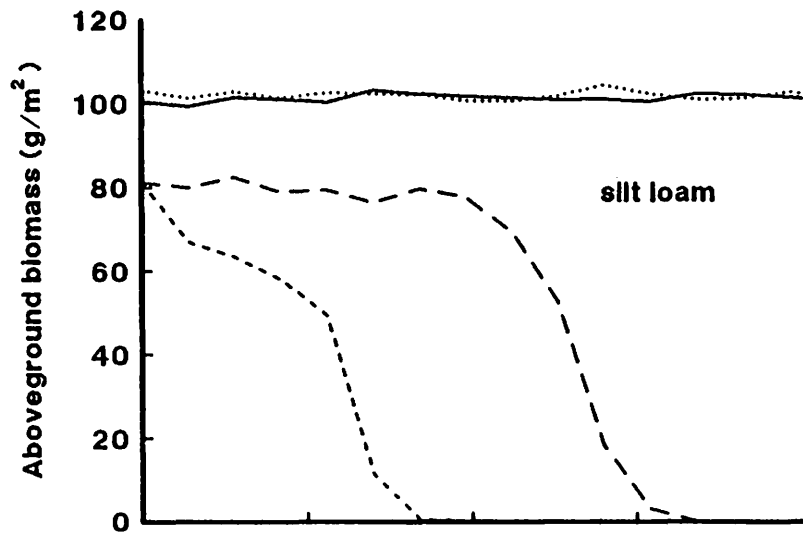


Figure 11



Simulated *B. gracilis* biomass at four times:

- year 50
- - - - - year 100
- year 150
- year 200

Figure 12

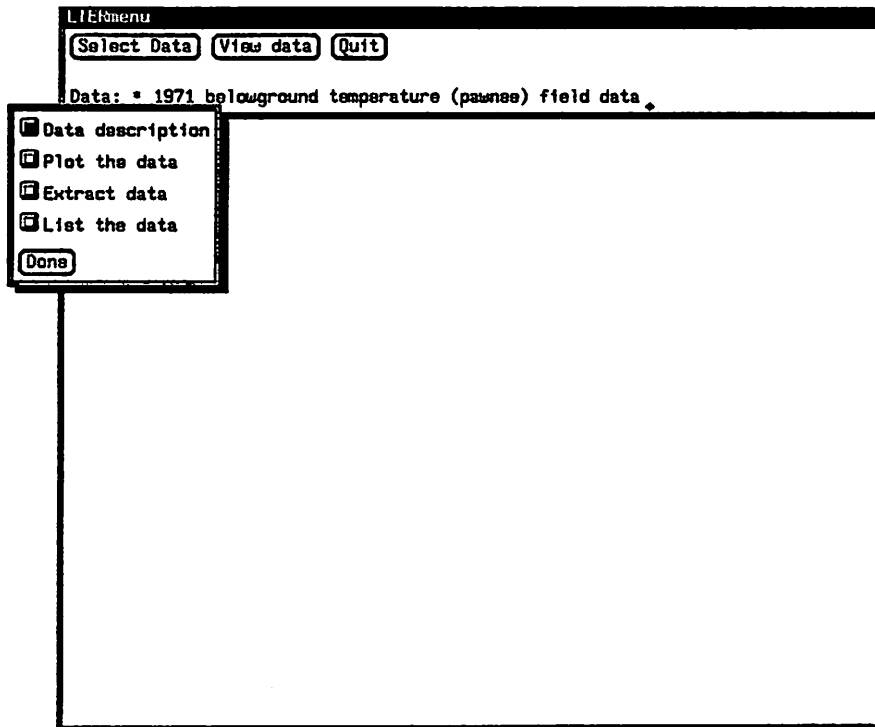


Figure 13

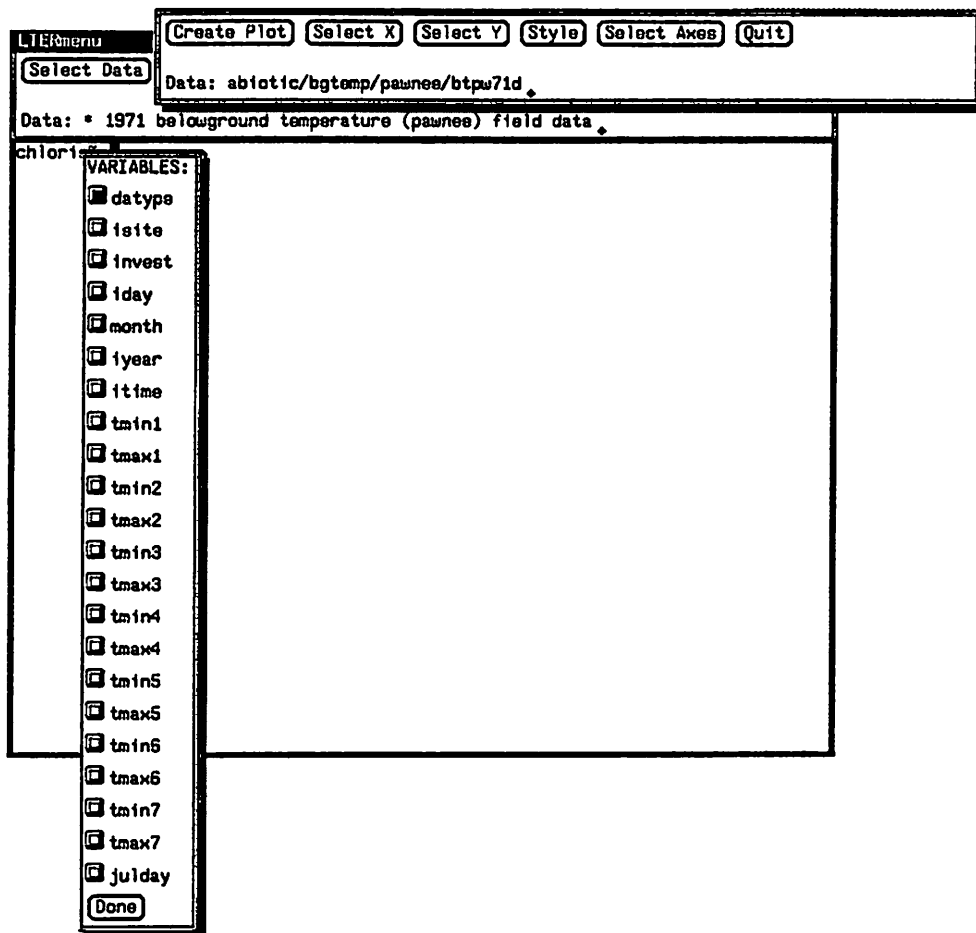
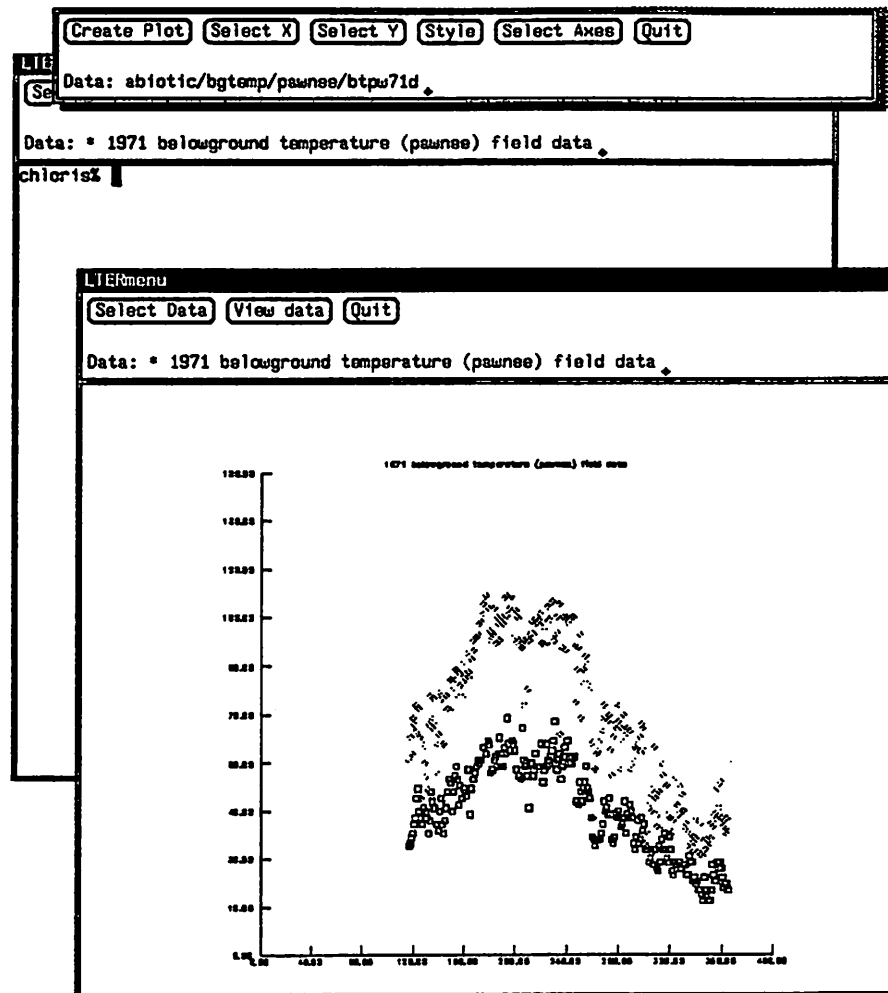


Figure 14



PUBLICATIONS 1988-1990
Central Plains Experimental Range LTER Project

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