TIEE

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ISSUES - DATA SET

Effects of Plant Biodiversity on Ecosystem Productivity within a Savannah Grassland Community

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THE ECOLOGICAL QUESTION:
How does plant biodiversity in a grassland savannah community affect ecosystem productivity?

ECOLOGICAL CONTENT:
grassland, biodiversity, biomass, productivity, sampling effect hypothesis, quadrat sampling

WHAT STUDENTS DO:
Students make Microsoft Excel graphs to examine the effect of biodiversity on productivity for seven years of data. This leads students to hypothesize the possible reasons for this effect, including sampling effects and niche differences among species, and to examine the challenges and implications of extrapolating these experimental data to biodiversity loss in general. Students discuss their hypotheses, analysis, interpretation, and conclusion orally and/or in writing.

SKILLS:
Using a computer spreadsheet to make simple graphs; writing, hypothesizing, thinking critically, analyzing, interpreting, and drawing conclusions.

ASSESSABLE OUTCOMES:
Graphs from spreadsheet data; written or oral analyses, interpretations, conclusions, and hypotheses.

SOURCE:
Cedar Creek Natural History Area Long-Term Ecological Research (LTER) archive data 1996 – 2002 (http://www.cedarcreek.umn.edu/research/exper/e120/)

Teaching Issues and Experiments in Ecology (TIEE) is a project of the Education and Human Resources Committee of the Ecological Society of America (http://tiee.ecoed.net).

OVERVIEW

Cedar Creek Natural History Area is part of the Long-Term Ecological Research (LTER) network. This unique network, funded by the National Science Foundation, supports long-term research at 24 sites located across the climates and habitats in North America and Antarctica (Hobbie 2003).

LTER Mission:

1. Understand ecological phenomena over long temporal and spatial scales
2. Create a legacy of well-designed and documented long-term experiments and observations for future generations
3. Conduct major synthetic and theoretical efforts
4. Provide information for the identification and solution of ecological problems

History (from the Cedar Creek Webpage):

Cedar Creek Natural History Area is a 2200 hectare (1 hectare = 2.47 acres) experimental ecological reserve operated by the University of Minnesota in cooperation with the Minnesota Academy of Science. It is located about 50 km north of Minneapolis and St. Paul. Cedar Creek lies at the boundary between prairie and forest. It is a mosaic of uplands dominated by oak savanna, prairie, hardwood forest, pine forests, and abandoned agricultural fields and of lowlands comprised of ash and cedar swamps, acid bogs, marshes, and sedge meadows. The soils of Cedar Creek are derived from a glacial outwash sandplain. Upland soils are nitrogen poor: numerous nutrient addition experiments performed in both old fields and native savanna have shown that nitrogen is the major soil resource that limits plant growth. Cedar Creek has a continental climate with cold winters, hot summers, and precipitation (66 cm/yr) spread fairly evenly throughout the year.

The Biodiversity/Productivity Experiment

This experiment was set up to examine the effects of manipulating species richness (ecologists often refer to the number of species present in an area as the ‘species richness’) on plant productivity and biomass. Human impacts are driving many species extinct locally and globally. These human impacts include habitat loss or fragmentation, habitat modifications such as pollution and introductions of exotic species, and climate change. Fragmentation or fast shifts in climate may limit the number of species that occur in a habitat simply because the seed of that species cannot reach that area. Our experiment is analogous to this situation in that we allow the seed of many species to reach some areas, and restrict the number of species able to reach other areas. We do not focus on the loss of a particular species, but rather ask whether the loss of biodiversity has any general, predictable effects. In particular, we focus on whether biodiversity affects productivity. Productivity here is the amount of plant biomass produced on a given area of land, over a given amount of time. We use aboveground plant biomass as a measure of annual productivity. In our system productivity ˜ biomass because no biomass from the previous year survives to the current year, it either dies and decomposes or is consumed in the spring fires we set. Productivity is an important ecosystem trait, as all higher trophic levels depend upon it directly or indirectly as a food resource. In addition, maximizing productivity is a goal of many pasture, forestry, and agricultural systems, and it is possible that insights about the effects of biodiversity can be applied to some of these systems.

The experiment is located in an old field at Cedar Creek Natural History Area, Minnesota. In order to get rid of the existing vegetation and seed bank, the field was herbicided and burned and 6-8 cm of topsoil was removed. The field was plowed and the 168 9 x 9 meter plots were established for this experiment. Each plot was planted with seed of 1, 2, 4, 8, or 16 grassland-savanna species. All plots received, in total, 10 g m^{-2} of seed in May 1994 and 5 g m^{-2} in May 1995, with seed mass divided equally among species.

Long-Term Ecological Research Projects

Since its inception in 1982, the overarching philosophy of the Cedar Creek LTER has been, and remains, the synthesis and integration of the principles and processes of population, community and ecosystem ecology. In our original (1981) LTER proposal we said: “Population and community ecology can be greatly strengthened by consideration of the long-term effects, the indirect effects and the feedback effects that the ecosystem approach emphasizes. Similarly, ecosystem ecology can be strengthened by detailed studies of the dynamics of interactions among individual species that play such a key role in the processes of productivity, energy flow and nutrient cycling. We believe this synthesis will only be possible when long-term experimental research combines population, community and ecosystem perspectives.”

We are pursuing this research in five inter-related types of long-term studies: (1) experimental manipulations of plant diversity; (2) N addition experiments; (3) fire frequency experiments; (4) experimental manipulations of herbivore and predator trophic levels; and (5) long-term observations of soils, plants, insects and mammals in a successional chronosequence and savanna.

References:

- Hobbie, J.E. 2003. Scientific accomplishments of the long-term ecological research program: an introduction. Bioscience 53:17-20.
- Tilman, D., D. Wedin, and J. Knops. 1996. Productivity and sustainability influenced by biodiversity in grassland ecosystems. Nature 379:718-720.
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STUDENT INSTRUCTIONS

Background Information

Cedar Creek Natural History Area is a 2200 hectare (1 hectare = 2.47 acres) experimental ecological reserve that includes prairie/savanna habitat and prairie plants growing in abandoned agricultural fields. Prairies in Minnesota are dominated by bunchgrasses such as little bluestem, big bluestem, and Indian grass, and also include a large number of species of forbs such as lupine, purple prairie clover, milkweeds, and goldenrods. Savanna consists of scattered trees within a continuous stand of prairie grassland. Fire is common in these systems and the trees are restricted to a few fire-resistant species, primarily bur oaks.

The Biodiversity/Productivity Experiment

This experiment was set up to examine the effects of manipulating species richness on plant productivity and biomass. Human impacts are driving many species locally and globally extinct. These human impacts include habitat loss or fragmentation, habitat modifications such as pollution and introductions of exotic species, and climate change. Fragmentation or fast shifts in climate may limit the number of species that occur in a habitat simply because the seed of that species cannot reach that area. Our experiment is analogous to this situation in that we allow the seed of many species to reach some areas, and restrict the number of species able to reach other areas. We do not focus on the loss of a particular species, but rather ask whether the loss of biodiversity has any general, predictable effects.

In particular, we focus on whether biodiversity affects plant productivity. Productivity is the amount of plant biomass produced on a given area of land, over a given amount of time. If a grassland were being used to produce hay, its annual productivity would be the amount of hay that it could produce each year. We use aboveground plant biomass as a measure of annual productivity. In our system productivity ˜ biomass because no aboveground plant biomass from the previous year survives to the current year. Each year, aboveground plant biomass either dies and decomposes or is consumed in the spring fires we set. Productivity is an important ecosystem trait, as all higher trophic levels depend upon it directly or indirectly as a food resource. In addition, maximizing productivity is a goal of many pasture, forestry, and agricultural systems, and it is possible that insights about the effects of biodiversity can be applied to some of these systems.

In 1993 the vegetation and seed bank were removed from an abandoned agricultural field. In spring of 1994, 168 plots, each 9 m x 9 m, were seeded to contain 1, 2, 4, 8, or 16 grassland-savanna species. All plots received, in total, 10 g m^{-2} of seed in May 1994 and 5 g m^{-2} in May 1995, with seed mass divided equally among species. Treatments were maintained by weeding 3 or 4 times/year. Plots were sampled in mid-August for aboveground living plant biomass by clipping, drying, and weighing four 0.1 x 3.0 m vegetation strips per plot from 1996 through 1999, and eight strips per plot in 2000. Different areas were sampled each year.

You will use the Excel spreadsheet software and provided data to create the following graphs and answer the following questions.

1) Biodiversity Dataset 1

   a) The first column shows the number of species planted in a plot, each row represents a different treatment. In this experiment, the treatment is the number of species planted, which ranged from 1 to 16. Each treatment was applied to dozens of plots (ranging from 29 to 39 depending on the treatment). Each column to the right represents a different year, from 1996 to 2002. The first group of columns gives the value for aboveground biomass, averaged across all the plots of a given treatment. The next group of columns gives the standard error. The standard error is a measure of “confidence,” and tells us how much the average value is expected to vary if the experiment were to be run again. Small standard error bars indicate that our confidence in the accuracy of the estimate is high and large standard error bars indicate that our confidence is low.

   b) We will make a scatter plot graph to visualize the relationship between biomass and species richness and to help us interpret our data. As described below, you can use the chart wizard to create this graph. Although there are many types of graphs to choose from in Excel’s chart wizard, the two primarily used by scientists are the “scatter plot” and the “column.” Species richness is the experimentally manipulated variable, referred to as the predictor variable. By convention, we use the horizontal, or x-axis, to indicate our predictor variable, and the vertical or y-axis to represent our response variable. Species richness is a variable that can be represented quantitatively, and we therefore choose a scatter plot to graph our data. If we had categorical data (e.g., plots characterized simply as “low,” “medium,” and “high” diversity) we would choose a column graph.

   c) Make a graph of the average aboveground biomass versus species richness (i.e., the number of species). Start by highlighting the first two columns and clicking on the chart wizard. Select scatter plot on the graph wizard, select the plot sub-type “scatter with data points connected by smoothed lines,” and then select finish. This shows the patterns for the year 1996. We can now add years by selecting “add data” under the chart menu (NOTE: Excel often produces a graph of gibberish if you try to graph all the years at once). Select the new data, including the heading, for the years you would like to add. You can add the years one at a time to see how the changing patterns are revealed. Remember to label your axes (you can edit the axes labels by double clicking on them). When you finish, look at the graph and describe the pattern that you see (to each other if you are working in a group). How would you describe the pattern to another student looking at the graph for the first time?

   d) Add error bars to the figure. Double-click on one of the data points for the year 1996. When the dialog box opens, select the tab y-error bars. Select “custom” and add the column for SE1996 to both the “+” and “-“ sections under custom error bars. Data points for which the error bars overlap are not significantly different from each other.

e) Questions:

i) Describe the relationship between the number of plant species and plant biomass.

ii) How does the relationship between biomass and species richness change over time? How does it stay the same? Do the standard error measurements change your interpretation this pattern? What is the advantage of having data from more than one or two years?

iii) What conclusions can you draw, or hypotheses can you make, about the effect of the loss of biodiversity in natural systems? What are the problems that need to be considered when extrapolating the results of this experiment to natural systems?

2) Biodiversity Dataset 2

a) The numbers presented here show the percentage of plots with biomass exceeding the highest monoculture biomass. These data can address the sampling effect hypothesis: diverse plots have more biomass because they are more likely to contain a dominant species with high biomass. Under this hypothesis, one or a few high biomass species are good competitors and dominate the plots in which they are present. Consequently, the total biomass of communities containing these species is predicted to be the same as the biomass of these species when grown alone. In this scenario there should be an increase in the average biomass across diversity gradients, but **no** increase in the maximum amount of biomass across the diversity gradient.

b) Questions:

i) Do the data support or reject the hypothesis that there is no increase in the maximum biomass? Does the answer to this question depend upon the year (if so, state how the years differ)?

ii) What is the relationship between species richness (the number of species) and productivity within this savannah grassland?

iii) How does the relationship between species richness/productivity change over time?

iv) Why might a diverse plot contain more biomass than even the highest monoculture plot? Why might two species be better than one when it comes to biomass production?

3) Bonus Biodiversity Dataset

   a) This dataset contains the “raw” data from the first three years of the experiment. These data were the source of the averages and the standard errors in Dataset 1. Make a graph similar to the one you made for Dataset 1.

   b) Questions:

      i) Can you answer the questions from #4 above using this graph?

      ii) What is the advantage of using the summarized data in Dataset 1 versus using the raw data in the Bonus Dataset?

      iii) What might be a disadvantage of using the summarized data?

   c) This dataset also contains information on the presence/absence of functional groups in each plot and can be used to illustrate the utility of different statistical approaches. The functional groups of plants in this experiment are: trees, C3 grasses, C4 grasses, legumes, and non-leguminous forbs. C3 grasses have the C3 photosynthetic pathway, while C4 grasses have the C4 photosynthetic pathway. Forbs are broadleaved herbaceous species. Legumes are forbs that have a symbiotic association with a bacterium which enables them to use atmospheric nitrogen (N_2) directly.

Is the increase in biomass with increasing diversity associated more with the presence of some functional groups than of others? How would you test this hypothesis? While previous data analyses used graphs with one numerical predictor (species richness), this question involves several categorical predictors. Simple linear regression is a statistical technique applicable to situations with one continuous predictor, whereas Analysis of Variance (ANOVA) is applicable to situations with several categorical predictors.

NOTES TO FACULTY

Available Datasets

There are two datasets (plus one optional Bonus Dataset) with which students can work. The one(s) you choose will depend upon your goals for this exercise, available time, and your students' skills with spreadsheets plus their level (e.g., sophomores versus seniors). Each dataset is explained below along with suggestions on how to use the data. In addition, you may choose to have students complete a writing exercise involving critiques of the Cedar Creek and other biodiversity experiments (the exercises for Datasets 1 and 2 should be completed before attempting this writing exercise). The ideas behind these critiques are also discussed below.

Dataset 1: contains average plant biomass and standard errors for each species richness level. These data show an increasingly positive relationship between species richness and productivity over time.

Dataset 2: shows the percentage of plots that exceeded the maximum monoculture biomass. This second dataset allows a test of the sampling effect hypothesis (as stated below), and finds that the initial years are consistent with the sampling effect hypothesis while three of the last four years are not.

Bonus Data: presents the raw data (as opposed to the averages presented in Dataset 1) and presents information on the presence/absence of functional groups. Graphs from this data are rather cluttered and difficult to interpret, illustrating why we use the averages. There are a large number of analyses that are possible with the functional group data. We have generally found significant effects of both C4 grasses and legumes and of their interactions. We have included this richer data set as an opportunity for teachers and students to be creative and have therefore left the exercise quite open-ended. Teachers electing to use these data should determine what exactly they want students to do with the data and provide more explicit instructions than we do here.

Species List: shows the functional groups, genera and species, plus common names of the plants used in the experiment.

Teaching Suggestions
Dataset 1

As explained in the Overview, the key issue addressed here is the relationship between species diversity and productivity as a measure of "ecosystem function." The history and importance of this research is explained on the Cedar Creek website (http://cedarcreek.umn.edu/research/biodiversity.html) which also leads you to numerous papers and figures (see also Tilman et al., 1996, 1997, 2001, listed below).

You can use these data in a basic ecology class so that students better understand why the diversity/productivity relationship is of so much interest. Having students work with this dataset is a good preparation for a lecture on species diversity; you could also use it as a follow-up on a lecture about this topic.

From nature shows and other sources students may believe that high species diversity is “good,” but they likely could not explain why this might be so. “Ecosystem function” can be a pretty abstract idea, so working with and discussing these data can help to make that idea more concrete. The Resources (link to section below) section of this TIEE dataset provides links to numerous Web sites on species diversity. You can use these to get ideas to present in class. (There are also websites about grasslands in the Resources section if you know little about grassland ecology.) Alternatively, you can ask students to look at one or two Web sites for homework; this would be a useful set-up for discussion following the lab.

These data also show students the importance of long-term data and you can discuss this with them using the context of data interpretation and experimental design (e.g., how can scientists come to similar or different conclusions using similar experiments if the time course is different?)

The Excel directions are fairly explicit, but anticipate the time your students will need to make their figures. (To save time in class, you can have them work on Excel for homework or give one of the Excel tutorials in the Resources section ahead of time.) As a note, briefly explain what a standard error is and why it is useful.

The student questions (repeated below) emphasize data description and interpretation. You can use these as discussion points, homework essay questions, and/or test questions. Depending on your students’ experience with data analysis, you may need to help them see all the details in the figure they developed (see question 2). The third question can stimulate discussion about the trade-offs of controlled ecological experiments and foreshadows issues discussed further in the “critiques” section.

1. *Describe the relationship between the number of plant species and plant biomass.*
2. *How does the relationship between biomass and species richness change over time? How does it stay the same? Do the standard error measurements change your interpretation this pattern? What is the advantage of having data from more than one or two years?*
3. *What conclusions can you draw, or hypotheses can you make about the effect of the loss of biodiversity in natural systems? What are the problems that need to be considered when extrapolating the results of this experiment to natural systems?*

Dataset 2

These data are the next “step up” from the first dataset. They move students from describing the observed pattern to testing a hypothesis about the mechanism behind a pattern. This dataset is appropriate for a more advanced ecology class or with basic ecology students if you have time to discuss the issue with them.

As the Student Instructions section explains, the sampling effect hypothesis suggests that diverse plots have more biomass because they are more likely to contain a dominant species with high biomass. Under this hypothesis, one or a few high biomass species are good competitors and dominate the plots in which they are present. Consequently, the total biomass of communities containing these species is predicted to be the same as the biomass of these species when grown alone. In this scenario, there should be an increase in the average biomass across diversity gradients, but **no** increase in the maximum amount of biomass across diversity gradients.

The questions and answers for Dataset 2 are discussed here.

1. *Do the data support or reject the hypothesis that there is no increase in the maximum biomass? Does the answer to this question depend upon the year (if so, state how the years differ)?*

   The answer depends upon the year. Specifically the years 1996, 1997, 1998 and 2001 show no change in the percentage of monoculture-biomass-exceeding plots across the diversity gradient. The years 1999, 2000, and 2002 show an increase in the percentage of monoculture-biomass-exceeding plots ($P < 0.05$ for all three years).

   Note that the percentage of plots that have a higher biomass than any of the monoculture plots is sensitive to sampling variation in monoculture biomass (i.e., some years may have unusually low or high values for monoculture biomass). Therefore, it is important to test for biodiversity effects by asking whether this percentage increases with biodiversity, rather than whether this percentage differs from zero. For example, the data from the year 1996 show that the percentage of plots was significantly greater than zero ($P = 0.003$), but this percentage did not increase with biodiversity ($P = 0.45$). This may be explained by sampling error causing a low monoculture biomass for that year rather than by a biodiversity effect.

2. *What is the relationship between species richness (the number of species) and productivity within this savannah grassland?*

   These data show, as did the data in Dataset 1, that productivity increases with species richness.

3. *How does the relationship between species richness/productivity change over time?*

   In the early years, the percentage of plots that have higher biomass than any of the monoculture plots was constant across species richness, but this percentage increases with species richness in 3 of 4 later years.

4. *Why might a diverse plot contain more biomass than even the highest monoculture plot? Why might two species be better than one when it comes to biomass production?*

   There are a number of possible answers to this question. The most common explanations for this phenomenon are:

1. Interactions between grasses and legumes. Legumes can access nitrogen from the atmosphere and make it available to other plants. Grasses have large root systems that are efficient at capturing and retaining soil nitrogen.
2. Differences in the timing and depth of nutrient uptake among species, such that diverse communities have more complete capture of available resources over space and time.

The Sampling Effect Controversy

The topic of Sampling Effect has been quite controversial (Huston 1997, Wardle 1999, Kaiser 2000, Wardle et al. 2000, Loreau 2001). You may want to have a classroom discussion based on students' answers to Question 3: "What does this suggest about the effect of the loss of biodiversity in natural systems? What are the problems that need to be considered when extrapolating the results of this experiment to natural systems?"

Emphasize to students that they are working with real data from an experiment at the heart of this controversy. The following material may be useful in presenting some of the issues raised by this and similar studies. You may choose to handout the following critiques and responses and have the students write a one page argument in favor of one of the critiques or responses. Students can also debate the issue by choosing one side or the other (Wardle et al. 2001 and Kaiser 2000 are quite readable for less advanced student).

A number of critiques have been leveled towards biodiversity experiments. Three critiques and responses are summarized below.

1. **Critique:** The positive relationship between plant species richness and productivity can be attributed to the higher probability of one or a few high biomass species occurring in diverse plots. This assumes that these high biomass species are good competitors and dominate the plots such that the total biomass of communities with these species is essentially the same as the biomass of these species when grown alone. In this scenario, there should be an increase in the average biomass across diversity gradients but no increase in the maximum amount of biomass across diversity gradients.

   Response: Such a pattern was observed initially, but later years show that the maximum biomass increases across the diversity gradient. Thus, this long-term experiment suggests that the mechanisms behind the biodiversity-productivity relationship may have changed over time.

2. **Critique:** If a positive relationship between biodiversity and productivity is due to a "sampling effect" and can therefore be attributed simply to a higher probability of being present at high diversity, this relationship should be considered an experimental artifact with no relevance beyond the experiment.

Response: Because by definition diverse communities contain more species, the higher probability of any given species occurring in diverse communities is a phenomenon that could have effects in many habitats outside of experimentally assembled communities.

3. **Critique:** Experimentally assembled communities with a design of random species loss cannot predict the effects of real species loss, which will not be random.

   Response: While real species loss will be biased, it is difficult to predict how it will be biased. Rare species are vulnerable to extinction, while disease may cause abundant species to become functionally extinct (e.g., Chestnuts) and nutrient pollution may eliminate slow growing or high root-to-shoot ratio species. Given this uncertainty, it is reasonable to first address the effects of random loss. An interesting question for future research is whether biased species loss will show similar effects as the random species loss simulated in this experiment.

Bonus Dataset

This dataset contains the “raw” data from the first three years of the experiment. These data were the source of the averages and the standard errors in Dataset 1 and can be used if you want student to calculate averages and errors. This would be a good idea in a more advanced ecology class.

As explained above, this richer dataset will allow teachers and students to be creative and the data work-up to be open-ended. These data would be appropriate for students in a plant ecology course or other advanced ecology class. For undergraduates or beginning graduate students, figure out what you want the students to do with the data and give them clear and specific instructions.

The Student Instructions provide guidance on using this dataset to assess whether an increase in biomass with increasing diversity may be due to presence of particular functional groups. Functional groupings are explained in the student section. As noted above, we have found significant effects of C4 grasses and legumes.

Assessment

Possible assessments include the accuracy and clarity of figures students make using the Excel spreadsheet, written description and analysis of these figures, discussion or analysis of one of the papers listed below, and a short essay on one of the discussion questions above or in the "Student Instructions" section.

Resources

Resources include links to sites about the Cedar Creek research, Biodiversity, Grasslands and Prairie, and Excel tutorials.

Cedar Creek

- www.cedarcreek.umn.edu
  Cedar Creek Natural History Area where the research was conducted; includes photos and descriptions of habitat and plant lists

Biodiversity

- www.nbii.gov/issues/biodiversity/
  National Biological Information Infrastructure; lists www sites on biotic and ecosystem diversity

- www.greatplains.org/resource/biodiver/biostat/biostat.htm
  The status of biodiversity on the Great Plains; The Nature Conservancy

- www.esa.org/science/Issues/
  ESA *Issues in Ecology*, includes "Biodiversity and Ecosystem Functioning" by Naeem et al.

Grasslands and Prairie

- www.npwrc.usgs.gov/resource/resource.htm
  USGS Northern Prairie Biological Resource list

- www.fs.fed.us/grasslands/
  USDA Forest Service; includes "select a state and grassland" link

- www.noble.org/imagegallery/grasses.html
  www.noble.org/imagegallery/forbs.html
  Noble Foundation Plant Image Gallery; Grasses and Forbs

- www.bellmuseum.org/mnideals/prairie/index.html
  Minnesota IDEALS; "On the Prairie" for kids but useful, includes a field guide

- www.sierraclub.org/ecoregions/prairie.asp
  Sierra Club North American Prairie Ecoregions

Excel Tutorials

- www.usd.edu/trio/tut/excel/
  Basic information: how to use functions, filling down, formatting, inserting, graphs and graphing

- www.homepage.cs.uri.edu/tutorials/csc101/pc/excel97/excel.html
  Basic information: from "what is excel" to "creating charts"; copyright of University of RI Computer Science Dept

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- www.fgcu.edu/support/office2000/excel/
  Florida Gulf Coast University; basic - includes visuals

- www.baycongroup.com/el0.htm
  Introductory information; BayCon Group - commercial site

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