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Annual Performance Report for Grant DE-FG05-89ER60879:

Testing the Scale-dependence of Models of Resource Competition and Environmental Conditions for Forest Structure and Dynamics

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Project Summary:

The goal of the proposed research is to evaluate and integrate two kinds of explanation of forest community structure and dynamics previously developed at different spatial scales. Gradient models describe species distributions and community composition in term of environmental factors, which can usually be associated with conditions for plant growth. Resource competition models explain community dynamics and resulting composition in terms of acquisition of limiting resources. Recent developments in resource competition theory (extending explanation to large-scale gradients), and in analysis of small-scale variations in conditions, make it increasingly clear that the potential scales of explanation for these two models are not mutually exclusive. We propose to compare qualitative predictions from both approaches at a set of scales where we have detailed data on forest composition and dynamics.

Prospects for a syntheses of these two approaches are good. Nevertheless, an essential part of determining the limits of each approach is to discover areas where the models make different predictions, and evaluate these differences in light of field data. We plan to develop and test regional gradient predictions of local patterns, with a set of intensive study sites representing major forest types on the coastal plain and piedmont of the Southeastern United States. We will also compare the results of empirical models of within- and across-site spatial and temporal distribution, i.e. gradient and stage-projection models, with heuristic results from a proposed resource-competition modeling system.

Technical Progress Report:

The first eight months of this project have emphasized development of techniques and the acquisition and testing of required equipment and software. Nonetheless, we can identify several areas of significant progress toward the research objectives of the project.

1) *"Test the degree of scale-dependence of two regional gradient models . . . by comparing them to within-site spatial patterns."* The data and models are nearly ready for a rigorous comparison of gradients within our intensive study sites with gradient models for regional vegetation in Texas and for two of three sites in North Carolina.

2) *"Develop statistics appropriate for permutation tests of differences between gradient models . . . at different spatial scales."* Simulations recently completed allow us to distinguish statistically "stable" axes in gradient analyses at 95% confidence levels--extending previous work (Knox & Peet 1989, Knox 1989) and setting the stage for tests.

3) *"Develop a method for finding the primary spatial scales for gradients within mapped forest plots. Also develop methods for testing . . . with measured environmental variables."* Preliminary work with forests mapped by measurement of interpoint distances (see Rohlf & Archie 1978) led us to conduct a formal evaluation of this approach. Work with model point patterns demonstrated a singular lack of robustness to moderate levels of field error (see Hall, enclosed ms.).

4) *"Explore the applicability of resource-ratio theory to southeastern forest systems. . . ."* We have adapted the computer model ALLOCATE (Tilman 1988) for easy use on Sun workstations and have begun modifying it to better reflect forest tree life histories. We have started greenhouse experiments to screen some of the dominant tree species for seedling resource limitation in soils from the Texas sites. Further, we have initiated a wide-ranging review of literature on resource limitation and resource-response curves in southeastern trees.

5) *"Identify and test crucial predictions that differ among gradient and resource-ratio models, . . ."* We have changed ALLOCATE to report species average abundances from multiple habitats in form suitable for gradient analysis and comparison with existing gradient models.

Gradient Modeling and Scale

Initially we gave priority to revising the regional gradient analysis for southeast Texas over refining more advanced gradient models from North Carolina (R.K. Peet, personal communication). The Texas gradient model (Marks & Harcombe 1981) has been refined through selection of optimal data transformations and use of canonical correspondence analysis (ter Braak 1987, 1988). Two axes now admit interpretation. Having developed a texture-based estimate of plant available water in soil (closely related to the first axis, $p < 0.01$), we are seeking to combine it with data on drainage and topographic position to strengthen the interpretation of the first axis as determined by moisture. The second interpretable, stable dimension is related to soil cation chemistry and exchangeable phosphorus. We will derive a more rigorous interpretation of the second axis from permutation tests on partial canonical correspondence analysis, holding constant the effects of an estimate of available moisture.

Within-site soil textures and soil chemical analyses have been completed for two of three sites in North Carolina. Some follow-up sampling may be appropriate after a full geostatistical analysis (see Burrough 1987, Robertson 1987). An initial series of soil measurements was collected for the Texas sites, and more are planned in the next budget year. Three types of information will be sought: scales of heterogeneity in soil and site physical properties, characterization of variation in soil cations, and coarse indices of resource availability (total N, total P) at the three Texas sites. (Fortuitously, last summer an extended period of very high water at the Texas floodplain site allowed us to quantify microtopographic variation there at minimal expense. After the water receded we rated flood damage to saplings, as part of a doctoral project investigating sapling demography at this site.)

Prior to further work on permutation tests for scale comparisons, we refined and extended previous work by Knox (1989, Knox & Peet 1989) on ordination stability. We now have simulations (see Minchin 1987) adequate to estimate 95% lower confidence limits for an estimate of the expected variability of each of four dimensions in an ordination of species that are not separated along gradients (see Fig. 1a-d). With this information we can distinguish gradient-like sequences of species responses from random dimensions. When combined with constrained ordination (such as canonical correspondence analysis) and permutation approaches now in development, stability statistics will let us distinguish the absence of a regional-level signal at smaller scales from the presence of a different signal. Later this spring and in the next budget year, we will be characterizing the approximate statistical power of the stability statistics to detect simulated patterns and using related simulations to select among permutation tests.

Modeling Competition for Limiting Resources

Tilman's (1988) model ALLOCATE has been installed on the Sun workstation, modified to read the characteristics of simulated species and habitats from external files, and modified to produce results in a format suitable for graphical analysis with S and for correspondence analysis. David Tilman visited Rice this March to tour our study sites, present some of his related recent work, and discuss theoretical characteristics and modifications of his models. We are exploring further program modifications to include more realistic tree life history characteristics. These include: differential loss rates for leaves, stems, and roots (and across species), a gradual onset of allocation to seeds, height/biomass allometry appropriate to trees, stem respiration not proportional to biomass, and some simple spatial structure. We are also continuing to process and summarize relevant demographic data from Harcombe's long-term studies. Recently processed field collections add two more years to our data on oak seed production at the Texas floodplain study site (see Streng et al. 1989).

To obtain values to use as parameters in physiological portions of this model, we have a literature review under way. To date we have identified and obtained copies of over 200 published papers, books, or reports dealing with responses to levels of limiting resources, either for our species or for related woody plants. We expect to complete the bulk of this survey this spring, but work on it will continue into the next budget year.

From discussions and literature review, litter nutrient content has emerged as a potentially crucial index of differences between our species and sites, which is relevant to resource competition models. We plan to conduct a small series of measurements of litter and tissue carbon, nitrogen, and phosphorus contents for the dominant species at the three Texas intensive study sites. (Should these results show the need for a larger series of measurements, we will seek funding from other sources to conduct a full-scale set of analyses in collaboration with Mark Walbridge of George Mason University.)

Greenhouse Experiments

An important criterion for evaluating ALLOCATE is to establish that resource limitation is likely and identify the limiting resources. Laboratory evidence for resource limitation will emerge from greenhouse experiments using shading, quantitative watering, and nutrient additions, with cores of field collected soil. In response to technical comments on our proposal and more complete results from pilot experiments, we are now collecting intact soil cores in 20 cm lengths of 4" PVC pipe instead of using small pots of sieved soil for these experiments. The lower ends of these tubes are closed with fine nylon mesh, to retain soil while allowing free drainage of moisture in excess of field capacity. This change also required that we design and fabricate portable equipment for collecting the cores.

This past autumn, at least 300 mature fruit were collected for *Quercus nigra*(2 sites), *Quercus stellata*, *Quercus lyrata*, and *Liquidambar styraciflua.* We have just completed collections of *Acer rubrum*(3 sites). We collected some additional seed from other species for germination and viability tests. Resource limitation experiments are now under way for *Quercus stellata* in sandy upland soils and *Liquidambar* in bottomland soils. (We are soliciting price quotes for the minor renovations required to make a second campus greenhouse usable for these experiments during the warm season.) *Acer rubrum* experiments will provide a vital comparison across sites. Experiments with *Quercus nigra* and *Pinus taeda* are also high priorities for the 1990-91 budget year.

Computer Equipment

With cost sharing by the Weiss School of Natural Sciences (and a large academic discount), we acquired a Sun SPARCstation 1 desktop workstation (19" monitor, 8 Mbyte RAM, RISC CPU rated at 12 MIPS/1.2 MFLOPS). Standard system software was installed and a SunFORTRAN compiler provided under a site license agreement. Connections to a campus computer network, and thus to NSFnet and Internet, were established as part of a renovation of facilities in the new department of Ecology and Evolutionary Biology. Also as part of the renovation, gateways and a local area network now provide the Sun access to POSTSCRIPT laser printers. We expect to outgrow our available disk storage space and, as planned, will need to expand it in the next budget year.

Data Analysis Software

Our most frequently used programs for vegetation analysis and bootstrapped ordination have been ported to the Sun workstation and tested in that environment, as were programs for generating point maps with interpoint distances and least squares minimization. This conversion included developing programs for Procrustes rotation of gradient analysis results, which do not require code from IMSL and thus can be distributed with future releases of Knox's BOOTDCA program for correspondence analysis.

The program package "Geo-EAS" was obtained from the EPA Environmental Monitoring Systems Laboratory. It will be used principally to develop semivariogram models of environmental and vegetational variation in the intensive study sites and perform related "Kriging" for spatial averaging and interpolation.

After examining options for statistical software and dynamic interactive graphics, we decided to purchase a license for the "Splus" extended and supported version of the S language for graphical data analysis and statistics (Becker et al. 1988). Installation proved to be relatively free of difficulty. (This contrasts with severe difficulties with dynamic loading reported by many users who obtained S directly from AT&T.) Graphical extensions for "brushing" and rotation of 3-D plots (see Becker et al. 1987) have allowed us to obtain new insights about the distribution of tree species across drier sites in southeast Texas. Standard S features have recently contributed to summarizing of simulation results for ordination statistics (bootstrapped ordination), evaluation and summary of simulation results with the ALLOCATE model, and testing of Rohlf & Archie's (1978) mapping methods.

Using network datalines, we have obtained copies of "nesi" (the New Environment for Statistical Inference) routines written in the S language, and other useful S packages for estimating data transformations for additivity, resistant analysis of variance, and estimation of growth curves from repeated measures.

We are also considering statistical program development in X-lisp-stat, and may install it when the most recent version proceeds past beta testing. The suite of programs developed for this project, if made available under S with X-windows or X-lisp-stat, could form the nucleus of a networked environment for vegetation analysis and comparison of patterns across scales. S includes more mature tools for non-parametric and exploratory data analysis, whereas X-lisp-stat has more flexible tools for building graphical ways of interacting with data. Our present plan is to continue software development in S while investigating X-lisp-stat as a basis for a later system to be made accessible thru Internet.

Literature Cited

Becker,R.B., Chambers,J.M., Wilks,A.R. 1988. The new S language: a programming environment for data analysis and graphics. Wadsworth, Pacific Grove, California.

Becker,R.B., Cleveland,W.S., Wilks,A.R. 1987. Dynamic graphics for data analysis. Statist. Sci. 4: 355-395.

Burrough,P.A. 1987. Spatial aspects of ecological data. In: Jongman,R.H.G., ter Braak,C.J.F., van Tongeren,O.F.R. (eds) Data analysis in community and landscape ecology. Pudoc, Wageningen. pp 213-251.

Knox,R.G. 1989. Effects of detrending and rescaling on correspondence analysis: solution stability and accuracy. Vegetatio 83: 129-136.

Knox,R.G. & Peet,R.K. 1989. Bootstrapped ordination: a method for estimating sampling effects in indirect gradient analysis. Vegetatio 80: 153-165.

Marks,P.L. & Harcombe,P.A. 1981. Forest vegetation of the Big Thicket, southeast Texas. Ecol. Monogr. 51: 287-305.

Minchin,P. 1987. Simulation of multidimensional community patterns: towards a comprehensive model. Vegetatio 71: 145-156.

Robertson,G.P. 1987. Geostatistics in ecology: interpolating with known variance. Ecology 68: 744-748.

Rohlf, F.J. & J.W. Archie. 1978. Least-squares mapping using interpoint distances. Ecology 59:126-132.

Streng,D.R., Glitzenstein,J.S., Harcombe,P.A. Woody seedling dynamics in and east Texas floodplain forest. Ecology (in press)

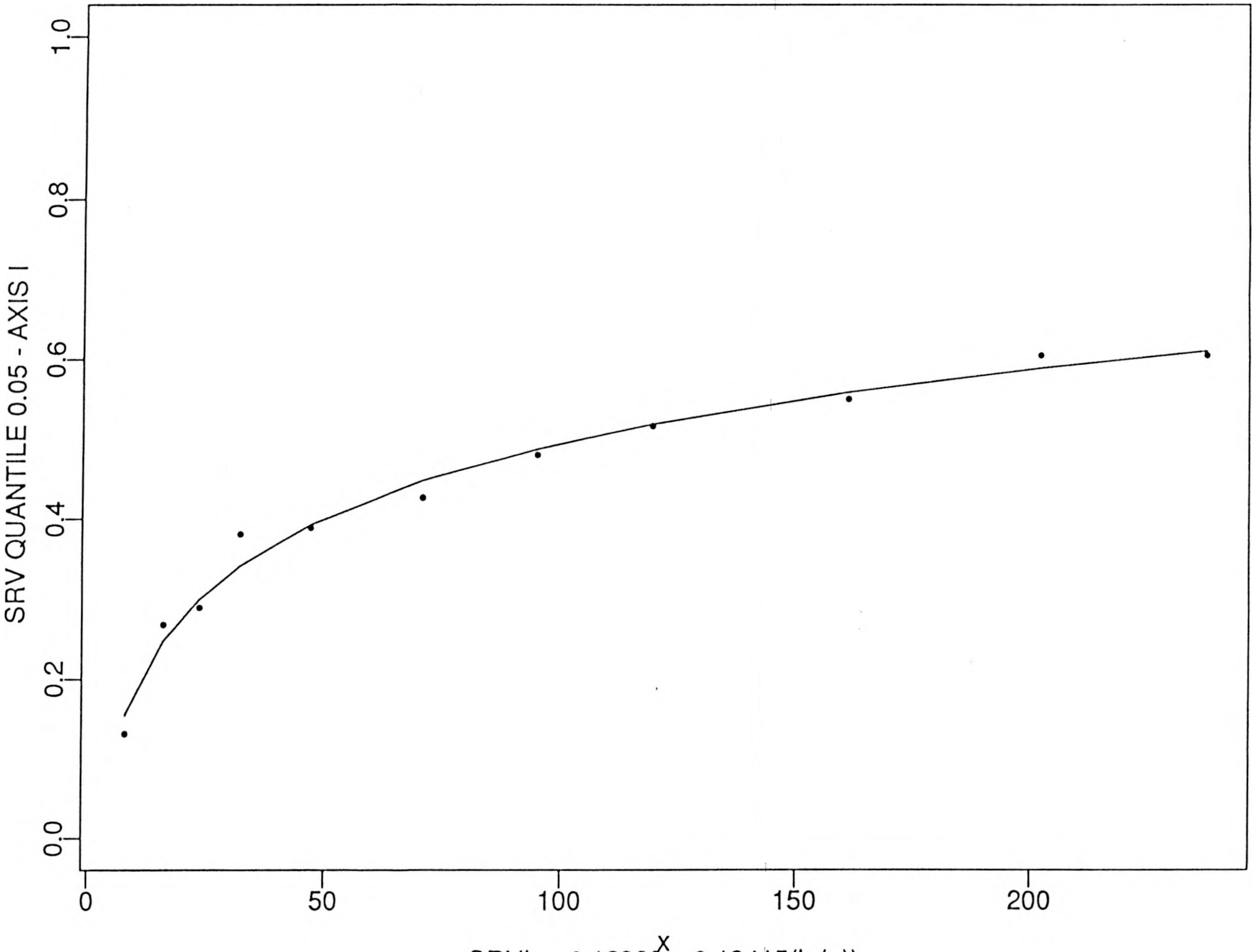
ter Braak,C.J.F. 1987. The analysis of vegetation-environment relationships by canonical correspondence analysis. Vegetatio 69: 69-77.

ter Braak,C.J.F. 1988. CANOCO - an extension of DECORANA to analyze species-environment relationships. Vegetatio 75: 159-160.

Tilman,D. 1988. Plant strategies and the dynamics and structure of plant communities. Princeton University Press, Princeton, New Jersey.

Fig. 1a

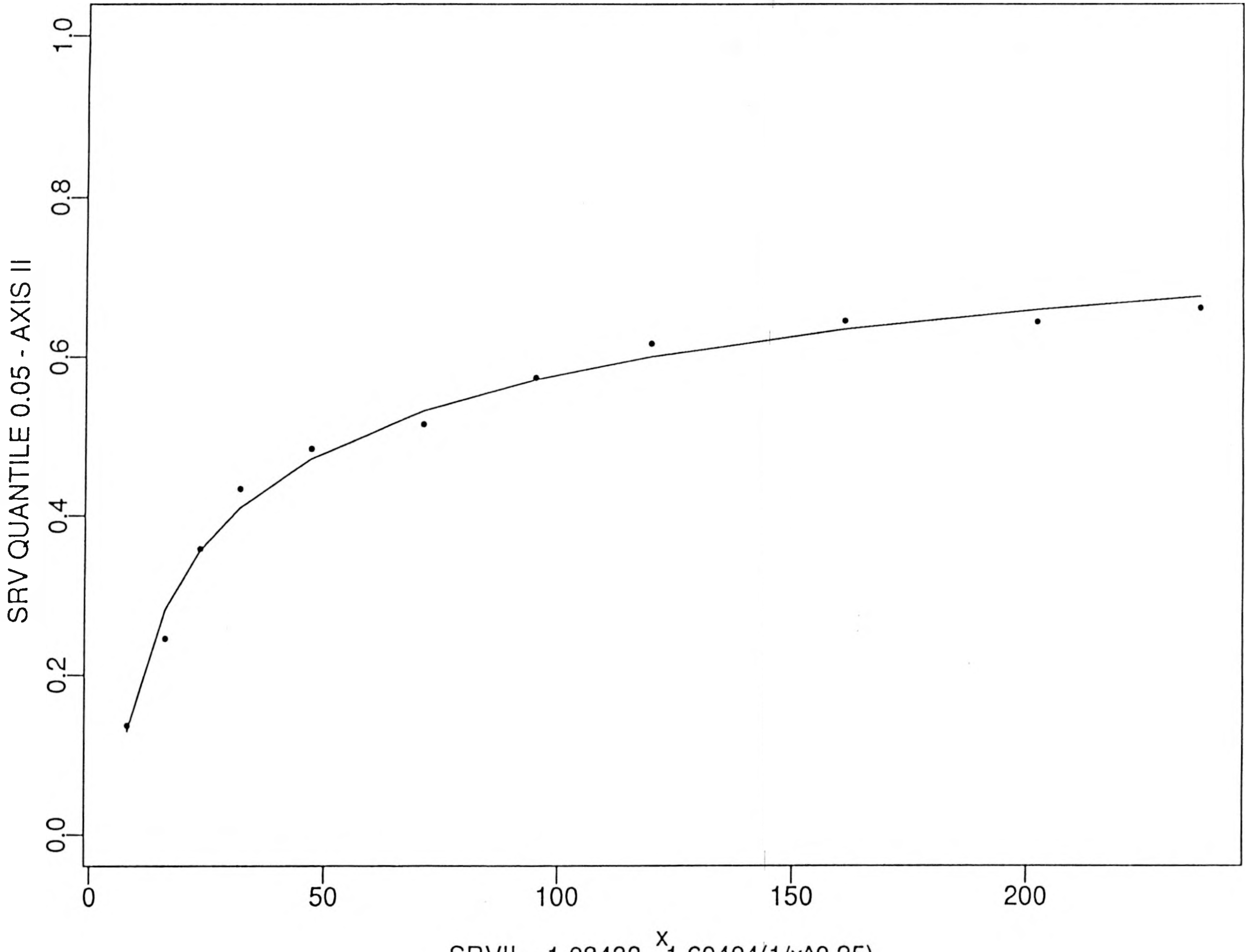
Approx. 95% confidence bound, curve fit with LS



SRVI = -0.12399 + 0.13415(ln(n))

Fig. 16

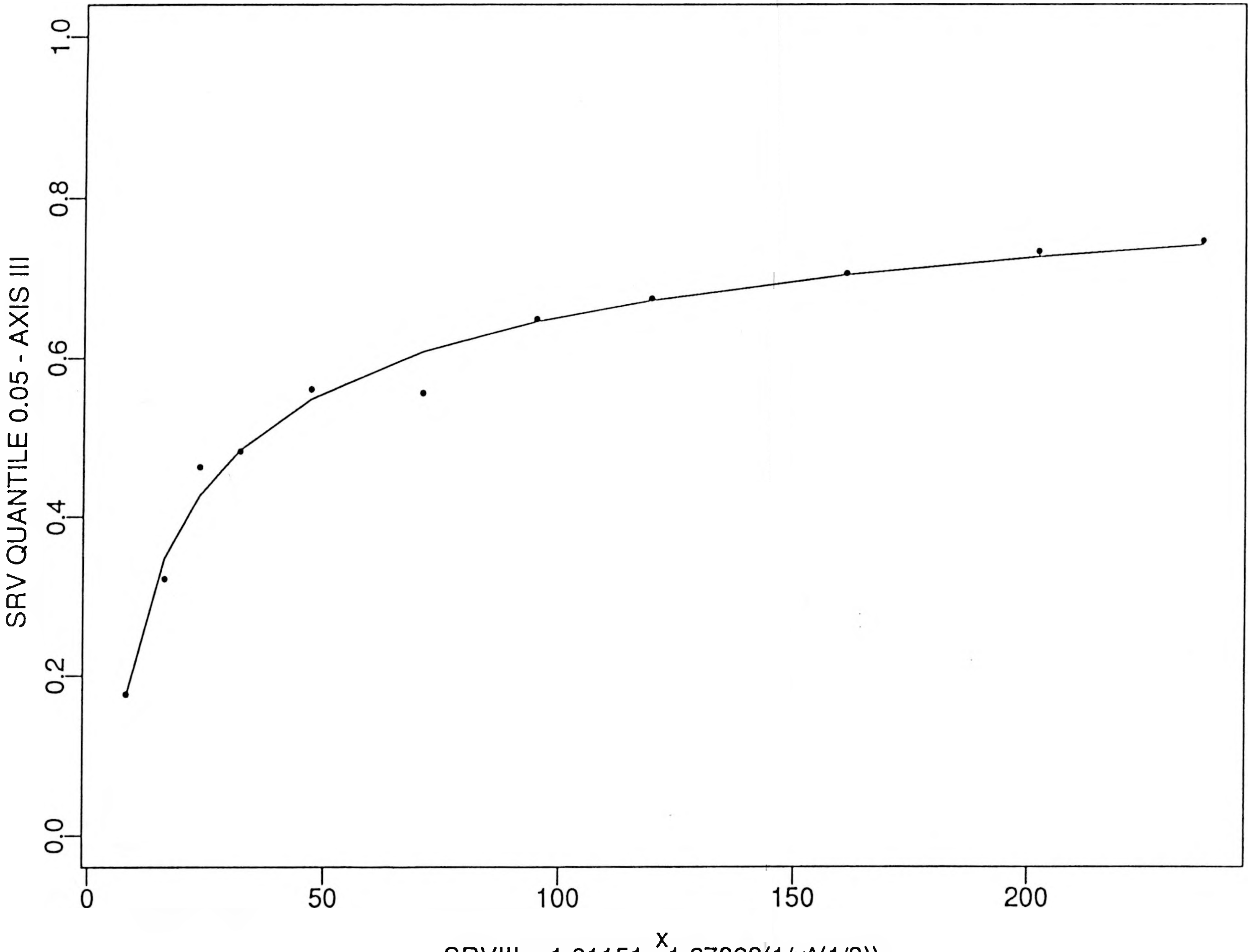
Approx. 95% confidence bound, curve fit with LS



SRVII = 1.08433 - 1.60404(1/x^0.25)

Fig. 1c

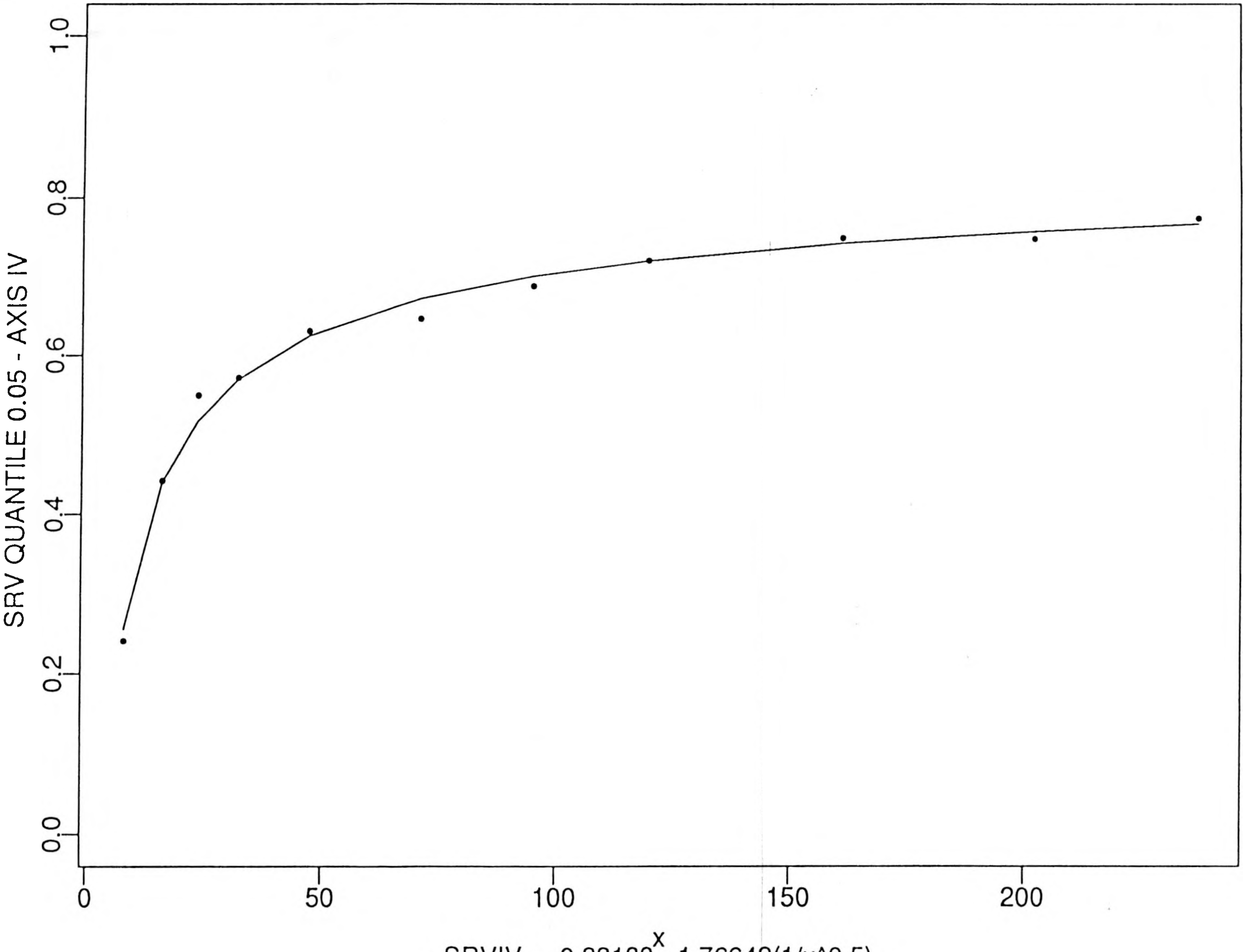
Approx. 95% confidence bound, curve fit with LS



SRVIII = 1.01151 - 1.67368(1/x^(1/3))

Fig. 1d

Approx. 95% confidence bound, curve fit with LS



SRVIV = 0.88133 - 1.76642(1/x^0.5)