BIOSYSTEMS MODELING

Abstracts of Current and Recent Work At

North Carolina State University

1981 Supplement

513 Cox Hall, N. C. State University, Raleigh, North Carolina 27650

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INTRODUCTION

Approximately two years ago, we assembled and distributed the booklet, "BIOSYSTEMS MODELING, A Collection of Abstracts of Current and Recent Work at North Carolina State University." The booklet was intended to serve as a medium of communication, a basis for initiation of collaborative interdepartmental projects, and as a record of the degree and type of activity at NCSU in biosystems modeling. The original booklet seemed to serve these purposes, and an update appears to be in order.

There are no clear boundaries as to what type of work should be included in such a collection. Most biological research will have some mathematical content (at least simple arithmetic) and most work in mathematical science and methodology is at least potentially applicable to biological systems. The intent is to include biological work in which mathematical methods play a central role, and mathematical work of clear relevance to biology.

The original booklet contained contributions from twenty-three departments, including one from our sister institution, North Carolina A&T State University. The present update contains contributions from fourteen departments.

The collection includes abstracts of published work, descriptions of work in progress, and potential applications. This last category includes descriptions of on-going biological work which might profitably be extended to include mathematical modeling, as well as models "in search of" experimental data for testing.

The subject index is compiled in terms of broad subject matter categories. In most cases, the keywords for the index were supplied by the contributors.

ARRANGEMENT

The abstracts are grouped by the department of the first-named author. In the case of entries with several authors, the entry is included in the
Listing by Department under each department. An author index is also provided.

REQUEST TO READERS

If the interest in this type of compilation continues, another update will be planned in about two years. We would warmly welcome any suggestions directed at improving its usefulness.
LISTING BY DEPARTMENT

Entries with authors from several departments are listed under each department.

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*Indicates Biomathematics Faculty.
MECHANICAL IMPEDANCE MEASUREMENTS OF HUMAN TISSUE

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Presented at the 32nd Annual Conference on Engineering in Medicine and Biology

Mechanical impedance, the ratio of force to velocity of a dynamically existed system, can be used to model dynamic response as a function of input frequency. The approach has the advantage of determining the overall response of the system by measuring force and velocity at the input point. Problems of transducer attachment and local phenomena are circumvented. While the input can be broadband, steps or impact, it is often convenient to excite the system sinusoidally at a series of frequencies in the range of interest.

Results, often plotted as impedance versus frequency, can be used to model the system as a combination of lumped parameter masses, dampers and springs. Data curves are presented for whole-body, hand-arm, head and mammary tissue. In general, these systems show a mass-like lower frequency response sometimes followed by a resonance but always followed by some degree of isolation so that the apparent mass (the amount of material actually vibrating) is significantly reduced at higher frequencies.
Many hand-held power tools produce uncomfortable, often unsafe, levels of vibration. Chain saws powered by internal combustion engines have been studied extensively because of their characteristically high vibration levels. Electric and air powered tools have also been found to produce high levels of vibration especially if the tool output is reciprocating or if there is impact, for example, between saw teeth or grinder wheel and the workpiece.

Typically, solutions to the problem have involved improvements in engine or motor balancing and isolation of the tool handles from the source of vibration. Isolators usually consist of blocks or bushings or rubber or similar materials which have both spring and damper characteristics. While many tools operate at rotational or cycle frequencies in the 100 to 200 Hz range, they usually produce significant levels of vibration at much higher frequencies. These higher frequencies are easily isolated by the method discussed below. Lower frequencies are more difficult to isolate. This is unfortunate because the hand-arm is most sensitive at the lower frequencies.

The rational design of handgrip isolators required that the dynamic response of the hands and arms be determined. With this information, it was then possible to determine the characteristics required in the isolators. Models predicted and observations confirmed that higher frequencies could be effectively isolated, but that lower frequencies were difficult to isolate.
MULTIPLYING HUMAN FORCE OUTPUT: SPRING LOADED IMPACT TOOL

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Presented at 1979 Winter Meeting of
American Society of Agricultural Engineers
New Orleans, LA Dec. 1979

In many work and sport activities energy is accumulated in the kinetic form in a moving tool or workpiece. This energy is then released rapidly to produce a high force to overcome the threshold levels of the job being done. Examples are cutting wood with an ax, digging with a pick or hitting a baseball with a bat.

The work summarized here involves the modelling and evaluation of human input force and power relationships, followed by the development and testing of a spring-loaded impact tool to develop known energy outputs without the aiming error inherent in kinetic tools, especially when multiple blows are required. It consists of a spring which is released at near full compression to accelerate a mass which impacts against the working tool. Selection of spring rate and length, mass weight, and tool weight give the design variation adaptable to a range of applications.

The concept appears to have the potential to increase efficiency and speed up many hand tool operations.
THE USE OF INDIRECT ORDINATION IN THE STUDY
OF APPLE ORCHARD WEED VEGETATION

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T. R. Wentworth
Department of Botany

W. A. Skroch
Department of Horticultural Science

The importance of 36 weed species were determined in 47 apple study
orchards in Henderson County, North Carolina. At the same sample sites,
data on a suite of environmental variables were collected. The data were
subjected to indirect ordination (principle components analysis [PCA] and
reciprocal averaging [RA]) to extract axes of compositional variation.
Environmental data were regressed against orchard RA axis 1 location to
determine which environmental factors best explain weed compositional
variation. Using PCA and Cluster Analysis, two major orchard subgroups were
identified. These groups were found to differ significantly in paraquat use.
The number of paraquat applications from 1976 to 1979 was the environmental
factor explaining the most amount of compositional variation in the first RA
axis for the high paraquat use (HPU) orchard subgroup. For the low paraquat
use (LPO) orchard subgroup, soil K and Na were the environmental factors
most associated with RA axes 1 and 2, respectively.
DIFFUSION FROM A CIRCULAR STOMA THROUGH A BOUNDARY LAYER
A FIELD-THEORETICAL ANALYSIS

J. R. Troyer
Department of Botany


The case of diffusion of a gas from a single circulator stoma through an unstimred boundary layer of finite thickness into a perfectly stirred atmosphere free of convective effects is examined theoretically, with the gas assumed to be at constant concentration across the stoma. The analysis employs a mathematical solution to an analogous problem in electrostatic physics previously obtained by Kuz'min (1972 Sov Phys Tech. Phys 17:473-476). The diffusion flux is shown to be no more than 1% greater than that into a perfectly unstirred atmosphere is the boundary layer is thicker than 40 times the stomatal radius. Under the conditions assumed, for realistic boundary-layer and stomatal dimensions, taking the diffusion flux through the boundary layer to be linear with the stomatal radius would usually involve no significant error. This result may indicate that the principal effect of wind velocity on mass exchange between leaf and atmosphere may be exerted through influencing convection outside the boundary layer rather than through determining the thickness of that layer.
VEGETATION ON LIMESTONE IN THE HUACHUCA MOUNTAINS, ARIZONA

T. R. Wentworth
Department of Botany

The Huachuca Mountains of southeastern Arizona support distinctive plant communities on soils developed from limestone. Vegetation patterns on limestone were determined through gradient analysis of coverage data from 77 0.1 ha quadrats located over a range of topographic positions from 1600 to 2100 m elevation. The sequence of major community types from most mesic to most xeric positions on open slopes is: (1) pine-oak woodland, (2) mesic phase Cercocarpus scrub, and (3) xeric phase Cercocarpus scrub. Deciduous woodlands and pine forests occupy low and high elevation limestone canyons, respectively. An environmental scalar developed to quantify site position in relation to elevation and topographic position was strongly correlated with an indirect ordination axis from reciprocal averaging of the coverage data.

The plant communities studied have generally high importance of species of Madrean affinity, but coverage of these species declines toward more xeric situations where a drought-adapted flora of widespread distribution predominates. Although vegetation on limestone in the Huachucas is similar to that in the Santa Catalina Mountains, it differs in composition, environmental relationships, and species diversity from that of the nearby Mule Mountains. The latter contrasts may be due to effects of mountain mass and differential rates of colonization.
DISTRIBUTIONS OF $C_4$ PLANTS ALONG ENVIRONMENTAL GRADIENTS
IN THE MULE MOUNTAINS, SOUTHEASTERN ARIZONA *

T. R. Wentworth and J. D. Elson
Department of Botany

The Mule Mountains are a small, semi-arid range with strong Mexican floristic affinity. Previous studies of vegetation on granite and limestone soils elucidated trends of community composition associated with gradients of decreasing temperature and increasing precipitation from low to high elevations. Reciprocal averaging (correspondence analysis) of compositional data provided sample vectors along which changes in coverage and diversity of $C_4$ species could be examined. Plants having the $C_4$ photosynthetic pathway (almost exclusively perennial bunchgrasses) form a conspicuous and diverse component of most vegetation types. On granite, both coverage and diversity of $C_4$ species increase gradually from high elevation pygmy conifer-oak scrub through low elevation desert grassland, where $C_4$ species are dominant. On limestone, $C_4$ species coverage and diversity increase slightly from high elevation Cercocarpus scrub through Mortonia-dominated Chihuahuan desert scrub of intermediate elevation, but then decline in low elevation Parthenium-Acacia Chihuahuan desert scrub. Recent replacement of grassland by desert scrub on low elevation limestone may account for relatively low importance of $C_4$ species there. Distributions of $C_4$ plants on calcareous bajadas (plains) below the Mule Mountains and on limestone slopes of the nearby Huachuca Mountains are currently under investigation.

SIMULATION MODEL OF BOLL WEEVIL CAPTURE IN PHEROMONE TRAPS

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R. E. Stinner
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A mathematical model was developed to simulate the capture of boll weevils, Anthonomus grandis Boheman, in a pheromone trap. The model considers the effects of rates of response to pheromone, location of boll weevils within the trap area, and the probability that responsible boll weevils are captured by traps. Capture efficiency as affected by trap density, male boll weevil density, and the cotton crop status are discussed.
SIMULATION MODEL OF BOLL WEEVIL DISTRIBUTION WITHIN A COTTON FIELD

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A mathematical model was developed to simulate mechanisms affecting the distribution of boll weevils within a cotton field. The model considers the effects of pheromone trap density, boll weevil population density, cotton crop status, mechanisms of in-field movement, population growth, and capture by pheromone traps. Simulation results of interest are the temporal and spatial clumping patterns produced around pheromone sources.
POPILLIA JAPONICA: STIMULATION OF TEMPERATURE-DEPENDENT DEVELOPMENT OF THE IMMATURES, AND PREDICTION OF ADULT EMERGENCE

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Robert L. Rabb and R. E. Stinner
Department of Entomology

The temperature-dependent development of the immature stages of the Japanese beetle is re-described. The effect of temperature on the development of overwintered third-instar grubs, and the reproductive maturation period of the adults are quantified. Emergence of adults was not affected by soil moisture. Simulations of immature-stages development and adult emergence compared favorably to field data.
POPILLIA JAPONICA: THE EFFECT OF SOIL MOISTURE AND TEXTURE ON SURVIVAL AND DEVELOPMENT OF EGGS AND FIRST INSTAR GRUBS

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Egg and first-instar survival as a function of soil texture and moisture was estimated under laboratory conditions. These stages were found to be resistant to extreme moisture conditions in various types of soils. Delays in egg development were observed particularly in saturated soils. These results are used in developing a mathematical model of survival of the early instars under variable moisture conditions, and simulations are compared with field data. Field survival was highly variable, and correlated only partially to model outputs. Probable causes of the discrepancies are discussed.
Japanese beetle populations were sampled continuously during the summer of 1978 and 1979 in two agroecosystems of eastern North Carolina. Patterns in trap capture were used to develop a conceptual model of the distribution and movement of the adults. Agroecosystems were partitioned into four categories of sites: (1) aggregation, or intensive production sites, (2) marginal production sites, (3) migration 'alleys', and (4) feeding sites. The effect of temperature on flight activity is also discussed.
CURRENT WORK IS IN SEVERAL AREAS OF INTEGRATED PEST MANAGEMENT IN APPLE

1. Temporal, spatial, and numerical dynamics of pest populations; approaches include:

   a. Evaluation of a widely distributed generalized model of insect
      phenology which is based on the degree-day concept;

   b. Assessment of the potential utility of degree days for predicting
      insect phenology by comparing predictions based on degree days with
      those based on julian date alone;

   c. Evaluation of a published model of codling moth inter-generational
      numerical dynamics based on a constant environment; and

   d. Development of a model of codling moth intra- and inter-generational
      population dynamics, incorporating environmental and management inputs.

2. Spatial and temporal distributions of pest populations, and sampling
   distributions based on direct census and pheromone trap methods of popula-
   tion assessment, and optimization or improvement of sampling procedures.

3. Pest-crop interactions, such as effects of crop and pest density, orchard
   parameters, fruit quality parameters, and environmental conditions on crop
   damage at harvest, and crop effects on pest dynamics.

4. Determination of time-dynamic economic thresholds for pest species; this
   includes:

   a. Knowledge of expected population density between decision point and
      harvest date;

   b. Age-specific damage rate of pest population;

   c. Value-structure of crop, including status of fruit quality and damage
      level and expected crop loss from other factors; and

   d. Uncertainty of knowledge of current pest level, future pest dynamics,
      efficacy.

5. Pesticidal effects on pest populations, using two approaches:

   a. Optimization of pesticide applications, considering degradation rates
      of pesticides, age structure and age-sensitivity relationship of pest
      population, dose-response curve of the pest, uncertainty of future
      environmental conditions, and imperfect knowledge of population para-
      meters; and
b. Evaluation of current pesticide application schemes, based on
determining risk to growers as a function of the relative toxicities,
persistences, and application frequencies and rates of pesticides
actually used in relation to the standard recommended rates, fre-
quencies, and materials.

6. Testing of population dynamics models (developing validation criteria),
particularly considering:

a. Which stage(s) of life cycle of pest should be used for testing;
b. How much error is acceptable, and how error should be measured;
c. Testing of submodels versus complete models; and
d. Evaluation of how rigorously published models have been tested,
and by what criteria.
A system of computer programs was written to simulate ignition and spread of a forest fire under varying weather conditions and fuel types. Using a low-speed computer terminal, the user is required to input decisions concerning the request for and deployment of fire suppression units. The user is periodically given the opportunity to alter those decisions or to request information regarding the current status of the fire and of the suppression units.

The stated objective is for the user to contain the spread of the fire so that it is extinguished before it reaches the border of the area in which the fire occurs. The simulation is concluded by one of three occurrences; (1) the user requests termination, (2) the fire spreads out of the area, or (3) the fire is contained and extinguished.

The simulator is in use at several forestry schools for teaching forest fire management. No further developmental work is in progress at this time.
The genetic component of variation of enzyme activity in natural populations of \textit{Drosophila melanogaster} was investigated by using two sets of chromosome substitution lines. The constitution of a line of each type is: $i_1/i_1; +_2/+_2; i_3/i_3$ and $i_1/i_1; i_2; +_3/+_3$, where $i$ refers to a chromosome from a highly inbred line and $+$ refers to a chromosome from a natural population. The $+$ but not the $i$ chromosomes vary within a set of lines. By use of a randomized block design to test and estimate components of variance, 50 of the second- and 50 of the third-chromosome substitution lines have been screened for variation in the activity levels of seven enzymes. Six of the seven enzymes show a significant genetic component in at least one set of lines, and five of the seven enzymes show activity variations attributable to factors that are not linked to the structural gene. These unlinked activity modifiers identify possible regulatory elements. Analyses of covariance show that most of the genetic variation of enzyme activities cannot be accounted for by genetic variation of live weight or protein content. These results and the lack of strong correlations between the genetic effects on the activities of different enzymes indicate that the effects are mainly specific for individual enzymes.
ALLOZYME FREQUENCY CHANGES ASSOCIATED WITH SELECTION
FOR INCREASED GRAIN YIELD IN MAIZE (ZEA MAYS L.)

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Department of Statistics

Genetics 95:225-236, 5/1980

Frequency changes of alleles at eight enzyme loci were monitored in
four long-term maize selection experiments. The results indicate that
changes in frequencies of the alleles at these loci are associated with
changes due to selection for improved grain yield. The frequencies changed
more than is consistent with the hypothesis of selective neutrality. In
addition, significant deviations from a random-drift model were nearly
always accompanied by significant linear trends as would result if allozyme
frequencies respond to directional selection. Evaluations of linkages and
linkage disequilibria in the selected populations indicate that the eight
enzyme loci responded independently as selection progressed.
ON NUTRIENT SOURCES TO ONSLOW BAY, NORTH CAROLINA

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E. E. Hofmann
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Continental shelves have varying geomorphologies which result in fundamentally different nutrient regimes in the overlying waters. Deeper continental shelves or semi-enclosed seas such as the Eastern China Sea, North Sea or Gulf of Maine may have a nutrient reservoir at depth that may supply the euphotic zone through vertical mixing processes. Other continental shelf waters are shallower, have little or no deep reservoir and depend on outside sources, usually rivers or the ocean, for nutrients. In which case, as noted by Riley (1967), nutrient supply to shelf waters is controlled by such parameters as the width of the continental shelf, the magnitude of horizontal and vertical diffusive processes and river runoff. Since many continental shelves are broad and shallow, it is necessary to catalog the various sources and sinks in the system and the physical and dynamical constraints imposed on such as that relate to biological productivity. An additional process by which nutrients from the deeper ocean may be transported into the shelf waters is the gross advection of nutrient rich deeper ocean waters vertically and horizontally onto the shelf.

Studies of North Carolina shelf waters by Stefansson, Atkinson and Bumpus (1971) (hereafter referred to as SAB(1971)) concluded that two processes, cascading of shelf water and intrusions of Caribbean water contained in the Gulf Stream, probably controlled nutrient flux onto that shelf regime. Blanton (1971) elaborated on the Gulf Stream intrusion mechanism proposing a stranding mechanism by which intruding Gulf Stream waters (GSW) are isolated in Onslow Bay. While most of the controlling processes were thus revealed, it was apparent that the absolute flux of nutrients, the seasonality of nutrient influx and importance of late winter upwelling were unknown. To address these and ancillary questions, a large scale study of Onslow Bay was initiated in 1975. Many of the results of this latter study are now published and the data gathered, and the concepts developed for Onslow Bay as well as for other parts of the southeast United States continental shelf can be applied to the topic of advective nutrient dynamics in Onslow Bay.

Since recently developed concepts are critical to the discussion, we will first give a thorough review of relevant topics.

SAB (1971) stated that onshore intrusions of deeper GSW formed a lower layer in the Bay observed only in the spring and summer, implying that both stratification and wind were a causality. They noted van Arx (1962) had postulated that Gulf Stream meanders would periodically and presumably place cold water year round at the shelf break, but these authors firmly felt that seasonal dependence of GSW intrusions argued for partial wind control. While this greatly clarified, in a qualitative sense, the spring/summer situation, advective nutrient dynamics during other times of the year are less well known.
A TIME DEPENDENT MODEL OF NUTRIENT DISTRIBUTION IN CONTINENTAL SHELF WATERS

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A time dependent, vertical plane mathematical model of nitrate distribution in Onslow Bay, North Carolina, is developed using similarity theory and conventional numerical techniques. Inputs of nitrate into Onslow Bay are the result of Gulf Stream intrusions (Atkinson, et al., 1979) and this forcing is included as a boundary condition for this system. Advective and diffusive processes provide the mechanisms for transport of nitrate in Onslow Bay. The time dependence of the resulting nitrate fields is determined by the rate of phytoplankton removal of nitrate.

Nondimensional numbers, arising from model formulation, indicate the relative importance of various processes included in the model. Two non-dimensional numbers, H and P, and the non-dimensional ratio, P/H, indicate interactions of physical processes. Importance of the biological terms is determined by a third non-dimensional number, A. Model results are compared to nitrate data collected in Onslow Bay, North Carolina, during an intrusion.
LIFE HISTORY STRATEGY OF BEAVER (CASTOR CANADENSIS)

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Richard A. Lancia
Department of Forestry and Zoology

Current efforts are specifically directed toward developing a theoretical model of the genetic fitness associated with dispersal of subadults from their natal colony.
BEAVER FAMILY ORGANIZATION: ITS IMPLICATIONS FOR COLONY SIZE

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This paper develops a mathematical model to predict average size of beaver (*Castor canadensis*) colonies (family units). Based on a family social structure where only adults breed, the model predicts an upper limit to colony size. Although natality, mortality, and dispersal rates may vary as functions of population density to set the value of the limit, no density-dependent mechanism is required to establish the existence of the limit.

Further predictions include 'threshold' combinations of survival and dispersal rates, only above which 'typical' colony social structure can develop. Modeling predictions are consistent with ecological correlates expected for a K-selectionist species.
A NONLINEAR SYSTEM WITH SINGULAR VECTOR FIELD NEAR EQUILIBRIA

Stephen L. Campbell and Jack W. Silverstein
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The system \( \dot{N} = (N - \alpha)\omega + y, \quad \dot{\omega} = bN + a\omega^T \), \( N(t) \in \mathbb{R}^{mxm}, \quad \omega(t) \in \mathbb{R}^m \), which originally arose from a model for the pathological behavior of neural networks, is studied. Similar equations can arise in a variety of applications. It is shown that if \( N(0) \) is positive definite, then solutions exist for all time. Equilibrium points are determined. \( N \) is found to be singular at the equilibrium points, making the analysis of the asymptotic properties of the system non-trivial. The asymptotic behavior when \( y = 0 \) is completely described. Some results are proven on the asymptotic behavior of \( N \) and \( \omega \) when \( y \neq 0 \).

*Paper has been accepted for publication in Applicable Analysis, 1981.
A NONLINEAR IMPACT MODEL FOR A SPHERE WITH A FLAT PLATE

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Presented at the 1979 Winter Meeting of the
American Society of Agricultural Engineers.

With the development of the piezoelectric force transducer, it has become possible to measure directly the time dependent contact force during impact of a uniform viscoelastic sphere with a solid flat surface. This paper develops the second order nonlinear differential equation,

\[ \ddot{x} + c \frac{v_0}{v_t} (1 - 3 \frac{-t}{\tau}) \dot{x} + k(x + \gamma(1 - e^\gamma)) = -mg, \]  

(1)

and proposes it as a model for the motion of the sphere's center of gravity during impact. The seven parameters \((m, k, c, \tau, \gamma, v_0, v_t)\) are determined for a silicone rubber ball. These parameters are then used in a numerical solution of the differential equation and compared with the measured force of the impact. Three methods of direct measurement of the seven parameters from the contact force are also considered.

Our current work is going in two directions. The first is to develop ways of estimating the parameters in the differential given in the abstract. The second is to apply this model to fruit namely, blueberries and grapes. The main goal here is to show that the parameter \(k\) of the differential equation is directly related to the firmness and hence marketability of the fruit.
PERIODIC SOLUTIONS FOR CERTAIN PROTEIN SYNTHESIS MODELS

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We investigate the qualitative behavior of a class of deterministic models with delays that arise in the study of protein synthesis. We demonstrate the existence of non-constant periodic solutions to our system of differential-delay equations under certain conditions on the parameters. We conclude with a brief discussion of the biological significance of our results.
THE EXISTENCE OF PERIODIC SOLUTIONS FOR
INDUCTION - REPRESSION SYSTEMS IN PROTEIN SYNTHESIS

J. M. Mahaffy
Department of Mathematics

The genetic regulation of protein synthesis often involves both positive and negative feedback control or induction and repression. One particular example is provided by the lac operon in E. coli. Using this example, mathematical models are developed with enzyme kinetic approximations and delays for the biological processes of transcription and translation. The resulting differential equations with delays are analyzed for their qualitative behavior. By varying the parameter values the system can be shown to be locally unstable. For these parameter values cone mapping techniques are applied to prove the existence of periodic solutions.
A STOCHASTIC MODEL OF BEAVER POPULATION GROWTH

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A mathematical model of the growth phase of an unexploited beaver (Castor canadensis) population was developed based on field observations of the life history of beaver colonies and was compared with empirical observations of population growth in Massachusetts. Dispersal rates of subadults from their natal colonies were considered to be density dependent, i.e., as population density increased the rate of dispersal decreased. The rate of pair formation between dispersed individuals was varied as a function of the number of occupied colony sites within an area containing a fixed number of suitable sites.

The dynamics of natality, mortality, and dispersal were considered as flows between appropriate age classes, i.e., kits, yearlings, subadults, adults in newly established colonies, and adults in previously established colonies. The model described population growth as a system seeking homeostasis. Effects of colony site degradation were not considered.

A stochastic simulation computer program based on the model is explained and simulation results are given. By equating the number of breeding females to the number of established colonies, estimates of mean colony size and age composition are derived. The simulation results provide insight into the size of a "floating population" of dispersed subadults and the magnitude of rates of successful colony establishment.

Finally, the computer simulation was used to test a maximum sustained yield harvesting strategy.

In an irreversible monoenzyme system, the reaction scheme for free enzyme E and substrate concentration S is expressed by \( E + S = ES + E + P \).

When the effect of diffusion is taken into consideration, this reaction scheme leads to a reaction-diffusion equation in the form \( \partial S/\partial t = \nabla \cdot (D \nabla S) - v(t,x) \), where \( v \) is the so-called "initial reaction velocity." Three models in relation to the function \( v \) are considered in the present paper. These are given by (i) \( v = k_2 E_0 S / (k_m + S) \), (ii) \( v = \sigma S / (1 + bI + S) \) and (iii) \( v = -k_1 E S + k_{-1}^1 (E_0 - E) \), where \( k_1, k_{-1}, k_2, k_m, \sigma, b \) and \( E_0 \) are known constants. Model (i) is a simple reaction mechanism based on the Michaelis-Menton hypothesis, while model (ii) involves the inhibition concentration \( I = I(t,x) \) which is governed by a linear parabolic equation independent of \( S \).

In model (iii), the enzyme concentration \( E \) is governed by the differential equation \( \partial E/\partial t = -k_1 E S + (k_{-1}^1 + k_2^2) (E_0 - E) \) which is coupled with the equation for \( S \). In each of these models, the boundary condition is given in the form \( \alpha(x) \partial S/\partial v + \beta(x) S = 0 \). The object of this paper is to investigate various qualitative properties of the concentrations in the above systems. The mathematical problems include the existence and uniqueness of both time-dependent and time-independent solutions, iterative schemes for the construction of the solution, stability and instability of steady-state solutions, effect of the inhibition on the asymptotic behavior of the substrate concentration, rate of decay of the time-dependent solution, asymptotic limit of the product concentration, and finally a threshold result for the stability and instability problem of the substrate-enzyme coupled system.
COEXISTENCE AND STABILITY OF A COMPETITION - DIFFUSION SYSTEM IN POPULATION DYNAMICS *

C. V. Pao
Department of Mathematics

The coexistence and stability of the population densities of two competing species in a bounded habitat are investigated in the present paper, where the effect of dispersion (transportation) is taken into consideration. The mathematical problem involves a coupled system of Lotka-Volterra type reaction-diffusion equations together with some initial and boundary conditions, including the Dirichlet, Neumann and third type. Necessary and sufficient conditions for the coexistence and competitive exclusion are established and the effect of diffusion is explicitly given. For the stability problem, general criteria for the stability and instability of a steady-state solution are established and then applied to various situations depending on the relative magnitude among the physical parameters. Also given are necessary and sufficient conditions for the existence of multiple steady-state solutions and the stability or instability of each of these solutions. Special attention is given to the Neumann boundary condition with respect to which some threshold results for the coexistence and stability or instability of the four nonuniform steady-states are characterized. It is shown in this situation that only one of the four constant steady-states is asymptotically stable while the remaining three are unstable. The stability or instability of these states depends solely on the relative magnitude among the various rate constants and is independent of the diffusion coefficients.

DESCRIBING THE BEHAVIOR OF EIGENVECTORS OF RANDOM MATRICES USING SEQUENCES OF MEASURES ON ORTHOGONAL GROUPS *

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A conjecture has previously been made on the chaotic behavior of the eigenvectors of a class of n-dimensional random matrices, where n is very large [10]. Evidence supporting the conjecture has been given in the form of two limit theorems, as \( n \to \infty \), relating the random matrices to matrices formed from the Haar measure, \( h_n \), on the orthogonal group \( O_n \).

The present paper considers a reformulation of the conjecture in terms of sequences of the form \( \{ \mu_n \} \), where for each \( n \), \( \mu_n \) is a Borel probability measure on \( O_n \). A characterization of \( \mu_n \) being "close" to \( h_n \) for \( n \) large is developed. It is suggested that before a definition of what it means for \( \{ \mu_n \} \) to be asymptotic Haar is decided, properties \( \{ h_n \} \) possess should first be proposed as possible necessary conditions. The limit theorems in [10] are converted into properties on \( \{ \mu_n \} \). It is shown (Theorem 1) that one property is a consequence of the other. Another property is proposed resulting in the construction of measures on \( D = D[0, 1] \) which converge weakly. It is shown (Theorem 2) that under this necessary condition for asymptotic Haar, not only is the conjecture in general not true, but that the behavior of the eigenvectors of large dimensional sample covariance matrices deviates significantly from being Haar distributed when the i.i.d. standardized components making up the matrix differ in the fourth moment from 3.


COMPENSATORY GROWTH OF LEGHORN PULLETS

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System: Rearing replacement leghorn (egg-type) pullets.

Model: A mathematical model is needed which describes body weight gain from age 0 to 168 days as a function of protein (or limiting amino acid) intake. Additional considerations include caloric requirements for maintenance, body weight gain, carcass fat and temperature regulation. Additional information is needed on the relationship of body size, composition, photostimulation, environmental temperature and nutrient adequacy on age at sexual maturity.
USE OF COMPENSATORY GROWTH IN REARING EGG-TYPE PULLETS

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The growth rate of leghorn pullet chicks can be reduced during the first half of the 20 week growing period by feeding low protein (or lysine deficient) diets; subsequently, compensatory growth will occur during weeks 11-20. Theoretically, overall growth (0-20 weeks) will be accomplished more efficiently, i.e., with less consumption of protein, lysine the most limiting amino acid, and even calories than occurs with pullets fed sufficient protein and lysine to grow at the optimum of their genetic potential. This theory will be tested in a series of experiments between 1981 and 1985. Additional information will be obtained on (1) capability of genetic strains for compensatory growth, (2) the influence of environmental temperature on feed consumption (hence protein and lysine consumption and resultant compensatory growth), (3) minimum lysine requirement for growth, (4) effect of limiting growth rate (a) early or (b) late in the growing phase on age at sexual maturity and on subsequent egg production.

Observations on body weight, nutrient intake, and egg weight will be recorded at 2 week intervals. Equations will be developed to describe gain in body weight as a function of nutrient intake.
DEVELOPMENT AND DORMANCY OF APPLE TREE BUDS

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In the late summer, apple tree buds enter dormant period during which growth is sharply reduced. Two states of dormancy may be defined. Innate dormancy or rest is portion of the dormant period in which the cause of reduction of growth is due to endogenous factors and is not reversible by restoring favorable environmental conditions. Imposed dormancy or quiescence is induced by unfavorable environmental conditions and is reversible when shifting to favorable conditions. The quiescence, rest and breaking rest are three phases of a continuous process and are accompanied by changes in amounts (or concentrations) of growth promotors and inhibitors within buds. The amounts (or concentrations) of promotors relative to inhibitors are apparently important in determining the dormancy status. The ratio tends to decrease as buds enter quiescence phase and increases sharply at the termination of rest phase. The rate of increase appears to depend on the temperature during the rest phase. The optimum is around 5°C.

A model is proposed to account for a hormonal regulation of all phases of dormancy. It is intended to be used as a framework for quantitative experimental investigation into the bud development in relation to temperature and other environmental factors.
CURRENT STATUS OF THE CHARGE-STATE MODEL FOR PROTEIN POLYMORPHISM

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The stepwise or charge-state model of mutation for electrophoretically detected protein variants was formulated by Ohta and Kimura (1973). This model met three general, empirical features of protein polymorphism in natural populations, namely that (i) the most frequent variant at a locus is of intermediate mobility, (ii) electrophoretically silent alleles occur, and (iii) allelic mobilities diverge with time. We surveyed the theoretical developments and experimental testing of this model. Its assumptions and shortcomings were stressed. Yet the model is evidently useful for (i) theoretical population studies, (ii) testing observed allele frequency profile, and (iii) measuring genetic distance. In particular, the frequency moments test, or similar procedures based on expected profile frequencies, could indicate which of several loci might repay intensive biochemical and physiological study. Experimental studies of the Lap-5 locus in Drosophila willistoni supported this suggestion.
EXACT INBREEDING COEFFICIENTS IN POPULATIONS WITH OVERLAPPING GENERATIONS

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Genetics 89:591-614, 7/1978

A theory is given that allows inbreeding coefficients to be calculated exactly for populations with overlapping generations. Emphasis is placed on providing equations well suited for computer iteration. Both monoecious and dioecious populations are considered and family size is not restricted to being Poisson. One-locus and two-locus inbreeding coefficients are evaluated, although the reader may omit the two-locus sections. The exact treatment is shown to be preferable to approximate treatments in that it applies to both early and late generations for all population sizes. Inbreeding effective numbers found by the exact treatment are compared to various approximate numbers, and the approximate values are found to be generally very good.
QUADRATIC ANALYSES OF RECIPROCAL CROSSES

C. Clark Cockerham and B. S. Weir
Department of Statistics

Three different models, a two-way factorial model for familiarity, an orthogonalizing transform of this model to a diallel model, and a bio model more representative of the biological situation, are interrelated in terms of their components of variance and covariance. It is clarified that there are five components that can be reckoned with in the analysis of reciprocal crosses, including distinct maternal and paternal variances.

Estimation of the components and tests of hypotheses concerning them are outlined for the types of mating designs with reciprocals. One design involves a factorial mating design between two distinct sets of parents or parental lines and the other a diallel of all crosses from a single set of parents or parental lines. Both designs provide the same types of information and similar tests of hypotheses. At least some parts of the analyses corresponding to the factorial model are required to separate the maternal and paternal variances. A least squares partitioning of the sums of squares according to the diallel model, but with expectations expressed in terms of the bio model, provides most of the tests of hypotheses of interest. Worked examples are given.
THE VARIANCE OF INBREEDING AND COANCESTRY *

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One of the central parameters in population and quantitative genetics is the inbreeding coefficient, or the probability that an individual receives from its parents two genes at a locus that are identical by descent. For any particular locus, the genes are either identical or not, and this paper discusses the variation in actual amounts of inbreeding. Components of variance are defined and evaluated for loci within individuals, for individuals within populations, and for populations, with attention paid to linkage, population size and mating systems. For inbreeding at a single locus, variances are expressed in terms of Cockerham's higher order probability measures of identity (Genetics 69:235), while for inbreeding averaged over loci, it is necessary to use two-locus descent measures for all pairs of loci in the genome (Weir, Avery and Hill, *Theoretical Population Biology*, in press). The work is extended from inbreeding to coancestry coefficients.

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CHOOSING AMONG SAMPLING METHODS TO DETERMINE ABUNDANCE OF APPLE ORCHARD WEEDS IN HENDERSON COUNTY, NORTH CAROLINA

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A method is presented for determining which of a set of sampling techniques is most nearly optimum for sampling weed abundance. The method is applicable to all weed species and crop systems. To employ the method, one first needs to develop a set of sampling alternatives. A pilot survey then needs to be conducted to determine time costs and sampling and measurement error variances associated with each technique. The method was used to determine which of three plot sizes (0.6 x 0.6 M, 0.6 x 1.5 M, 1.2 x 2.1M) and two types of orchard scan is most nearly optimum for estimating weed abundance in apple orchards of Henderson County, North Carolina. The results indicate that orchard scans are optimal when less than 14.1 min ha⁻¹ of sampling effort is expended. If a lower variance of the mean is required, however, plot samples may be the better choice. Of the plots used, the 0.6 x 1.5M size was most nearly optimal.
STABILITY OF EQUILIBRIA IN
THEORETICAL PLANT HOST-PARASITE SYSTEMS

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In a theoretical host-parasite system with a typical gene-for-gene relationship between resistance in the host and virulence in the parasite, the stability of the polymorphic equilibrium point is of ultimate interest. Does the corporation of selection against unnecessary resistance in the host and selection against unnecessary virulence in the pathogen stabilize the system for all practical purposes? Two models have been analyzed; one in which only the pathogen evolves on a multi-line host population, as in agricultural systems, and another in which the host and pathogen co-evolve, as in more natural systems. In the former the polymorphic equilibrium was seen to be globally stable, but in the latter the equilibrium was more difficult to analyze. Because of the discrete nature of these systems, both models were formulated as difference equations and hence, for the co-evolving system, the question of whether both host and pathogen gene frequencies should change sequentially or simultaneously became important. It was shown that a simultaneous change implied a local instability for the equilibrium; however, with a sequential change in frequencies of first the pathogen and then the host, the linearization of the system was found to yield neutral stability (i.e., Lyapunov stability). When higher order terms were included, the sequential system was shown to have a locally stable or unstable focus depending upon parameter values for the system. Neither the sequential nor the simultaneous model precludes the occurrence of limit cycles which are implied by computer simulations. The behavior of other models emphasizing different aspects of this type of system will be studied with the hope of increasing our understanding of natural host-parasite systems. This new understanding could provide a better basis for planning strategies for optimal use of genetic techniques applied to disease resistance in important crop species.
MODELING OF MOVEMENT BETWEEN FIELDS
BY AN INSECT PEST SPECIES

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From a zoocentric viewpoint, the cultivated fields in an agro-
ecosystem may be described as stochastically predictable, spatio-temporal
island habitats. Mechanisms by which a given insect species utilizes these
temporary resource fields consist mainly of inter-field migration as well
as forms of dormancy (which could be considered as movement through time).
Stochastic models describing these inter-habitat "movements" will be formulated
and studied as to their applicability in population dynamics and pest manage-
ment. Spatial and temporal distributions of both host and pest species,
relative host suitability as well as environmental conditions will be
considered.
HOW WELL DO HOLOGRAPHIC AND VISUAL SYSTEMS CORRESPOND?

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There are some very suggestive similarities between holography and visual scene analysis when each system is characterized as sets of inputs and outputs linked by what will be called a black box function.

1) Each system consists of two stages, recording and reconstruction.
2) The inputs to the recording and reconstruction subsystems are pairs of object and reference wavefronts (assuming the neural wavefronts we have described actually exist).
3) The outputs in recording are permanent records of the same optic wave, and the spatial distributions of the recordings in each system have some characteristics in common.

These observations imply mapping identities exist for the recording and reconstruction subsystems, each involving the neural black box function and its analogous holographic function.

To press the correspondence further, the possibility of the black box functions being essentially the same can be checked by finding equations that govern the processes underlying these functions. The processes involved turn out to be quite different on closer examination. However, in the search for the processes that could produce a neural holography, a qualitative model of visual scene analysis arose. In this model, the inferotemporal cortex emits neural wavefronts that are independent of viewer position, which allows various neural wavefronts generated by a scene to be matched. Also proposed, is a role for the hippocampus in using recognition of novelty to initiate exploration and neural recording.
A FRAMEWORK FOR MODELING ENDEMIC-EPIDEMIC TRANSITIONS IN SOUTHERN PINE BEETLE*

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The framework set forth for modeling dynamics of the SPB-pine interaction comprises a hierarchy of four levels: the individual tree, local neighborhood, stand, and large region. Individual trees are described in terms of attack threshold, potential brood productivity, stress state and relative attractiveness to beetle attack, as well as emittance of beetles and their pheromones. Certain stress factors substantially reduce the attack threshold and also reduce the brood productivity of the tree. This effect is made on the basis of a distinction between endemic and epidemic modes of infestation within an individual tree. The degree to which epidemic mode trees dominate the dynamics of the neighborhood stand and region is made the basis of endemic/epidemic distinctions at these levels.

The region-wide description suggested is in terms of a mosaic of probability distributions. We would hope that these could be treated as being drawn from a common distributional family, parametrized separately for each stand. In the consideration of the dynamics of each stand, probability distributions must be adjusted for micro-heterogeneities, such as edge effects and proximity to infested trees. Consideration of each of the four levels of the hierarchy is therefore necessary for the understanding of the overall system.

*Paper presented at Work Conference on Population Dynamics of Forest Insects at Low Levels, August 9-10, 1979, North Carolina State University, Raleigh, N. C. Fred P. Hain, Editor.
MODELING AND STATISTICAL ANALYSIS OF A LABORATORY EXPERIMENT TO MEASURE CANNIBALISM IN HELIOTHIS VIRESCENS LARVAE

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see Biomathematics Series No. 4
Institute of Statistics Mimeo Series No. 1306
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A simple laboratory experiment was analyzed by means of biomathematical modeling and subsequent statistical analysis on the basis of the model. The observations, which had been made in the Entomology Department, consisted of a large number of replications of the following elementary experiment: put two neonate Heliothis virescens (F.) larvae in a cup with excess diet; rear them under controlled favorable circumstances, and, after a sufficiently long time, observe the number of pupae (0,1, or 2). Simultaneously, in the same controlled chamber, the elementary experiment was replicated a large number of times for each of eleven different geographic strains. The purpose of the experiment was for each of the eleven strains to determine if cannibalism is a mortality factor or not and to estimate the propensity for cannibalism in case it is. Achieving this purpose is made difficult by the fact that in the life of each pair of larvae in each cup two causes of death are confounded: "natural" or "random" death, and death by cannibalism.

Under certain routinely accepted assumptions, the three numbers, observable for each strain: (i) number of cups without pupae, (ii) number of cups with one pupa, (iii) number of cups with two pupae, are jointly distributed according to the trinomial distribution. This suggests that the statistical analysis might be handled by a chi-square test, and this had indeed been done, leading to a rejection of the null hypothesis that random death is the only cause of death, for most of the eleven strains. However, the goodness-of-fit nature of the chi-square test does not require the introduction of a parameter for cannibalism, and so the chi-square approach is unable to come up with an estimate of the propensity for cannibalism.

The parameters of the above-mentioned trinomial distribution depend on the intensities of both random death and death by cannibalism. Under certain precisely stated biological assumptions the trinomial parameters can be expressed
as functions of the two parameters: rate of random death, and rate of death by cannibalism. This is the crucial step. Now it became possible to apply the theory of Neyman structure tests, and thus to construct the optimal exact test of the null hypothesis that cannibalism is absent, and also to estimate the parameter for cannibalism. The exact distribution of the sufficient statistic for the problem turns out to be rather skew, so that the chi-square distribution as well as the normal distribution behind the chi-square are very poor approximations, except for excessively large sample sizes. Also, the chi-square test amounts to a two-sided test in terms of this sufficient statistic, whereas the model shows that a one-sided test is appropriate for this problem. A relatively simple computer program was written to compute the exact test, and extensive comparisons were made between the exact and the chi-square tests, both for critical region and power. The exact sizes of the approximate tests were larger than the nominal sizes. So from every angle the exact test is preferable, but it could not have been constructed without having the model first. Another advantage of constructing the model is that it points out in what directions the experimental procedure could be refined.
DEVELOPMENT OF A PLANT GROWTH MODEL
FOR SNAPBEAN UNDER OZONE STRESS

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W. W. Heck and J. F. Reynolds*
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A mechanistic mathematical model is being developed to simulate the dry matter production of Phaseolus vulgaris in climate controlled environments. Various submodels (e.g., gas exchange, photosynthesis, respiration, bean production, etc.) will be united into a model which can physiologically describe the snapbean plant. The model will predict dry matter contents of various compartments (leaf, stem, bean, and roots).

The model will be based on data collected in the Phytotron. A dataset, consisting of results from snapbean exposure to ozone obtained from experiments carried out over the last few years, is presently being assembled for use in model development and parameter estimation.

It is expected that a level of detail can be achieved which would allow testing various hypotheses for sites of action of ozone within the plant.

* Dr. Reynolds is currently on leave to the Glasshouse Crops Research Institute, West Sussex, England.
TOBACCO AND ITS ENVIRONMENT — RELATIONSHIPS AMONG CLIMATIC FACTORS AND AGRONOMIC AND CHEMICAL DATA FROM SELECTED FLUE-CURED VARIETIES GROWN IN NORTH CAROLINA *

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Analytical procedures were employed to relate between-year variation in yield, leaf quality index, nicotine, and reducing sugars of 15 selected flue-cured tobacco cultivars grown at five North Carolina locations during the period 1966 to 1977 to daily rainfall and maximum and minimum temperatures. Predictor variables were constructed by dividing the growing season at each location into 14 seven-day intervals, plus one interval of 10 days prior to transplanting and a 13-day terminal interval. Cumulative rainfall, mean daily maximum and minimum temperatures for each interval, and the variability in daily maximum and minimum temperatures within each interval were computed.

Different statistical techniques were employed to develop a prediction model in which the independent variables were the five climatic parameters. The best predictions were obtained using an unrestricted stepwise regression procedure in which the "best 20" variables gave coefficients of determination of 77% for nicotine and reducing sugars, 84% for yield, and 81% for leaf quality index.

Rainfall during the rapid development phase was directly correlated with yield, but was negatively correlated during the early post-transplant growth and maturation phases. Rainfall during the developmental phase generally was associated with increased nicotine concentration in the leaf but during the maturation phase was associated with decreased nicotine concentration. The effect of rainfall on the reducing sugar concentration was opposite that on nicotine. However, during the late maturation phase, rainfall was associated with a tendency for both reduced nicotine and reducing sugar levels in the leaf.

The effect of temperature on yield and leaf quality index was mainly through fluctuations in both maximum and minimum temperatures. Large variations in maximum temperature were positively correlated with yield during the developmental phase, but negatively correlated during the maturation phase. Fluctuations in minimum temperature during development and maturation generally were correlated with reduced leaf quality.

FORMALIZATION OF THE CONCEPTS OF VERBAL VERSUS NONVERBAL REPRESENTATION OF PERCEPTUAL KNOWLEDGE

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Department of Computer Science

It is a common observation that the external representation of a visual scene can be dichotomized into two extreme types: (a) a verbal, symbolic, linguistic, propositional type, e.g., a verbal description of the scene, (b) a nonverbal, analog, isomorphic type, e.g., a photograph of the scene. Therefore, in designing a system for internal representation of knowledge for machine vision tasks, one must deal with the question of whether a propositional type of scheme is adequate or whether the task must be aided by an additional nonverbal, analog, isomorphic type of representation (Fischler, 1978 and Kosslyn and Pomerantz, 1977). This is a difficult question to answer partly because the terms used in the arguments, i.e., verbal, nonverbal, symbolic, propositional, analog, isomorphic, etc. are not precisely or operationally defined within the current context with respect to the question posed. The mathematical definitions of topological or algebraic isomorphism or homomorphism are considered too restrictive to be applicable without major modification. This paper proposed a formal definition of the external verbal/nonverbal representation dichotomy by: (1) analyzing the distinguishing features of verbal and nonverbal representations; (2) delineating and formalizing relevant components of a perceptive system; (3) examining the underlying characteristics of the mathematical concepts of isomorphisms and homomorphisms with respect to (1) and (2) above. Based on this definition, a theory is proposed, which characterizes the internal operations and data structures needed for each of these external representation types.

References:

A new function is introduced that allows a significant shortening and simplification of proofs and a sharpening of some results in the Liapunov theory concerning autonomous systems. Under investigation is the question whether similar improvements are possible for non-autonomous systems. The new approach applies to both difference and differential equations.
INFERENCES ABOUT LINKAGE DISEQUILIBRIUM

B. S. Weir
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Biometrics 35:235-254, 1979

Existing theory for inferences about linkage disequilibrium is restricted to a measure defined on gametic frequencies. Unless gametic frequencies are directly observable, they are inferred from genotypic frequencies under the assumption of random union of gametes. Primary emphasis in this paper is given to genotypic data, and disequilibrium coefficients are defined for all subsets of two or more of the four genes, two at each of two loci, carried by an individual. Linkage disequilibrium coefficients are defined for genes within and between gametes, and methods of estimating and testing these coefficients are given for gametic data. For genotypic data, when coupling and repulsion double heterozygotes cannot be distinguished, Burrows' composite measure of linkage disequilibrium is discussed. In particular, the estimate for this measure and hypothesis tests based on it are compared to the usual maximum likelihood estimate of gametic linkage disequilibrium, and corresponding likelihood ratio or contingency chi-square tests. General use of the composite measure, whether or not random union of gametes is an appropriate assumption, is recommended. Attention is given to small samples, where the non-normality of gene frequencies will have greatest effect on methods of inference based on normal theory. Even tools such as Fisher's z-transformation for the correlation of gene frequencies are found to perform quite satisfactorily.
ANALYSIS OF TWO-LOCUS GENOTYPIC DATA *

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The fact that genes are transmitted in packages, or gametes, and then go through each generation in packages, or genotypes, tends to impose some associations between them. These associations may be strengthened by the sampling process inherent in the mating system or by linkage between the genes at different loci. One of the objects of analyzing population genetic data is to determine if there are frequencies consistent with these kinds of associations, or if there is evidence of further associations because some combinations of genes, within or between loci, confer a selective advantage to the individual in which they are located. Our studies of population genetic data should also take account of population subdivisions and of migration.

It is a trivial statement to say that analyses of genetic data are now routinely carried out on a computer, and we suggest that this increased computational sophistication should be accompanied by increased statistical sophistication. If expressions exist to give either biased or unbiased estimates for example, we may as well use the unbiased ones even if there is greater algebraic complexity. The additional computation is no longer a factor of great consequence in most cases.

We can also point out that most analyses of multi-locus data presently being conducted have taken one of two approaches. Sometimes multi-locus frequencies are compared to the products of corresponding gene frequencies or single locus frequencies, even though this tends to neglect possible types of association or disequilibrium. Other times linkage disequilibrium is reported, where gametic frequencies are compared to the products of corresponding gene frequencies, but this ignores the genotypic structure of the data altogether.

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EFFECT OF MATING STRUCTURE ON VARIATION IN INBREEDING

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An analysis is made of the variation among individuals in fine populations of the proportion of their genes which are identical by descent. There are two causes of this variability: variation in pedigree among individuals and linkage causing whole blocks of genes to be identical or non-identical by descent.

The variation between and within populations is computed for several mating systems: monoecious populations with and without random selfing and dioecious populations with and without a hierarchical mating structure. Some cousin or maximum avoidance schemes are also considered. Transition matrices for two-locus descent measures are given for each system. Total variability is obtained by integrating these measures over the distribution of map distances over whole chromosomes. Approximate methods are also developed for unlinked loci.

Unless populations are very small, there is little variation in inbreeding between populations. For unlinked loci, the coefficient of variation in actual nonidentity is about $1/\sqrt{3N_e}$ for random selfing, $1/\sqrt{6N_e}$ for monogamous matings and $1/\sqrt{12N_e}$ for monoecy with selfing excluded or dioecy with random pairing. Except for species with few chromosomes, these values are increased rather little in early generations in small populations, but more later.

The relation of the quantities to variation in heterozygosity and in quantitative traits is discussed.
ESTIMATION OF LINKAGE DISEQUILIBRIUM
IN RANDOMLY MATING POPULATIONS

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The maximum likelihood method for estimating linkage disequilibrium from genotypic data for randomly mating populations is studied. Instead of iterative methods for finding a root of the cubic equations for one of the gametic frequencies (Hill, 1974), it is recommended that the cubic be solved completely. For data with some missing genotypic classes, it is further recommended that explicit solutions for the cubic be used.
EFFECT OF MATING STRUCTURE ON VARIATION IN HETEROZYGOSITY

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It is convenient to be able to characterize the amount of genetic variation in a population with a single summary statistic. Such a quantity should be easy to both calculate and interpret, and should take full advantage of the multi-locus data that is routinely available to population geneticists. The usefulness of any statistic is enhanced by knowledge of its sampling variance, and it is variances with which we are concerned in this paper. We will examine the effects of sampling implicit in the mating process as well as in the choice of a census sample, so that this work complements our previous studies on inbreeding (Weir, Avery & Hill, 1980) and on linkage disequilibrium (Weir & Hill, 1980).

The most common measure of variation is simply the frequency of heterozygotes, whether at a single locus or averaged over several loci, and it is relatively simple to develop the variance for this quantity. Another measure often used (e.g., Nei & Roychoudhury, 1974) is the gene diversity, which for one locus is one minus the sum of squares of gene frequencies. This is different from heterozygosity only when there are departures from random mating. We can also mention the measure of Brown, Feldman & Nevo (1980) which was also designed to reflect variation in inbreeding species. It is formed by scoring the number of unlike allelic pairs over several loci when all gametes from a sample of individuals are compared in pairs. Our discussion will bring out the similarities and differences between all of these measures.

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THE EFFECTS OF LINKAGE AND LINKAGE DISEQUILIBRIUM ON THE COVARIANCES OF NONINBRED RELATIVES*

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The effects of linkage and linkage disequilibrium on the genetic variances and covariances of noninbred relatives are formulated for quantitative traits with additive and dominance effects, but without epistasis. Assortative mating is excluded. Linkage disequilibrium between two loci introduces a covariance between their additive effects and between their dominance effects. The usual coefficients of additive and dominance variances found by counting paths through common ancestors suffice to express the covariances of relatives, which now include the additive and dominance covariances. The linkage parameter, or recombination fraction, comes into play only when relating the additive or dominance covariances from one generation to another.

*Heredity (in press).
EFFECT OF MATING STRUCTURE ON VARIATION IN LINKAGE DISEQUILIBRIUM

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Measurement of linkage disequilibrium involves two sampling processes. First, there is the sampling of gametes in the population to form successive generations, and this generates disequilibrium dependent on the effective population size \(N_e\) and the mating structure. Second, there is sampling of a finite number \(n\) of individuals to estimate the population disequilibrium.

Two-locus descent measures are used to describe the mating system and are transformed to disequilibrium moments at the final sampling. Approximate eigenvectors for the transition matrix of descent measures are used to obtain formulae for the variance of the observed disequilibria as a function of \(N_e\), mating structure, \(n\), and linkage or recombination parameter.

The variance of disequilibrium is the same for monoecious populations with or without random selfing and for dioecious populations with random pairing for each progeny. With monogamy, the variance is slightly higher, the proportional difference being greater for unlinked loci.
ANGIOTENSIN CONVERTING ENZYME ACTIVITY
IN PARAQUAT-TREATED EXPERIMENTAL ANALYSIS*

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We have studied a profile of angiotensin converting enzyme (ACE) activity in paraquat (PQ)-treated experimental animals (mice and hamsters) as a model for respiratory distress syndrome.

The preliminary results of our work (see references) show that pulmonary ACE activity can be elevated in response to acute insult of PQ in experimental mice despite a seriously decreased lung protein concentration. This finding seems relevant to an ultrastructural evidence that Type I cells and capillary endothelial cells of the rat were selectively damaged by PQ (Kimbrough, R.D., et al., Envir. Res. 6:265, 1973) and to an enhanced level of ACE in idiopathic respiratory distress syndrome of the newborn infant (Mattiolo, L., et al., J. Pediatr. 87:97, 1975). These observations offer a concept that profile of pulmonary ACE activity may specifically reflect a functional status of the integrity of pulmonary microvasculature. A linear time-response relationship of ACE level in our study also suggests a significant association between ACE concentration and intensity of PQ toxicity upon pulmonary system with progressively increasing lung weight and marked reduction in lung protein concentration. The increased activity of ACE with concomitant decrease of the level of total lung protein in PQ-poisoned lung indicates that a regulatory mechanism may exist for the sustained activity of ACE. It seems, therefore, that the rate of production and/or accumulation of ACE may have been greater than the rate of ACE degradation. It also appears conceivable that impaired machinery of lung protein homeostasis caused by PQ challenge may well contribute in part to the distorted picture of pulmonary surfactant system which many authors reported to be an important factor for the severity of the pulmonary lesion in PQ toxicity.

Our data also reveal that PQ is responsible for the increased kidney ACE activity, and suggest the presence of a modulating machinery for its prolonged activity during the experimental period in PQ challenged nephrotoxicity.

Of particular interest is a recent report which an ACE inhibitor, namely captopril, dramatically induced sustained improvements in clinical status and reneal function in patients with severe congestive heart failure (Dzau, V. J., et al., N. Engl. J. Med. 302:1373, 1980).

In light of these encouraging findings, we plan to pursue this project further with special emphasis on the following aspects.

1. Isolation and culture of pulmonary capillary endothelial cells, and ACE activity profile in in vitro system.

2. Pulmonary alveolar macrophage profile as a source of ACE activity.

3. Pulmonary function profile. This portion of our project will be conducted in collaboration with Dr. John O'Neil at U.S. Environmental Protection Agency, Research Triangle Park, NC.
Kim and Roberts

4. Hemodynamic profile in relation to ACE activity. This phase of our project will be conducted in collaboration with Dr. Arthur B. DuBois at John B. Pierce Foundation, Yale-New Haven Medical Center, Yale University School of Medicine, New Haven, Connecticut.

Publications Resulting from this Publication*


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PLANT COMMUNITIES AS FOOD PRODUCERS FOR THE EASTERN GRAY SQUIRREL

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Forest communities in the North Carolina Piedmont were characterized by a weighted averaging procedure as to their suitability as food producers for Eastern gray squirrel (*Sciurus c. carolinensis* Gmelin). Gradient analysis (reciprocal averaging or correspondence analysis) of the same communities indicated that compositional variation is related to successional status and to site moisture and fertility. Squirrel habitat suitability is correlated with successional development, increasing in an exponential fashion from early- and mid-successional deciduous forests. Replacement of light-seeded species by mast producers is responsible for this pattern. No consistent relationship between habitat suitability and stand location on the topographic moisture-soil fertility gradient was observed. We feel that gradient analysis can be an effective means of estimating habitat quality for wildlife species and relating quality to environment and successional status.
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