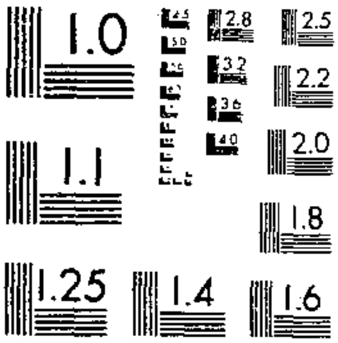
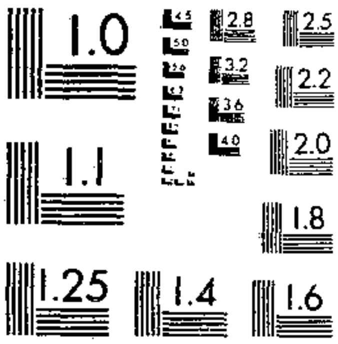
TB 1630 (1980) USDA TECHNICAL BULLETINS UPDATA
MODELING SOUTHERN PINE BEETLE POPULATIONS SYMPOSIUM PROCEEDINGS ASHEVILLE
1 OF 2

START



MICROCOPY RESOLUTION TEST CHART
NATIONAL BUREAU OF STANDARDS-1963-A



MICROCOPY RESOLUTION TEST CHART
NATIONAL BUREAU OF STANDARDS-1963-A

MODELING SOUTHERN PINE BEETLE POPULATIONS

SYMPOSIUM PROCEEDINGS

Asheville, N.C., February 20-22, 1980

Edited by

Fred M. Stephen, Janet L. Searcy, and Gerard D. Hertel

Technical Bulletin No. 1630
U.S. DEPARTMENT OF AGRICULTURE   FOREST SERVICE

Expanded Southern Pine Beetle Research & Applications Program

September 1980

TABLE OF CONTENTS

Dynamics of Bark Beetle-Fungus Symbiosis

THE SOUTHERN PINE BEETLE
POPULATION MODELING SYMPOSIUM--
AN INTRODUCTION AND OVERVIEW

Fred M. Stephen and Robert N. Coulson[1]

The impetus for this symposium came from a result of conversations initiated in meetings of the Expanded Southern Pine Beetle Research and Applications Program Technology Transfer Team concerned with population sampling and predictive modeling. This team has three primary charges: (1) to identify the accomplishments realized from the ESPBRAP in population sampling and predictive modeling; (2) to inform technical specialists, foresters, and forest managers that SPB population trends and associated damage can be reliably estimated using the new technology; and (3) to participate in developing a means for marketing this technology in a form compatible with user needs and technical capabilities.

We believe that the ultimate benefactors of the models we have developed will be those practitioners who are concerned with pest control decisionmaking in the forest environment. However, an intermediate "user" who was clearly identified in a previous symposium (Ciesla 1979) and who also needs to be considered in this overall process of technology transfer is the research scientist. Since mathematical modeling is a technique to abstract pertinent information about complex systems, a particular model can always be considered as incomplete. Nevertheless the modeling approach forces researchers to objectively conceptualize and define the particular system being investigated. Therefore, there is good reason to examine periodically the assumptions, the logic, and the techniques being used in development, validation, and implementation of models. Our technology transfer team thus conceived this symposium as a vehicle to reach scientists. It represents an effort to draw together and present in a single forum a synthesis of the SPB population and damage prediction models that have been formulated to date.

The importance to research scientists of examining intermediate results is clear from an iterative approach to model building proposed by Hamilton et al. (1969). They suggest that following preparatory work and initial formulation of a model, computer experimentation, examination and evaluation of new research findings, and model validation using new and old data all contribute to the refinement and reformulation of the initial model. These processes following initial model formulation are repeated until an acceptable model is developed. In simpler terms, we all can profit from examination and criticism of our work both internally and externally as we progress with our research efforts. We hope this symposium will provide a suitable forum for this process.

Defining the organization of the symposium presents several problems. A holistic treatment of those models, which may be appropriate for the development of an SPB pest management system, is much broader than what we have elected to include. However, a traditional view of insect population models excludes some of those topics we propose to incorporate. We found it difficult to delineate clearly the spectrum of papers. For example, is a model that uses measurements relating to SPB-infested trees as input and output properly considered a southern pine beetle population model? It is certainly apparent that the trees would not be of interest if some level of SPB population had not killed them. But bugs and trees are not synonymous. Population dynamics researchers have been trying for years to make this point with those making pest control decisions. We aren't planning on abandoning the fact now but nevertheless feel that a too-narrow view of what constitutes a population model might provide an unnecessarily biased and limited summary of the modeling efforts relating to SPB and its impact. This reasoning was used as the basis for including models concerned with SPB infestation trend prediction, as well as prediction of pine plantation growth and the impact of beetle populations therein. We did not, however, choose to cover those models

---

[1] The authors are, respectively, Associate Professor, Dept. of Entomology, University of Arkansas, Fayetteville; and Professor, Dept. of Entomology, Texas A. & M. University, College Station.

concerned primarily with hazard ratings, silvicultural systems or site-stand classifications and the beetle. Various economic models were likewise excluded.

What then is the organization plan for this symposium, and how was it conceived? The Expanded Southern Pine Beetle Research and Applications Program management, as elucidated by Leuschner (1979), suggests four types of impact or damage models that are defined by geographic and temporal boundaries and the use to which the models will be put. Briefly summarized, these include (1) models for short-term (1 to 6 months) prediction of beetle population growth and related damage in discrete spots; (2) models also of a short-term, predictive nature but directed toward multispot infestations over a wide area; (3) those models that focus on a more long-term (1 to 5 years) projection of damage over a wide area; and (4) areawide models that predict impact on a long-range basis (5 to 50 years). The definition of these models focuses primarily on the spatial area of concern and the time frame for impact prediction. The orientation of these model-group definitions provides a useful framework for their consideration in planning forest management strategies but does not provide enough detail to define sessions within this symposium. We hope that the organization of the sessions in a slightly different framework, based not only on spatial and temporal resolution but also on biological aspects of the SPB life system, will be useful.

It may then be appropriate here to preview the different symposium sessions and in a very brief manner to provide a synopsis of their contents.

Considered in the first session are those models concerned with the dynamics of beetle populations within trees and discrete spots, and with prediction of population change through time. Two models of this nature have been developed, one as a cooperative effort between the Entomology and Industrial Engineering Departments at the University of Arkansas and the other as a cooperative venture between the Biosystems Research Division (Industrial Engineering) and Entomology at Texas A. & M. University. Both of these models have similarities. The models are flexible, each being able to use numbers of infested trees or measurements of actual beetle populations as input or output; and each is based on aspects of SPB reproduction and survival. The modeling approaches differ, however, as will be evident from the presentations given here. Also included in this session is an examination of sensitivity analysis and how it can be used to assess the importance of particular rates and variables in the Arkansas population dynamics model.

In the second session, the speakers will present models that are related to specific processes in the southern pine beetle life system. Included here are those models often considered esoteric by ultimate users (i.e., forestry practitioners). These very models, however can be essential elements of more damage-oriented population prediction models, and can aid our understanding of the dynamics of the SPB life system. Some of these models have already been incorporated into the predictive systems discussed in the first session. The temperature/development studies by Gagne et al. at Texas A. & M. are, for example, essential components of both the Arkansas and Texas models. The biophysical modeling approach taken by the Texas group should eventually lead to the inclusion of part or all of the models on gallery construction and oviposition, host habitat changes relating to tree drying, and pheromone dispersion. The models of gallery initiation and landing and component life-cycle processes provide alternatives for examining elements of SPB colonization, reproduction, and development. A quantitative look at the impact of a major SPB predator, *Thanasimus dubius*, is provided from studies conducted in Mississippi. Finally in this session, North Carolina researchers present a model for the transition of SPB activity from the endemic to epidemic state. The model is formulated as a multilevel hierarchy proceeding from the individual tree level to the level of the large geographic region.

In session three, discussion centers on those models concerned with damage prediction via models not based primarily on beetle population dynamics. The influence of selected site and stand factors on the rate of expansion of individual SPB spots is considered. Also, attention is given to a regional SPB damage projection system based on site and stand parameters and applicable over a 1-year period. The incorporation of this model into a long-term, areawide damage projection system will be presented, along with models for host dynamics. This session will close with an examination of trend prediction systems that are based on beetle population-related measurements and secondary factors and that are used for prediction of timber mortality in the Georgia Piedmont and Gulf Coastal Plain.

Following the discussion of damage projection and trend prediction, an evaluation of what we have (or what we should have) included in this symposium will be conducted. We hope here to gain some insight into how those who are not closely tied to SPB population modeling view the progress we have made over the past several years. Constructive criticism should assist us as we move toward implementation of these models in field situations, and as we attempt to develop integrated forest and pest management systems that must be built around the predictive models we are about to discuss in this symposium.

LITERATURE CITED

Ciesla, W. M. 1979. Evaluation of control tactics for southern pine beetle: have user needs been met? *In* Evaluating control tactics for the southern pine beetle: symposium proceedings. [Many, La., Jan. 1979.] J. E. Coster and J. L. Searcy, eds. p. 112-116. U.S. Dep. Agric. For. Serv., Tech. Bull. 1613. Comb. For. Pest Res. Develop. Prog., Pineville, La.

Hamilton, H. R., S. E. Goldstone, J. W. Milliman, A. L. Pugh, E. B. Roberts, and A. Zellner. 1969. Systems simulation for regional analysis: an application to river-basin planning. MIT Press, Cambridge, Mass.

Leuschner, W. A. 1979. Impact analysis, interpretation, and modeling. *In* Current topics in forest entomology. W. E. Waters, ed. p. 50-53. U.S. Dep. Agric. For. Serv., Gen. Tech. Rept. WO-8.

MODEL FOR PREDICTING SOUTHERN PINE BEETLE POPULATION GROWTH AND TREE MORTALITY

Gail S. Hines, Hamdy A. Taha, and Fred M. Stephen[1]

Abstract.--The concept of systems dynamics is applied to populations of the southern pine beetle, *Dendroctonus frontalis* Zimm., in presenting a deterministic model to predict timber losses. The model can be used by forest practitioners and requires a minimal amount of entomological data for initialization. Population development is primarily a function of temperature, with growth being regulated by a series of variables affecting mortality and production rates. Results of the simulation include a prediction at weekly intervals of the numbers of dead and infested trees plus the expected monetary loss reflecting local stumpage prices.

INTRODUCTION

Considerable research has been done on various aspects of the biology of the southern pine beetle, *Dendroctonus frontalis* Zimmermann, in an effort to develop management strategies to minimize timber losses from this pest. Accurate predictions in forecasting the growth of the pest population are an essential component of a pest management system to achieve these goals (Waters and Ewing 1974).

In this paper we present a model for predicting timber losses in discrete infestations (i.e., spots) as a function of changes in southern pine beetle population over time (ca. 4 months or less). The model is designed for use by forest management personnel and does not require intensive sampling to obtain direct measurements of the various SPB life stages as they exist within infested trees. Rather, surveys requiring a minimum of specialized equipment can supply measures of certain initial conditions that govern the state of infestation and site and stand conditions. The facts that measurements of the population can be made by a forest technician and that a deterministic approach is taken--i.e., a treatment of variables as constants choosing average effects as parametric values--have resulted in a fairly simple and inexpensive simulation model.

The model utilizes principles of systems dynamics (Forrester 1968) developed initially for the simulation and study of continuous systems usually involving economic or industrial processes as a function of time. These concepts may be applied to biological systems (e.g., Paulik and Greenough 1966) and are applicable for modeling insect populations based on the assumption that the life cycle of a holometabolous insect and its interactions with its host, parasites, and predators are analogous to a production process (Berryman 1974). The production levels describe the quantities of insects in the various stages of development, and the systems dynamics rates regulate the flow of life forms between these levels as determined by the conditions of the system at a given point in time.

Systems dynamics has been employed in an insect population model (SIMECOB) for the European corn borer (Loewer 1976). SIMECOB considers population growth in each of the stages of insect development to be a continuous system, with probabilities for passages of insects to a succeeding level determined by weather conditions. Many biological factors, including the population density of natural enemies, host variety resistance, and migration, are not included.

BASIC DESIGN OF THE MODEL

The model is conceptually designed to represent the life cycle of the southern pine beetle by considering the influence of physical and biotic factors in the forest environment of the various beetle life stages. Figure 1 depicts the flow of beetles through the life stages and production of a subsequent generation. Each rectangle represents a developmental level containing numbers of SPB in specific life stages. As shown in figure 1, the population of adult beetles (BAA) that are arriving at trees

---

[1] The authors are, respectively, Assistant Professor, Dept. of Industrial Engineering and Dept. of Forestry, Auburn University, Auburn, Ala.; Professor, Dept. of Industrial Engineering, and Associate Professor, Dept. of Entomology, University of Arkansas, Fayetteville.

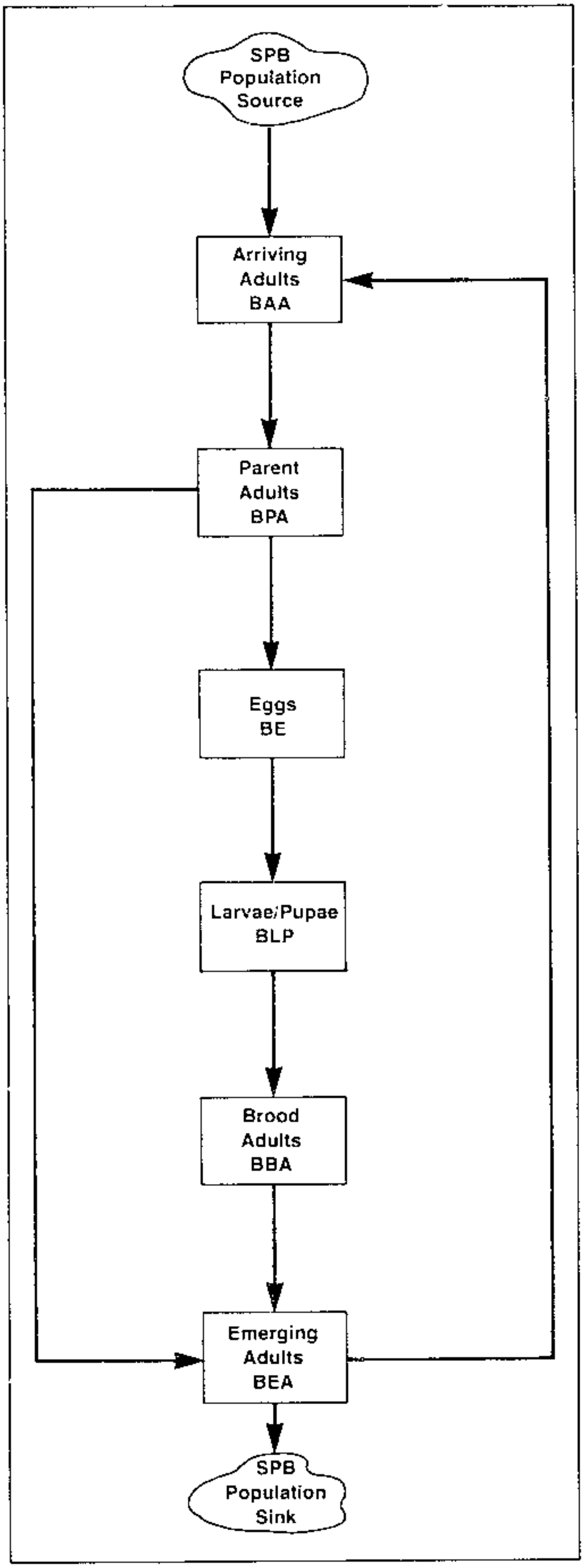


Figure 1.--Graphic representation of the basic flow paths within the SPB model.

can come from two sources. If no previous beetle activity has occurred in the immediate vicinity, the arriving adults must immigrate from an external source population. But in most spots the arriving adult population is produced from emerging and reemerging adults in the immediate vicinity.

As colonization of trees is successful, the arriving adults become parent adults (BPA) and initiate a new generation via gallery construction and egg production (BE). Two paths then exist for production of emerging adult beetles (BEA). Parent adults can reemerge, at which time they are arbitrarily classified as emerging adults. The alternate path results from within-tree development of eggs to larvae-pupae (BLP) and brood adults (BBA), both of which subsequently contribute to the new emerging adult population. Although the model is now designed to include both brood and reemerging adults in the emerging adult level (BEA), the two variables could be considered separately.

The effect of selected physical and biotic factors on the basic southern pine beetle life cycle is introduced in figure 2 by overlaying the various rates (bottlenecks) and variables (circles) that control the magnitude of changes in each level through time. A solid line represents the flow of material (SPB) between levels, whereas a dashed line represents the flow of information affecting the values of levels, rates, and variables. The irregular closed curves represent population sources, or sinks, which are external to the system being modeled.

The model is expressed in terms of rates of change in the form

$$\frac{dY_{i+1}}{dt} = f(X, Y_i)$$

where Y_i is the vector of state variables describing the bark beetle population by age structure at time *t*. These rates govern the movement of beetles through the various life stages and the production of a subsequent generation. The vector X contains a collection of variables that affect the state variables. This collection of independent variables includes mortality rates computed from life tables for the various life-stage levels and reflects attrition due to parasites and predators.

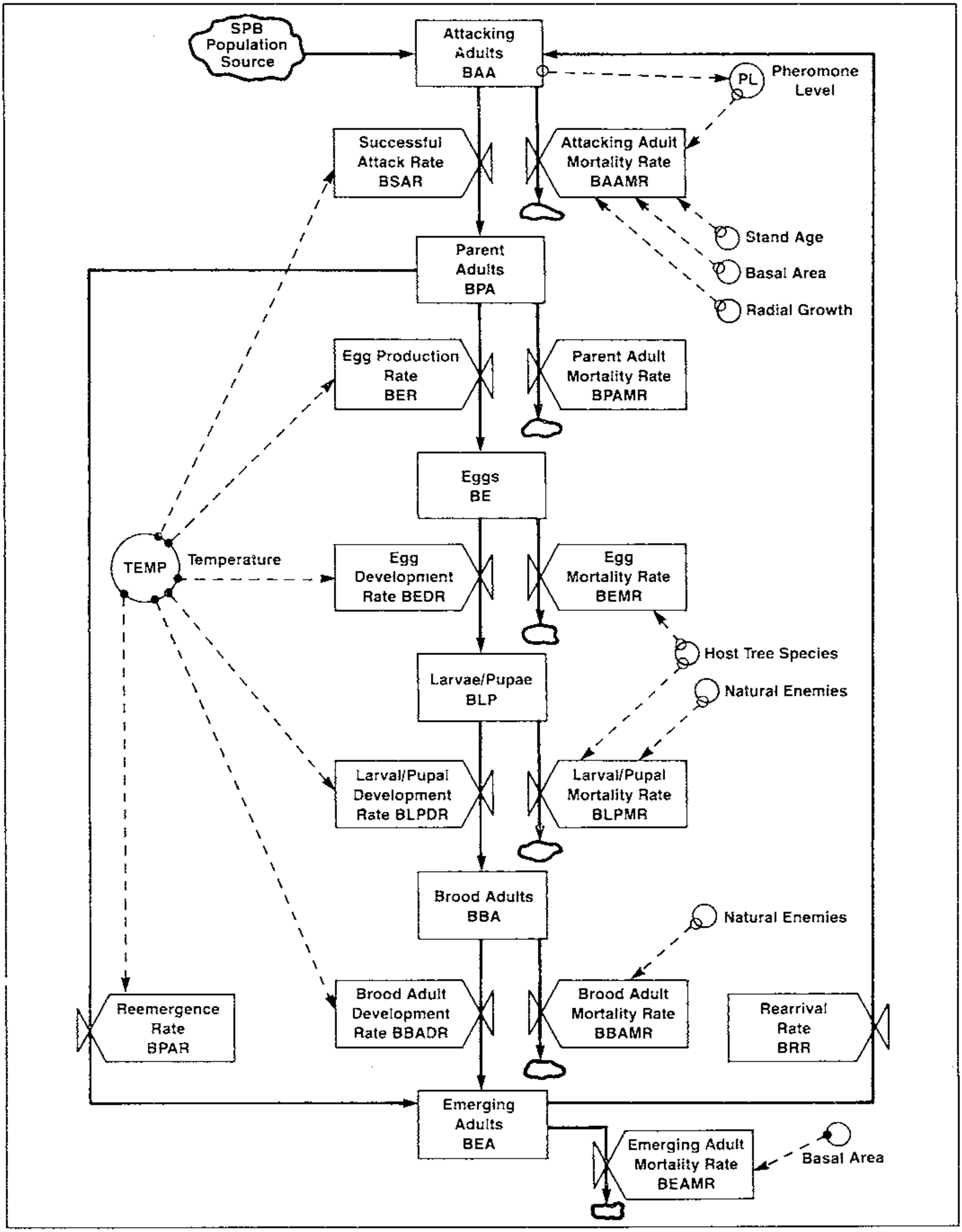


Figure 2.--Graphic representation of levels, rates, and paths of information flow within the SPB model.

Production Rates

Since temperature is the primary determinant of maturation and reproduction, the model possesses a subsystem that simulates environmental conditions. Information reported by the environmental subsystem is used to modify the production rates. This environmental subsystem produces a profile of hourly temperature readings that can be made site-specific by accessing recorded maximum and minimum temperatures for the appropriate date and geographical location (Ballard 1974). Estimates of the declination of the sun and the equation of time using Fourier analysis determine the time of sunrise. Three half-cosine waves are then fitted through readings of successive daily high and low temperatures. The time of sunrise determines the frequency of each wave, based on the assumption that each day's minimum temperature occurs 1 hour after sunrise and the maximum occurs 3 hours past noon. The model has the capability of modifying the ambient temperature profile to simulate conditions under the forest canopy.

The egg development rate of the southern pine beetle (BEDR) under a series of constant temperature regimes was determined by J. A. Gagne at Texas A. & M. University. Successful egg development occurs within the range of 50° to 92.1° F. The maximum rate of development at constant temperature occurs at approximately 81.5° F, as depicted in figure 3. Rates of development for other SPB life stages are described as functions of temperature bearing this same relationship (Gilbert et al. 1976) but altered proportionately, based on Gagne's experimental laboratory data and our field observations on total time required for within-tree development. Table 1 lists the temperature-dependent developmental rates and gives a description of the developmental processes that each rate controls. The egg production rate (BER), which is not a developmental rate but regulates the number of eggs deposited per female per time unit, is also temperature dependent. At approximately 81.5° F, BER will cause production of 28 eggs per female over a 4-day period. The rate controlling the rearrival on newly colonized hosts of the emerging and reemerging population (BRR) is a constant chosen such that half the colony will have amassed on an adjacent tree within 0.1 day. Flight ceases at temperatures less than 57° F. (Kinn 1978).

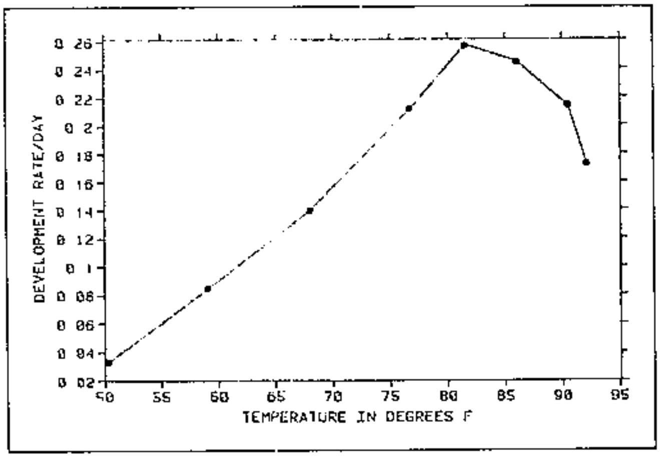


Figure 3.--SPB egg development rate per day as a function of temperature (° F).

Table 1.--Temperature-dependent production rates

Process	Controlling rate
Successful attack rate	BSAR
Gallery construction, oviposition, and parent adult reemergence rate	BPAR
Egg development rate	BEDR
1st instar through pupa	BLPDR
Brood adult to emergence	BBADR

Mortality Rates

A variety of physical and biological factors affect survival between successive levels of the developing within-tree brood. For graphic purposes the different causes of mortality affecting each level are combined and referred to collectively as mortality rates (fig. 2). In actuality the equations for these mortality rates are composed of a number of factors, including natural enemies, competitors, and other measurable causal agents of mortality (table 2). The analysis of additional data may provide further identification of the impact of each of these factors on mortality.

Data collected at test plots in southwest Arkansas suggest that mortality of within-tree stages is seasonally dependent and affected by the host pine species. Parasite and predator densities in addition to stand age and vigor, also influence mortality of within-tree SPB stages. The rates regulating the mortality of the attacking and emerging segments of the population area are altered

Table 2.--Variables affecting mortality rates

Pine basal area

Hardwood basal area

Host pine species

Season

Stand age and vigor

Density of attacking SPB population

Parasites and predators

Competitors

Table 3.--Data required for model initialization

- Date infestation was observed
- Length of simulation
- Site and stand conditions
  - Geographical location
  - Pine and hardwood basal areas
  - Host species composition
- Infested tree data
  - Growth rate
  - Age
  - d.b.h.
  - Tree count by SPB life stages
- Average height at top of infestation
- Current stumpage prices

depending on the hardwood and pine basal areas, the age and vigor of the stand, and the density of the attacking population (fig. 2).

The mortality rate of the attacking adult population is used to simulate the effect of the southern pine beetle pheromone during the initial period of an attack. The rate, when equated to one, has the effect of allowing a convergence of attacking beetles (i.e., mass attack) in numbers sufficient to overcome the resistance of the host. Once this threshold of resistance has been reached, the attack commences with the mortality rate reset at a level dependent on environmental conditions, as previously discussed. The attack continues until the cumulative number of attacks reaches a predetermined density level. At this time the numbers of emerging and reemerging beetles disperse to infest adjacent trees.

MODEL FORMULATION

The model is cast in terms of rates of changes of numbers of beetles in each of the life stage levels and formulated in a set of differential equations. The balance equation for change in the level of arriving adults in a given time interval is

$$\frac{d(BAA)}{dt} = (1-BEAMR) \times BEA \times BRR - BAA \times BSAR \qquad (1)$$

Equation (1) describes the amount of change in a given level of arriving adults as the difference between the numbers of surviving emerging adults and the numbers that successfully attack the host to become parents. Periodically, each rate is adjusted to reflect changes in the environment. In this way, the model can account for continuous variation in time.

Similarly, changes during an update interval in the remaining levels are regulated by the following equations:

$$\frac{d(BPA)}{dt} = (1-BAAMR) \times BAA \times BSAR - BPA \times BPAR \qquad (2)$$

$$\frac{d(BE)}{dt} = (1-BPAMR) \times BPA \times BER - BE \times BEDR \qquad (3)$$

$$\frac{d(BLP)}{dt} = (1-BEMR) \times BE \times BEDR - BLP \times BLPDR \qquad (4)$$

$$\frac{d(BBA)}{dt} = (1-BLPMR \times BLP \times BLPDR - BBA \times BBADR \qquad (5)$$

$$\frac{d(BEA)}{dt} = (1-BPAMR) \times BPA \times BPAR + (1-BBAMR) \times BBA \times BBADR - BEA \times BRR \qquad (6)$$

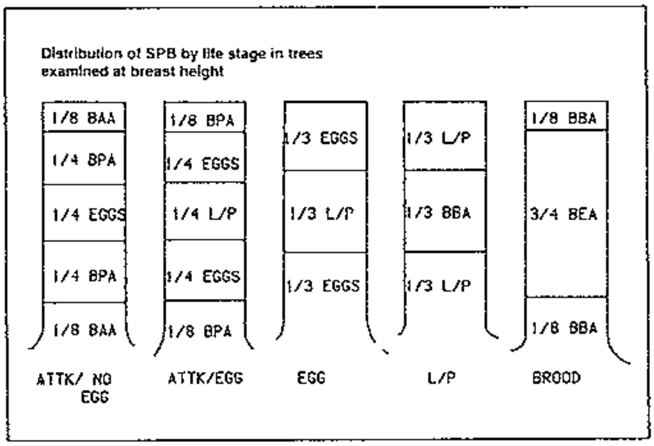


Figure 4.--Hypothetical distribution of SPB by life stage in trees examined at breast height.

The model, then, is a sequence of levels representing the life stages of the southern pine beetle, with movement through the various levels regulated by rates which are determined by environmental conditions.

INITIALIZATION OF THE MODEL

An existing infestation can be surveyed by forest technicians and the levels within the model initialized to represent the current status of the spot. The information needed to initialize the model is outlined in table 3. A field manual describing the measurements to be taken and the level of their precision, and a user's manual providing model documentation to assist in computer implementation of the system are available upon request.

As noted earlier, the model is designed for use by forest management personnel and thus does not require intensive sampling to obtain direct measurements of the various within-tree southern pine beetle life stages. Examination of the boles of ca. 200 infested trees suggests that various stages of SPB development may be found along an infested bole, and that these stages may be described by the stage of development observed at breast height. Forest technicians determine the numbers of infested trees that contain each of the brood stage levels at breast height. The model converts the infested trees to beetle life forms present within those trees, for input into the various developmental levels in the model. This conversion process uses the allocation method graphically illustrated in figure 4, an estimate of infested area, and an average density of beetles per bark area (dependent upon the life stage present).

An estimate of the amount of infested bark area can be obtained by measuring the d.b.h. of each infested tree, and determining the average height at top of infestation within the spot by climbing or felling a minimal number of trees (Stephen and Taha 1979a). A more accurate estimate of infested bark area can be made by recording for each infested tree in the spot its height at base and top of infestation plus the circumference at breast height and at top of infestation (Stephen and Taha 1979b).

The survey crew's assessment of the average amount of growth of the stand during the past 5 years, the average age of the stand, the species composition, and the pine and hardwood basal areas will be needed to modify the mortality rates of selected life stages. Additional data required for initialization of the model include the geographic location of the stand and date of survey so that appropriate temperature files may be accessed and rates initialized at values appropriate for the season. The current stumpage prices reflect local market conditions, and a description of the stand by d.b.h. class is used to determine volumetric timber losses.

ACCURACY OF SIMULATION

To determine the validity of the model simulation, actual field results were compared to the predicted tree mortality for several infested spots in two geographic areas. Climatic data were obtained for each location.

A comparison of field observations and simulated predictions from infestations in south Arkansas studied in 1976 and 1978 indicates very good predictive capability in some spots and considerable deviation from reality in others. For example, Plot 4 (fig. 5) was first checked in early June (Julian date 160, 1976). At that time there were 39 infested trees, which was also the total number of dead trees. The spot was growing very rapidly, and when checked in early July (194, 1976) there were 73 infested trees and a total of 113 dead trees. Our model prediction for that period was 86 infested and 121 total dead trees, a reasonably good forecast. By mid-August (226, 1976) there were 137 infested and a total of 273 dead trees. Our simulated infestation had 141 infested and 259 dead trees, again a close prediction. When the final ground check was made at the end of September (271, 1976), the spot contained 433 infested

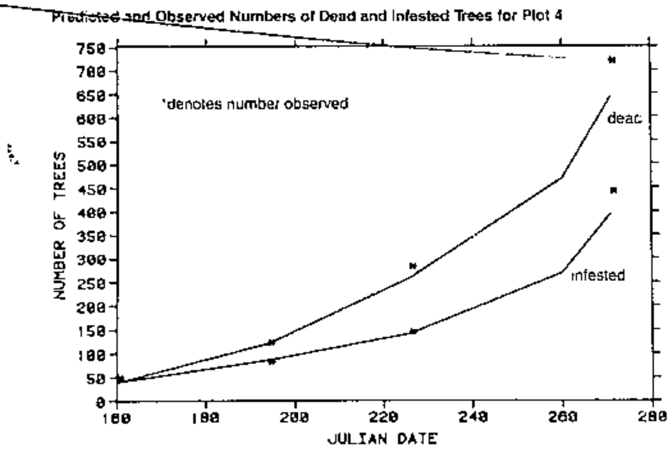


Figure 5.--Comparison of simulated infestation growth v. observed numbers of infested and dead trees in Plot 4, 1976.

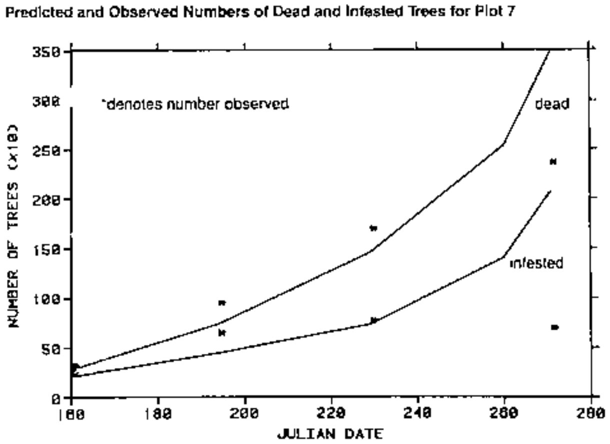


Figure 8.--Comparison of simulated infestation growth v. observed numbers of infested and dead trees in Plot 7, 1976.

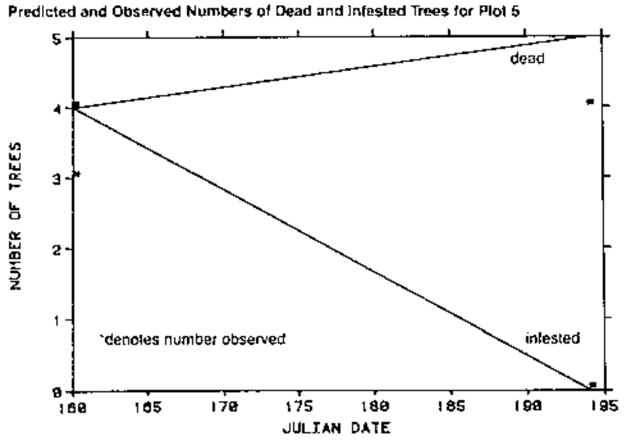


Figure 6.--Comparison of simulated infestation growth v. observed numbers of infested and dead trees in Plot 5, 1976.

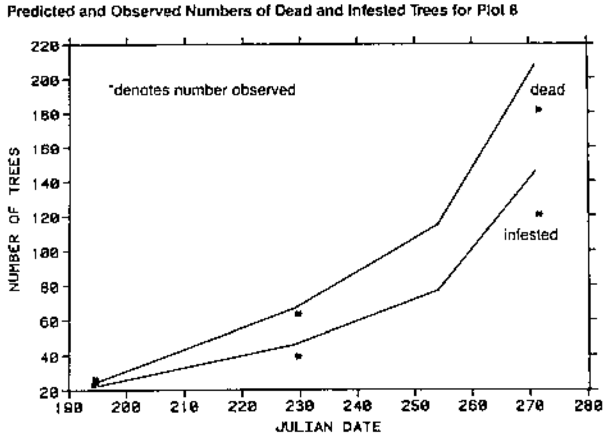


Figure 9.--Comparison of simulated infestation growth v. observed numbers of infested and dead trees in Plot 8, 1976.

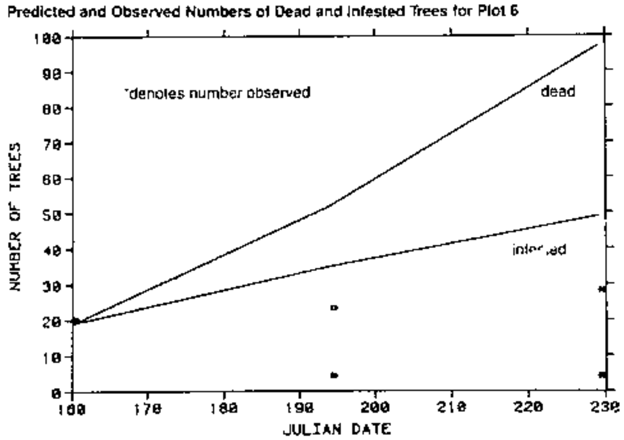


Figure 7.--Comparison of simulated infestation growth v. observed numbers of infested and dead trees in Plot 6, 1976.

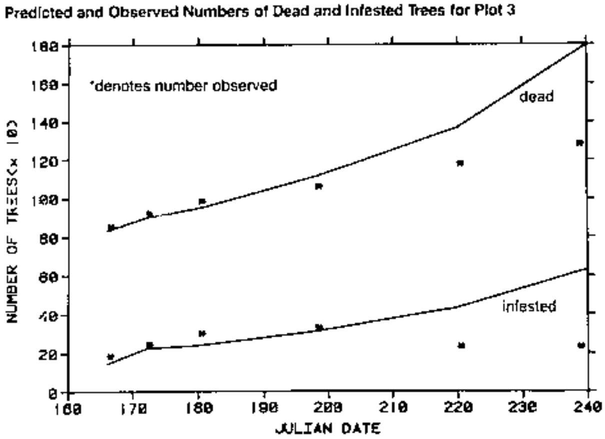


Figure 10.--Comparison of simulated infestation growth v. observed numbers of infested trees in Plot 3, 1978.

trees and 710 total dead trees. The simulation at this point predicted 393 infested and 641 total dead trees. The more rapid growth of the actual spot between J.D. 226 and 271, 1976, may be explained by SPB immigration into the study area from a very large spot about 1.5 km away that was being salvaged. This immigration was unaccounted for in the simulation.

Other examples of the accuracy of prediction are illustrated in figures 6 through 10. We correctly predicted the decline of the small plot, number 5 (fig. 6), but did not correctly predict that Plot 6 would also decline (fig. 7). Predictions of beetle population and spot growth for plots 7 and 8 were quite close to what was observed (figs. 8 and 9), except that the simulated growth of plot 7 exceeded the observed growth after J.D. 229.

In 1978 we monitored two plots. We correctly predicted that one of these would decline. For the other plot, our simulation was very good for both infested and dead trees over a 50-day period, but we predicted much more rapid spot growth than was observed for the next 25 days (fig. 10).

We will use data collected in Georgia during 1979 to check the accuracy of the model predictions further.

OUTPUT OF THE MODEL

Output from the model includes a forecast at weekly intervals of the numbers of dead and infested trees classified by life stages of the beetle. This prediction is obtained by converting numbers of beetles in each of the various life stages to an equivalent amount of infested bark area and then to numbers of dead and infested trees, given the average amount of infested bark area per tree. These calculations provide an estimate of total tree loss and afford a check on the prediction through time. A comparison with actual stand conditions should enable the manager to determine if additional measurements on the status of the infestation are required.

Assuming the d.b.h. distribution of the trees killed by the southern pine beetle is representative of the stand as a whole, the model yields a volume estimate of timber loss. The current stumpage price is then used to assign a monetary value to the loss.

CONCLUSIONS

Since our original objective was to mimic the general features of beetle populations, absolute correspondence between predicted and observed results is not completely necessary. The validation tests show that the model simulated the behavior of observed SPB populations reasonably well, as evidenced by a comparison of the numbers of observed and predicted dead trees in a limited number of test plots. Further validation of the model under a considerably wider range of geographic conditions and SPB population levels will be necessary before the model is ready for adoption by forestry practitioners.

LITERATURE CITED

Ballard, J. L. 1974. A population model for the *Heliothis zea* (Boddie). Unpubl. Ph.D. thesis. Univ. of Arkansas, Fayetteville.

Berryman, A. A. 1974. Dynamics of bark beetle populations: towards a general productivity model. Environ. Entomol. 3:579-585.

Forrester, J. W. 1968. Principles of systems. 2nd ed. Wright-Allen Press, Cambridge, Mass.

Gilbert, N., A. F. Gutierrez, B. D. Frazer, and R. E. Jones. 1976. Ecological relationships. W. H. Freeman, San Francisco.

Kinn, D. N. 1978. Diel emergence patterns of the southern pine beetle *Dendroctonus frontalis* Zimm. J. Ga. Entomol. Soc. 13(1):80-85.

Loewer, O. J. 1976. Insect management through weather based computer simulations. Trans. Am. Soc. Agric. Eng. 19(3):539-544.

Paulik, G. J., and J. W. Greenough, Jr. 1966. Management analysis for a salmon resource system. *In* Systems analysis in ecology. K.E.F. Watt, ed. p. 215-253. Academic Press, New York.

Stephen, F. M., and H. A. Taha. 1979a. Tree mortality, infested bark area, and beetle population measurements as components of treatment evaluation procedures on discrete forest management units. *In* Evaluating control tactics for southern pine beetle: symposium proceedings. [Many, La., Jan 1979] J. E. Coster and J. L. Searcy, eds. p. 45-53. U.S. Dep. Agric. For. Serv., Tech. Bull. 1613. Comb. For. Pest Res. Develop. Prog., Pineville, La.

Stephen, F. M., and H. A. Taha. 1979b. Area-wide estimation of southern pine beetle populations. Environ. Entomol. 8:850-855.

Waters, W. E., and B. Ewing. 1974. Development and role of predictive modeling in pest management systems-insects. *In* Modeling for pest management: concept, techniques, and applications. R. L. Tummala, D. L. Haynes, and B. A. Croft, eds. p. 19-27. Michigan State Univ., East Lansing.

ACKNOWLEDGMENTS

The authors wish to thank J. A. Gagne for providing SPB development rate data and M. L. Lih, W. Draper, and M. Motamedi for their valuable suggestions and technical assistance.

SENSITIVITY ANALYSIS AND
UNCERTAINTY IN ESTIMATION OF
RATES FOR A SOUTHERN PINE BEETLE MODEL

Hamdy A. Taha, Fred M. Stephen, and Mahmoud Motamedi[1]

Abstract.--A common problem encountered in simulating the dynamics of an insect population arises in estimation of some rates that control survivorship between insect life stages. In this paper sensitivity analysis is used to rank the rates of the model according to their degree of importance in affecting the output of the model. Based on this information, researchers can direct their efforts to obtaining reliable estimates of the most important rates of the model. Although the procedure presented here is general, its implementation is demonstrated by application to a predictive model of southern pine beetle (*Dendroctonus frontalis* Zimm.) population dynamics.

INTRODUCTION

The population dynamics model developed by Hines, Taha, and Stephen (1980) is designed to predict the future status of southern pine beetle infestations. The overall organization of the model is a representation of the life cycle of the beetle using a series of levels linked together by material flow paths. The *levels* represent numbers of the beetles in their different life stages. The transformation of one life stage to another through material flow paths is controlled by *rates*, which control the magnitude of changes in each level through time. A flow chart of the model is given in figure 1, with the levels depicted by rectangles and the rates by bottlenecks.

Implementation of the model requires two types of data: (1) values of the rates, and (2) initial status of the SPB-infested spot. The values of the rates are considered as part of the model construction, while the initial conditions normally apply to the infested spot under study. As a result, all the rates must be accurately estimated before the model can be successfully implemented.

Ideally, the rates should be determined based on the results of analyses of experimental data. However, due to the complex nature of the interactions of the beetle and its environment, it is quite difficult to secure experimental data for the estimation of certain rate functions. Table 1 summarizes the 13 rates of the SPB model and describes each rate and its method of determination.

The rates of the model which are *not* estimated from experimental data are normally determined from intuition and experience, either directly with southern pine beetle or with other insects having more or less similar biological characteristics. Trial-and-error simulations also provide means for checking the validity of assumptions concerning some rates.

The purpose of this paper is to develop a method for ranking the rates for which no data are available in order of "degree of importance." By degree of importance we mean the degree of sensitivity of the output of the model to small changes in a given rate. Such information is useful in determining the rates that have the most effect on the results of the model. Given this knowledge, researchers can then concentrate on finding reliable means for estimating those rates that are most critical in obtaining accurate predictions from the model.

To illustrate the idea of testing the model's sensitivity, figures 2 and 3 demonstrate the variations in number of dead trees over time as a result of varying the values of the parameters BSAR (successful attack rate) and BEAMR (inflight mortality rate of reemerged and brood adults). In each case the parameter to be evaluated was varied from 50 to 140 percent of its initial value while not altering any other parameters in the model. Figure 2 shows the extreme sensitivity to these changes of inflight mortality (BEAMR), as the number of dead trees can vary from about 75 to 2,000 at the end of a 3-month period. In figure 3, on the other hand, we can clearly see that although successful attack rate (BSAR) was also varied to the same extent as inflight mortality, almost no change in the output was produced.

---

[1] The authors are, respectively, Professor, Dept. of Industrial Engineering; Associate Professor, Dept. of Entomology; and Graduate Research Assistant, Dept. of Industrial Engineering, University of Arkansas, Fayetteville.

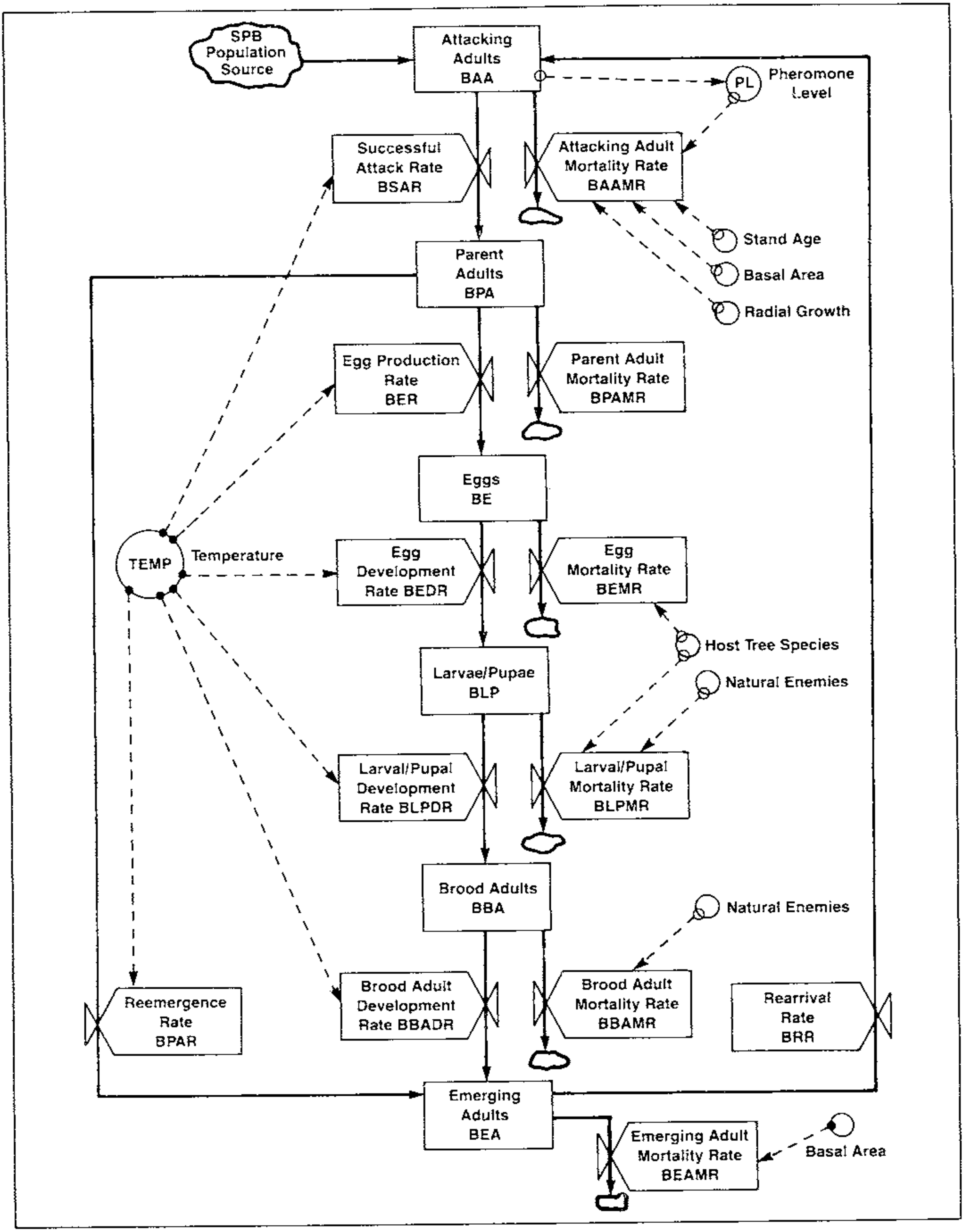

SPB Population Source
Attacking Adults BAA
PL Pheromone Level
Successful Attack Rate BSAR
Attacking Adult Mortality Rate BAAMR
Stand Age
Basal Area
Radial Growth
Parent Adults BPA
Egg Production Rate BER
Parent Adult Mortality Rate BPAMR
Eggs BE
TEMP Temperature
Egg Development Rate BEDR
Egg Mortality Rate BEMR
Host Tree Species
Natural Enemies
Larvae/Pupae BLP
Larval/Pupal Development Rate BLPDR
Larval/Pupal Mortality Rate BLPMR
Brood Adults BBA
Natural Enemies
Reemergence Rate BPAR
Brood Adult Development Rate BBADR
Brood Adult Mortality Rate BBAMR
Rearrival Rate BRR
Emerging Adults BEA
Emerging Adult Mortality Rate BEAMR
Basal Area

Figure 1.

Table 1.--Process description of model rates and summary of methods of determination

Temperature-dependent production rates	
BSAR:	Successful attack rate--indirectly estimated as a function of the egg development rate.
BPAR:	Parent adult reemergence rate--indirectly estimated as a function of the egg development rate.
BER:	Egg production rate--determined via search procedures and model simulation.
BEDR:	Egg development rate--determined by laboratory rearing under different constant temperature regimes.[1]
BLPDR:	Larva-pupa development rate--indirectly estimated as a function of the egg development rate.
BBADR:	Brood adult development rate--determined by laboratory rearing under different constant temperature regimes.[1]
Mortality rates	
BAAMR:	Attacking adult mortality rate--based on a combination of intuition and trial-and-error experimentation.
BPAMR:	Parent adult mortality rate--based on parent adult reemergence data of Cooper and Stephen 1976.
BEMR:	Egg mortality rate--based on egg sample dissection data.
BLPMR:	Larva-pupa mortality rate--based on analysis of X-ray sampling data.
BBAMR:	Brood adult mortality rate--estimated from X-ray and laboratory emergence data.
BEAMR:	Reemerged and brood adult inflight mortality rate--based on intuition, trial-and-error experimentation, and unpublished data.[2]
BRR:	Adult beetle rearrival rate--based on intuition and trial-and-error experimentation.

---

[1] Data from J. A. Gagne. Texas A. & M. University.

[2] Unpublished data from P. E. Pulley and R. N. Coulson. Texas A. & M. University.

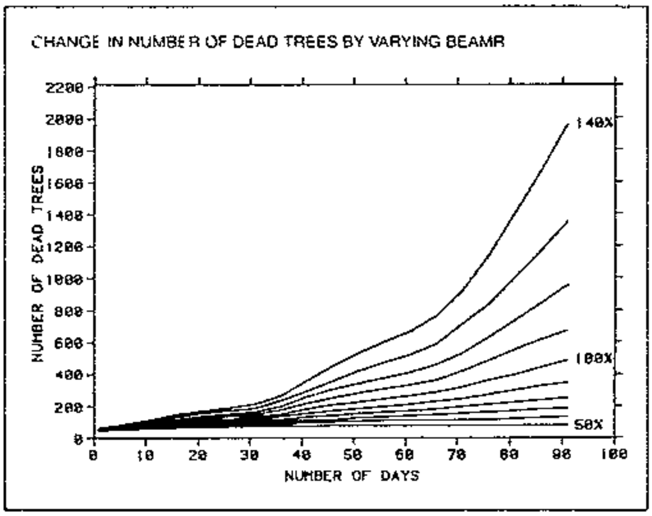


Figure 2.

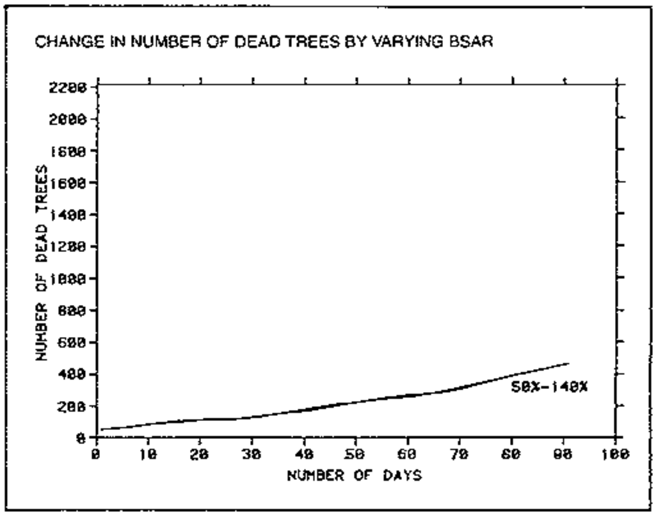


Figure 3.

RANKING PROCEDURE BY SENSITIVITY ANALYSIS

Sensitivity analysis in insect population modeling is a well-established technique (Gilbert and Hughes 1971; Gilbert and Gutierrez 1973; Miller, Wiedhaas, and Hall 1973; Miller 1974). Miller (1974, 1975) appears to be the first to use sensitivity analysis to establish the relative importance of the different parameters or rates for models simulating a mosquito population. The present work extends the general ideas of Miller for the purpose of ranking the rates of the SPB model (Stephen, Hines, and Taha 1980) according to their importance in affecting model output.

To apply sensitivity analysis, we need to express the output of the model in terms of a single variable, if possible. In the SPB model, the final output can be expressed in terms of the number of dead trees accumulated after the infestation has progressed for a certain period of time. Let

$P(t)$ = number of dead trees after t days of infestation growth

r_i = rate *i* of the SPB model, $i = 1, 2, \ldots, 13$.

We then write $P(t)$ as a mathematical function of r_i and *t* as follows:

$$P(t) = f\ (r_1, r_2, \ldots, r_{13}; t)$$

In the normal sense, a sensitivity coefficient $c_i(t)$ of $P(t)$ with respect to the rate r_i is given by

$$c_i(t) = \frac{\delta\ P(t)}{\delta\ r_i}$$

Since, in general, the output measure $P(t)$ is normally defined at discrete points, determining $c_i(t)$ by taking partial derivatives is impossible. As a result, we may use the approximation

$$c_i(t) = \frac{\Delta\ P(t)}{\Delta\ r_i}$$

where $\Delta\ P(t)$ is the change in $P(t)$ resulting from changing the rate r_i by $\Delta\ r_i$. The approximation assumes linearity and is thus correct for *very small* $\Delta\ r_i$.

For the purpose of *ranking* the rates r_i, $i = 1, 2, \ldots, 13$ of the model, the direct use of the sensitivity coefficients $c_i(t)$ is not suitable because there is no basis for effecting the comparison. What we really need is a coefficient that will measure change in $P(t)$ $(=\Delta\ P(t))$ resulting from changing the rate r_i by a given percentage. We formalize the concept as follows. Let

r_i^o = best initial estimate of the rate r_i, which is determined either experimentally or intuitively.

u_i = fractional change in rate r_i relative to its initial value r_i^o, $0 \le u_i < 1$.

Thus, to study the effect of changes in r_i on $P(t)$, we consider r_i in the range

$$r_i^o\ (1-u_i) \le r_i \le r_i^o\ (1+u_i),$$

which means that r_i is changed around its initial value by the percentage ± $100\ u_i$. In this case, we have

$$c_i(t) = \frac{\Delta\ P(t)}{\Delta\ r_i} = \frac{\Delta\ P(t)}{2\ u_i\ r_i^o}$$

Notice that $c_i(t)$ is computed under the assumption that $r_k = r_k^o$ for all $k \neq i$.

In order for $c_i(t)$ to be used for comparing the effect of the different rates on the output $P(t)$, it must be modified so that its value becomes independent of the specific value of r_i^o. This can be achieved by defining a new factor $d_i(t)$ as

$$d_i(t) = c_i(t)\ r_i^o = \frac{\Delta\ P(t)}{2\ u_i}$$

The factor $d_i(t)$ measures the changes in the output of the model (number of dead trees) as a result of changing r_i by ± $100\ u_i$ around its initial value r_i^o. As a result, the larger the value of $d_i(t)$, the more sensitive is the model to changes in r_i. In other words, we can now rank r_i, $i = 1, 2, \ldots, 13$ in order of the values of $d_i(t)$.

There are two points that we must clarify here: (1) Why don't we use the same percentage change ± 100 u for all the rates? (2) What effect does the simulation period *t* have on the relative values of $d_i(t)$?

To answer the first question, we must remember that the definition of $d_i(t)$ assumes linearity in the rate of change of $P(t)$ with respect to r_i. Since the shape of $P(t)$ changes with r_i, by specifying different u_i for each r_i we are in a better position to satisfy the condition of linearity by choosing suitable u_i for each *i*.

As for the effect of the simulation period *t* on the values of $d_i(t)$, it is obvious that the length of *t* would not be important if $P(t)$ varies *linearly* with *t* for all values of r_i. Unfortunately this is not the case, as illustrated by

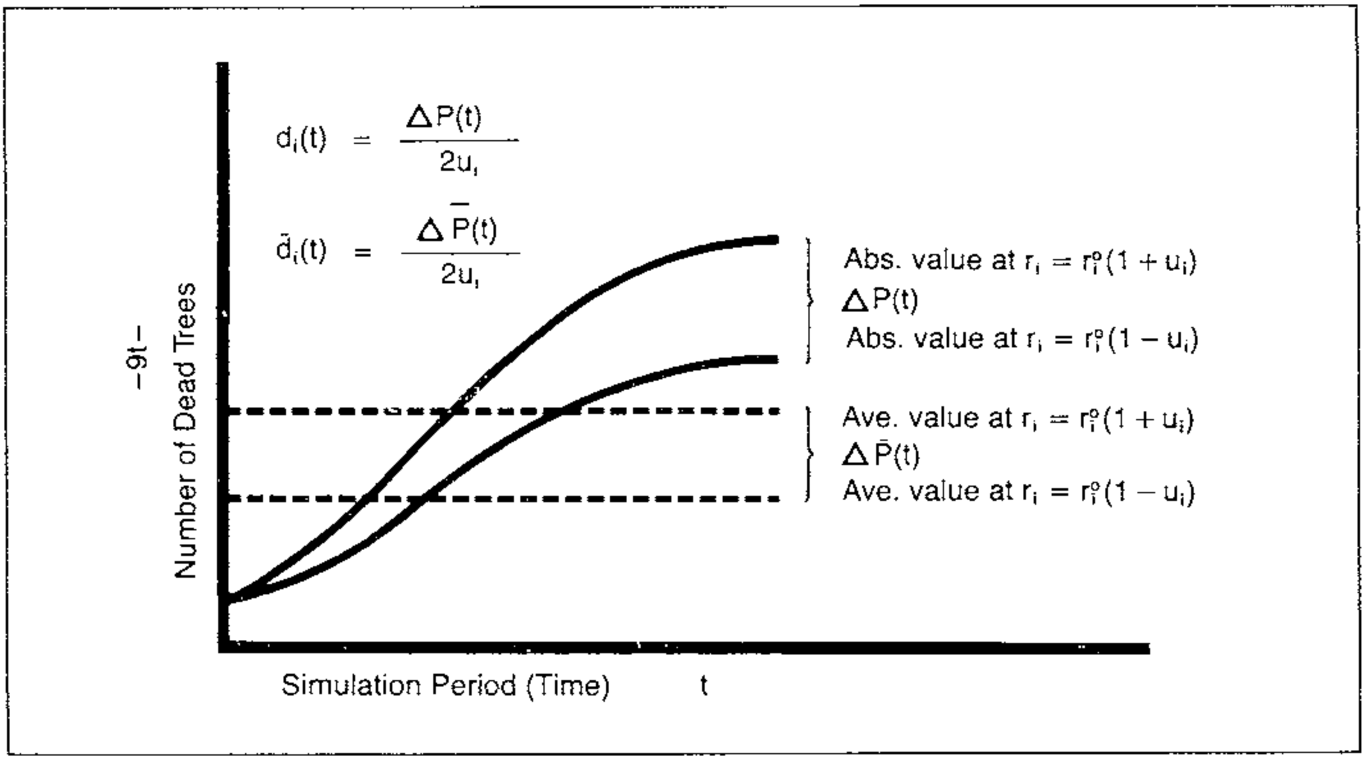


Figure 4.

figures 2 and 3. As a result, we need to modify the definition of $d_i(t)$ to "dampen" the effect of nonlinearity. The modification is achieved as follows.

The definition of $d_i(t)$ as given above, namely

$$d_i(t) = \frac{\Delta P(t)}{2\,u_i}$$

is based on measuring the change $\Delta P(t)$ in the number of trees at the *end* of the simulated period *t*. We shall say that this procedure is based on the *end value* change in P(t). A better procedure that will account (somewhat) for the nonlinear change of P(t) with r_i calls for replacing the change in the values of P(t) at *t* with the change in the *mean values* of P(t) over the period (0, t). Given

$\bar{P}(t)$ = mean value of P(t) over the period (0, t)

$$= \frac{\text{Area under } P(t) \text{ in the interval } (0,\, t)}{t}$$

In this case we define a new coefficient $d_i(t)$ as

$$\bar{d}_i(t) = \frac{\Delta \bar{P}(t)}{2\,u_i}$$

For convenience, we shall refer to the ranking process based on $d_i(t)$ as the *absolute value* method, while that based on $\bar{d}_i(t)$ as the *average value* method. Figure 4 demonstrates the two methods graphically.

The ranking procedure can now be summarized as follows:

1. Fix all the rates r_i, i = 1, 2, ..., 13, at their best initial values.

2. With the rates taken *one at a time*, change rate i by $\pm u_i$, $0 \le u_i \le 1$, and compute $d_i(t)$ or $\bar{d}_i(t)$ for a predetermined simulation period *t*.

3. Rank the rates according to the ascending order of $d_i(t)$ or $\bar{d}_i(t)$. The most important rate is the one having the largest value of $d_i(t)$ or $\bar{d}_i(t)$.

To illustrate the use of the absolute and average value methods, consider the rate BEAMR given in figure 2. The simulated period is *t* = 91 days. From the figure, we have the following results.

	Absolute value		Average value	
u	$\Delta P(91)$	$d(91)$	$\Delta \bar{P}(91)$	$\bar{d}(91)$
±10%	325	1625	9243	46218
±20%	700	1750	18671	46678
±30%	1160	1933	29941	49903
±40%	1825	2281	44752	55940

We notice from figure 2 that the values of $d(t)$ and $\bar{d}(t)$ will vary with the specific choice of t due to the nonlinearity of $P(t)$. We further notice that the effect of nonlinearity will be less pronounced with the average value method, which points to the advantage of using $\bar{d}(t)$ rather than $d(t)$. Another point we notice in figure 2 is that the values of $d(t)$ and $\bar{d}(t)$ need not be linear in the range ± u. It appears that further ramifications are needed to account for this point. This is one of the topics that we will continue to investigate in connection with the uses of the coefficients $d(t)$ and $\bar{d}(t)$.

PRELIMINARY RESULTS

Table 2 summarizes the results of ranking the 13 rates of the model by the two methods. The model was run based on the data available for a specific plot that was intensively monitored in 1976. The table shows that the two methods yield distinctly different results as far as the ranking is concerned. Both methods, however, show that the rate BEAMR (inflight mortality of emerging and reemerging adults) is the most important in the sense that the model is most sensitive to changes in its value. From table 1 we note that the value of this rate as used in the model is estimated via intuition, trial and error, and from data in unpublished studies at Texas A. & M. Whether this rate can be accurately estimated experimentally is not yet clear. We must emphasize, however, that the objective of sensitivity analysis is to point out the degree of importance of the rate rather than to estimate its value.

Because the ranking in table 2 is based on the data from only one plot, it will be necessary to repeat the same average values of the factors $d_i(t)$ and $\bar{d}_i(t)$ obtained from all plots.

CONCLUSION

In this preliminary study we presented a sensitivity analysis procedure for determining the degree of importance of the different rates of the southern pine beetle model. Work is continuing on refining the ranking procedure. Also, we are considering the possibility of compensating for the lack of accuracy in the estimation of rates by expressing their values in terms of a probability distribution. The results of this approach would be to express the output of the model (e.g., number of dead trees) in terms of a confidence interval.

Table 2.--Ranking of the rates by the absolute and average values methods

Rank	Absolute value method		Average value method	
	Rate i	$d_i(t)$	Rate i	$\bar{d}_i(t)$
1	BEAMR	2083	BEAMR	51981
2	BLPMR	964	BAAMR	27866
3	BAAMR	903	BLPMR	27152
4	BPAR	826	BBAMR	22199
5	BEDR	623	BEMR	20655
6	BPAMR	609	BEDR	18656
7	BEMR	601	BPAMR	15929
8	BBAMR	581	BLPDR	15535
9	BER	538	BPAR	14663
10	BLPDR	528	BER	11542
11	BBADR	120	BBADR	4502
12	BRR	22	BRR	192
13	BSAR	11	BSAR	133

Additional sensitivity analyses will be conducted to determine if simultaneous variation of the parameters in question produces unexpected results. This difficulty has been encountered in at least one study (Scolnik 1973 as cited by Holling 1978), where small variation of individual parameters indicated the model was stable. But when small (< 10 percent) simultaneous variation of several parameters was tested, the results changed dramatically. Tests of this nature may be important in studying the behavior of our model and will be performed in the near future.

The influence of other variables in the model on the expected output can also be tested via sensitivity analysis procedures. Alteration of such rate modifying variables as basal area and species composition, and application of the sensitivity analysis procedures described above must also be completed as model validation progresses.

LITERATURE CITED

Cooper, M. E., and F. M. Stephen. 1978. Parent adult reemergence in southern pine beetle populations. Environ. Entomol. 7:547-577.

Gilbert, N., and A. P. Gutierrez. 1973. A plant-aphid-parasite relationship. J. Anim. Ecol. 42:323-340.

Gilbert, N., and R. D. Hughes. 1971. A model of aphid population--three adventures. J. Anim. Ecol. 40:525-534.

Hines, G. S., H. A. Taha, and F. M. Stephen. 1980. Model for predicting southern pine beetle population growth and tree mortality. *In* Modeling southern pine beetle populations: symposium proceedings. [Asheville, N.C., Feb. 1980.] F. M. Stephen, J. L. Searcy, and G. D. Hertel, eds. U.S. Dep. Agric. For. Serv., Tech. Bull. 1630. Comb. For. Pest Res. Develop. Prog., Pineville, La.

Holling, C. S. (ed.). 1978. Adaptive environmental assessment and management. International Ser. on Appl. Systems Anal. 3. 377 p. Wiley & Sons, New York.

Miller, D. R. 1974. Sensitivity analysis and validation of simulation models. J. Theor. Biol. 48:345-360.

Miller, D. R. 1975. An experiment in sensitivity analysis on an uncertain model. Simulation today. No. 26, Simul. Councils, Inc., LaJolla, Cal.

Miller, D. R., D. E. Weidhaas, and R. C. Hall. 1973. Parameter sensitivity in insect population modeling. J. Theor. Biol. 42:263-274.

Scolnik, H. D. 1973. On a methodological criticism of the Meadows World 3 Model. 10 p. Tech. Rep. Dept. Math., Fundación Bariloche, Argentina.

THE USE AND STRUCTURE OF THE TAMBEETLE SPOT DYNAMICS MODEL

Richard M. Feldman, Guy L. Curry, and Robert N. Coulson[1]

INTRODUCTION

The mathematical description of *Dendroctonus frontalis* infestation dynamics is of extreme importance for the determination of optimal or near-optimal control strategies during southern pine beetle outbreaks. A computerized mathematical model of infestations, TAMBEETLE, has been developed at Texas A. & M. University under the auspices of the ESPBRAP. The purpose of TAMBEETLE is to predict the number of trees killed and the population growth (or decline) of SPB within an established spot. The model is based on an assembled set of scientific hypotheses formulated from both laboratory and field experimental research. TAMBEETLE is structured so as to benefit both scientific and field personnel. Scientific users normally require accurate estimates of the initial beetle populations derived from extensive field sampling; forest managers frequently need to obtain predictions based on limited data from ground surveys. A flexible input routine allows for both types of data requirements.

A biophysical modeling approach has been used to develop TAMBEETLE. This methodology initially separates the system into component parts. The individual components are analyzed, when possible, based on the physical and mathematical laws governing their behavior. The components are then integrated to produce the resulting system model. Finally, the integrated system model is validated through field data on infestation growth. The incorporation of complex biological models describing the components increases the ability of the system model to reflect infestation responses to environmental changes accurately. Most of the complexity is internal to the submodels and is not "seen" by the user. Therefore, it is possible to utilize TAMBEETLE with very simplistic data. Most of the data needed as input are used to estimate the initial conditions of a spot, i.e., the beetle population and site-stand status present at the start of the modeling time period.

The purpose of this paper is to present the uses and structure of TAMBEETLE. The mathematical details are omitted and the conceptual ideas behind the model emphasized. A detailed description of the mathematical structure is given in Feldman, Curry, and Coulson (1980).

USE OF THE INFESTATION MODEL

The southern pine beetle infestation model has a wide range of potential applications. They range from the highly theoretical use of testing scientific hypotheses to the applied use of aiding in the decisionmaking process of forest managers for spot control. The inputs needed for TAMBEETLE depend upon the user's specific application and, thus, options in the input routine are being developed which minimize data requirements for some applications.

The computer program consists of two separate routines. The major portion of the program deals with the mathematical description of SPB infestation dynamics. Independent of the mathematical model is the input routine. There are two options possible for input. The first option is a simplified version that does not involve the concise tree sampling procedures needed for the accurate population estimates described in Coulson et al. (1976). The concepts behind this simplified input option are based on the work of Stephen and Taha (1979). It should be emphasized that the complexity of the mathematical model results from the complexity of the ongoing biological processes and does *not* dictate a complex input routine. The input parameters are needed to determine the initial conditions, and the simplified option can be used whenever it is not necessary to know the initial conditions precisely. The second input option involves more detailed quantitative sampling procedures. Table 1 summarizes the input parameters needed for the two options.

---

[1] The authors are, respectively, Associate Professor and Professor, Dept. of Industrial Engineering; and Professor, Dept. of Entomology, Texas A. & M. University, College Station.

Table 1.--Input parameters illustrating different requirements depending on need

STANDARD INPUT	
Temperatures	Mean bark thickness
Mean and variance of tree d.b.h.	Mean radial growth last 5 years
Mean and variance of tree height to bottom of crown	

SIMPLIFIED OPTION	DETAILED OPTION
Number of infested trees	Number of infested trees
D.b.h. of each infested tree	D.b.h. of each infested tree
Predominant SPB life stage at breast height	Height of infested bole
	Bark thickness of each infested tree
	Disc sample counts of SPB on selected trees

The most immediately practical application of TAMBEETLE is to use it in predicting the growth of ongoing infestations. A forest manager may be faced with a limited budget for the control of SPB and a large number of infested regions needing control. Many decisions might be obvious; that is, based on previous experience some infestations could quickly by classified as no-risk regions and other regions might obviously be in need of immediate control. However, there may also be several similar regions and a lack of available resources to control all of them. In such circumstances, an SPB model would be invaluable in discerning which region warrants control or where the limited control actions would yield the greatest benefit.

The utilization of TAMBEETLE as an aid to experimentalists in feasibility studies for potential control strategies has been well documented (Coulson et al. 1979b). The major benefit of an infestation model for evaluating treatment tactics is that a costly field experimental program can be simulated with the computer for a very small fraction of the experimental expense. In this fashion, field programs need not be instituted for control strategies yielding marginal benefits.

The full implications of scientific hypotheses are often unknown without their mathematical representation. Based on experiences and/or field experimental programs, a scientist often proposes a hypothesis to explain a given phenomenon. Because the physical and biological processes within a spot involve many interdependencies, the effect of the proposed hypothesis cannot be known until it has been rigorously defined and integrated into the full biological system.

STRUCTURE OF THE INFESTATION MODEL

The mathematical model of southern pine beetle infestation dynamics that is incorporated into TAMBEETLE is divided into four major components: immature development and emergence, gallery construction and oviposition, adult reemergence, and adult attack/allocation. Submodels have been developed and validated for each of the components and are discussed below.

Immature Development and Emergence

The variation in mean developmental time due to varying temperature regimes is often handled in biological models by the use of a "physiological" time scale. In many instances, a degree-day scale has been used (Gutierrez et al. 1975, Wang et al. 1977). The degree-day scale can be generalized and given a biological meaning by using a constant temperature rate function. The integration of this rate function, as driven by the changing microclimate temperature, establishes the mean developmental completion time. A model for the constant temperature rate function, utilizing high and low temperature enzyme denaturation, was proposed by Sharpe and DeMichele (1977). The parameter values for this poikilotherm rate function were obtained for SPB through the extensive laboratory experimentation of Gagne et al. (1980).

Due to the large variation in individual developmental times for southern pine beetles, it is appropriate to model the immature developmental process using only mean values. Utilizing the experimental data of Gagne et al., we obtained a probability density function for individual developmental times. The probability density function is on the physiological time scale, and, thus, the effects of temperature are realized by varying the scale according to the poikilotherm rate function. The computational procedure used in combining the rate function and the probability density function into a predictive model is given in detail by Sharpe et al. (1977). The theoretical justification and implications for the procedure are given by Curry, Feldman, and Sharpe (1978a) and Curry, Feldman, and Smith (1978b).

In order to determine the number of southern pine beetles emerging on any given day, not only must the timing be known but the effects of mortality must be included. The general characteristics of within-tree mortality are described by Coulson et al. (1977). Utilizing the poikilotherm rate function for the physiological scale, we found that the functional form for the fraction of immatures surviving to a given age is an exponential decay function with an asymptote equal to the (temperature-dependent) fraction of ultimate survival. The functional form for egg to brood adult survival, based on constant-temperature laboratory data calibrated to mimic field survivalship, is well approximated by the density function of a normal distribution, with mean of 22° C and standard deviation of 8° C factored up so the maximum survivorship is 25 percent. In summary, there are three basic aspects to immature development: (1) a mean physiological time scale, (2) the inherent stochastic variation in developmental time, and (3) within-tree survival of immatures.

Validation

The egg-to-adult emergence time and the proportional survival were calibrated from Plot 21 data (Coulson et al. 1979a) (fig. 1). The bimodal nature of the model response is due to the use of an average survival fraction, while the experimental data has three trees with unusually high numbers and survival fractions contributing to emergence around day 200. Figure 2 displays selected trees (14-15) and (36-38) from Plot 21. These and other selected tree comparisons indicate the model agrees quite well with the field data. The timing aspect of emergence was calibrated by factoring the laboratory developmental rates by 0.7 for field comparisons with Plot 21.

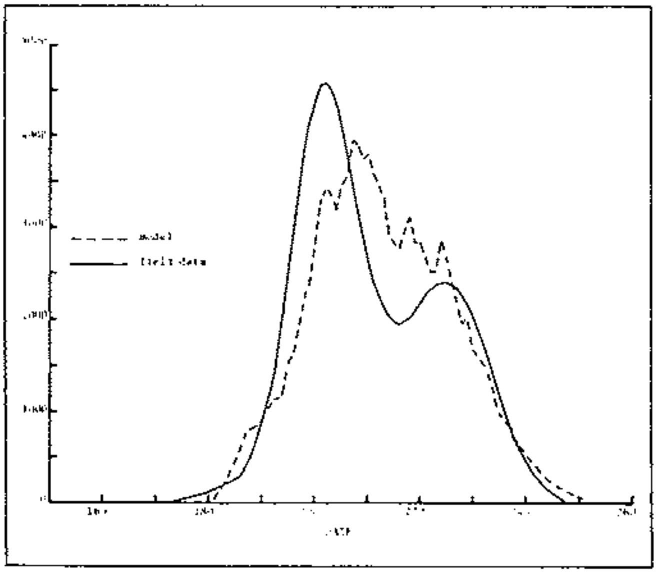


Figure 1.--Model and field comparisons for Spot 21 for daily emergence for all trees in the spot. Model was calibrated to agree with mean timing and average survival.

Validation of the emergence model is accomplished by comparisons with 1977 field Plots 20 and 22 (Coulson et al. 1979a). The magnitude for Plot 20 is very good with timing being slightly fast (fig. 3). For Plot 22 the timing is very good, whereas the model survival magnitudes are slightly high (fig. 4).

Oviposition

Wagner et al. (1980) developed a detailed mathematical description of oviposition based on an extensive laboratory experimental program. The methodology presented by Wagner et al. with revised parameters is used in TAMBEETLE and incorporates four factors that influence ovipostion: temperature, beetle density, female size, and female type. It was observed that females emerging in February oviposited more eggs than beetles emerging later in the year. Thus, a variable called "type" was defined to quantify this apparent seasonality factor.

The procedure used is to separate oviposition into two components that independently predict total egg produc-

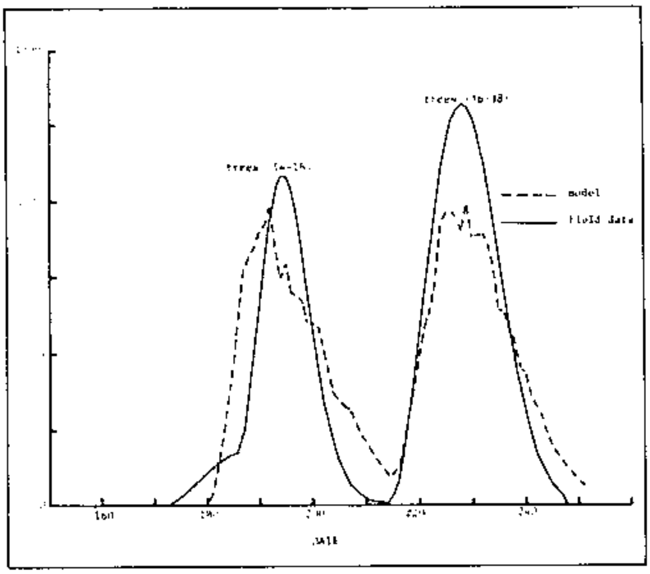


Figure 2.--Model versus field data daily emergence for selected trees within Spot 21.

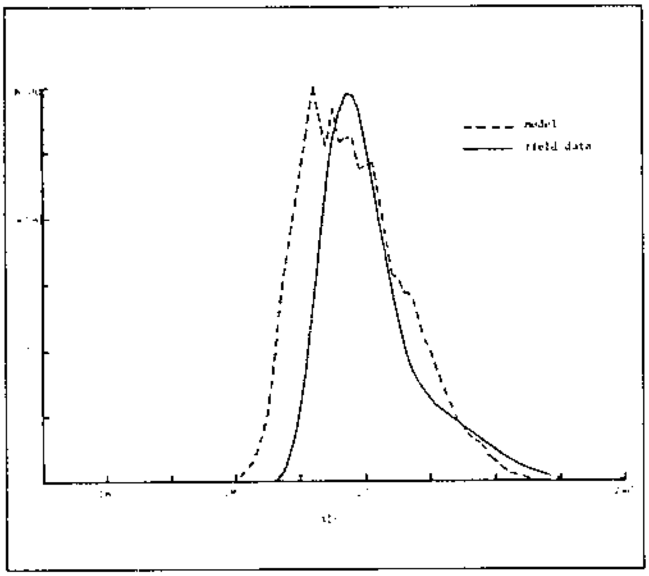


Figure 3.--Model and field data daily comparisons for emergence in Spot 20.

tion and the daily cumulative proportion of eggs oviposited. The function describing the daily cumulative proportion of eggs through time is called the "reproductive profile." Although size had no apparent effect on the profile, temperature, density, and type did. For a fixed type, the influence of temperature and density on daily proportional reproduction is described by a single profile using normalizing constants to define a physiological time scale (see Curry et al. 1978a, p. 405, and 1978b, Section 5). Because both temperature and density for a fixed type affected the time scale, two normalizing rate functions were used.

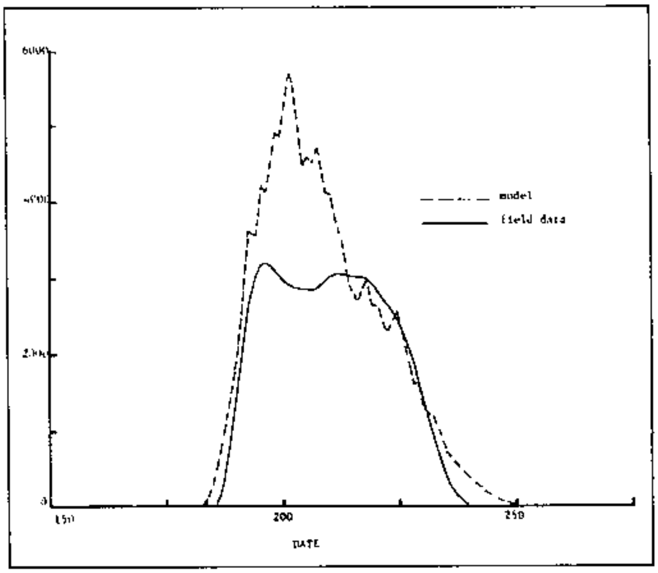


Figure 4.--Model and field data comparisons for emergence in Plot 22.

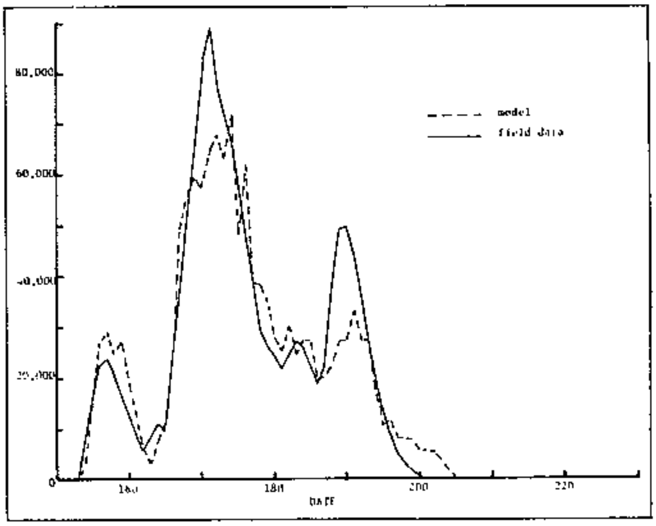


Figure 5.--Model and field data comparisons for Plot 21 for total eggs laid in the spot by day. Model cumulative total calibrated to match field total.

Validation

The total number of eggs by day for Plot 21 is compared with the model results in figure 5. The total number of eggs laid in the plot was used to calibrate the model to field conditions. The temperature-dependent reproduction profile was scaled up by multiplying the whole function by the factor 1.94. Thus, the total eggs for the experimental data and model were forced to agree. However, no model parameters with respect to timing were adjusted. Using the resulting field-calibrated model, the time-varying egg production for Plots 20 and 22 were predicted. These are compared with the field data in figures 6 and 7. Again, this constitutes a validation of the reproduction model as no model parameters were varied after the Plot 21 calibration and Plots 20 and 22 are independent data sets. Time magnitudes for both the validation runs are reasonable. The model simulates the individual trees as well as the total infestation response. Figure 8 displays the model predictions and the field results for a specific tree in Plot 21.

Reemergence

The laboratory studies of Gagne et al. (1980) indicate that reemergence is a temperature-dependent phenomenon that is independent of density. Therefore, a rate of reemergence can be derived similar to immature development. Parameter values for a poikilotherm rate function and a probability function describing reemergence were obtained by using the data of Gagne et al.

Validation

For field calibration, Plot 21 (1977) data were used to obtain a multiplicative constant that adjusts the laboratory data to field developmental times. This process resulted in a 1.2 adjustment factor for converting to the field reemergence rates. Figure 9 compares the Plot 21 reemergence data with the model results for total reemergence within the infestation over time. The timing of reemergence is very good, with the model mean time differing from the experimental average by only 0.54 days. The model deviation for the experimental data in figure 9 are largely due to the extreme variations in measured adult reemergence proportions for selected trees within the spot.

An independent validation of reemergence was performed by comparing the model with reemergence counts from Plots 20 and 22 (1977). These comparisons are displayed in figures 10 and 11, respectively. The shape and magnitude for Plot 20 is very good, with timing being slightly offset. In Plot 22, on the other hand, shape, magnitude, and timing are all in good agreement.

Attack/Allocation

The mechanism for modeling the attack process is an allocation procedure involving the daily number of flying southern pine beetles. This pool is composed of all beetles that reemerged, emerged, or immigrated into the spot during that day. The number of beetles in the flying pool are reduced to represent between-tree mortality and emigration out of the spot. Although these factors are dynamic, the lack of quantitative data at this time necessitates the treatment of between-tree mortality as a constant proportion. Finally, the remaining beetles are allocated to attractive trees and their neighbors according to the attractiveness of each tree. The specific allocation algorithm and the determination of a tree's attractiveness are discussed below.

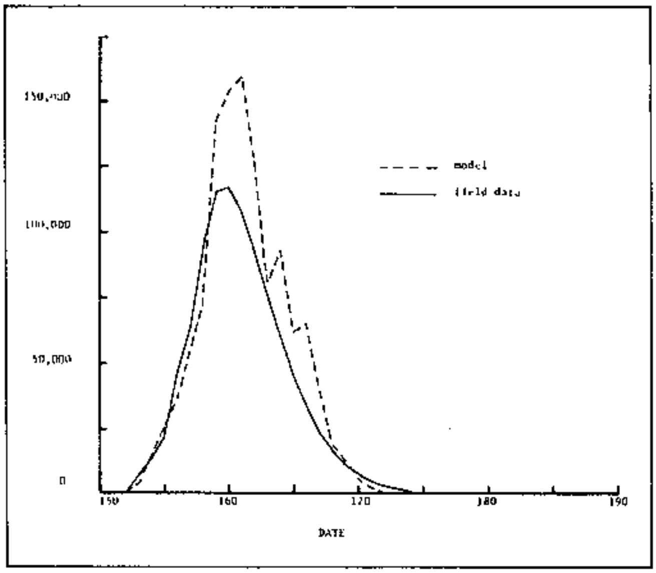


Figure 6.--Model and field data comparisons for Plot 20 for total eggs laid in the spot over time.

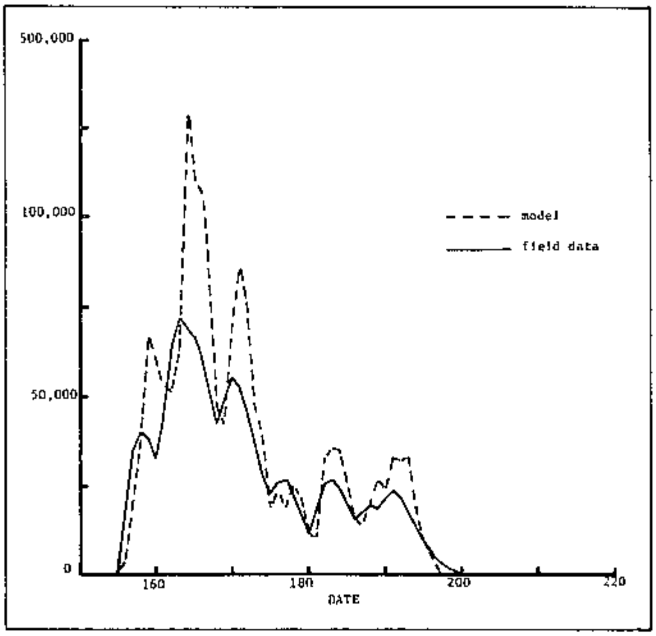


Figure 7.--Model and field data comparisons for Plot 22 for total eggs laid in the spot over time.

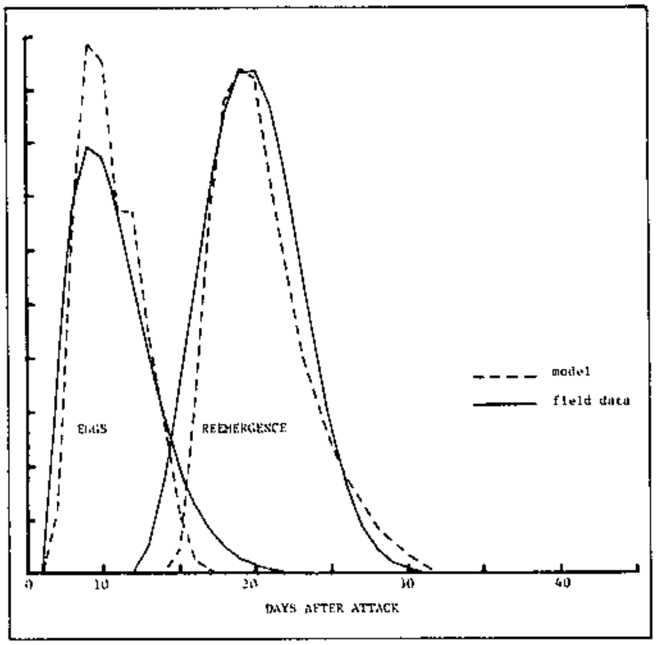


Figure 8.--Tree 14 in Spot 21 daily oviposition and reemergence comparisons between the model and the field data.

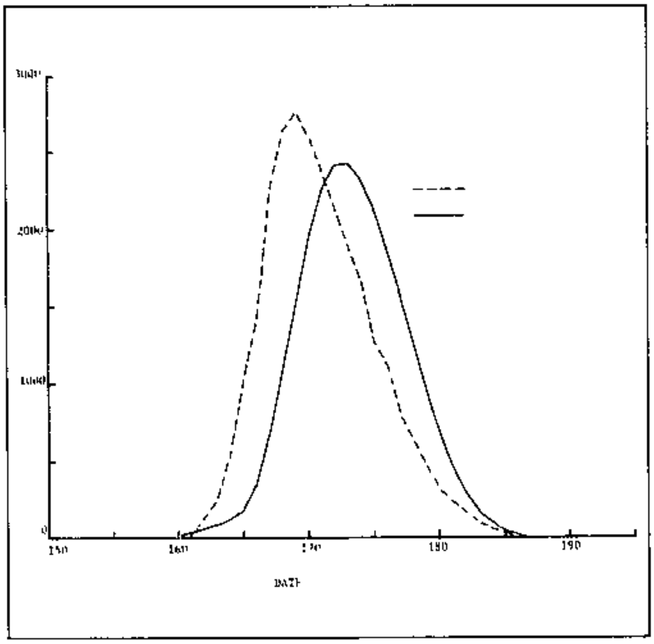


Figure 10.--Model and field comparisons for total reemergence by day for Plot 20.

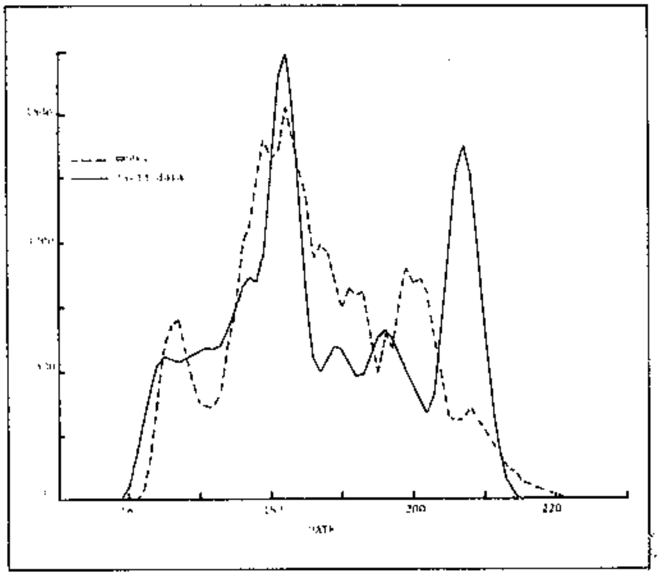


Figure 9.--Model and field comparisons for total reemergence by day for Plot 21.

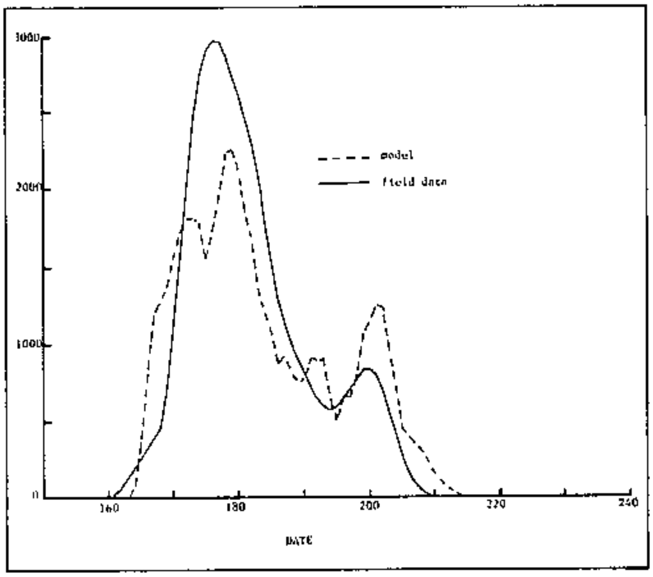


Figure 11.--Model and field comparisons for total reemergence by day for Plot 22.

Allocation to Attractive Trees

The basis for allocating southern pine beetles to host trees is an attractiveness term associated with each tree that is an indicator of the tree's pheromone production. As each beetle successfully initiates gallery, a quantity of chemical releasing compounds is generated (beetle frass and tree resins being two such compounds). The amount of volatiles emitted from this source declines due to evaporation of these chemicals from the source material. Thus, each beetle can be thought of as contributing an initial quantity of attractiveness that decays over time. The total attractiveness of a tree is, then, the sum of the initial attractiveness of recently attacking beetles plus a fraction of the contribution from beetles attacking the previous day plus a smaller fraction of those attacking 2 days before, etc.

The total attractiveness for the infestation is the sum of the attractiveness of all trees. This sum then determines the proportion of emigration from the infestation. As this total attractiveness decreases to zero, the proportion of flying SPB that emigrates from the infestation increases to one. Conversely, as the total attractiveness gets very large, the proportion of flying SPB available to attack trees approaches the fraction surviving between-tree mortality.

Southern pine beetles are allocated to individual trees from the remaining flying population as a function of the tree's attractiveness. This allocation is made to each tree in direct proportion to the tree's total attractiveness.

Insects allocated from the flying population to an attractive tree may actually attack a neighboring, nonattractive tree. At first most of the insects attack the attractive tree, with this proportion declining as inhibitor compounds build up, thus increasing attacks on neighboring trees.

Allocation of Neighboring Trees

Flying southern pine beetles are attracted to pine trees currently undergoing mass attack due to the volatiles being emitted. Only a proportion of the beetles attracted to a given tree actually attacks that tree. The remainder of these attracted SPB are thus available to attack neighboring (nonattractive) trees. Since the infestation spreads in a patchy environment, the number of neighboring trees that absorb SPB changes throughout the life of the attack. The number of beetles attacking nonactive trees depends on the number of beetles available, the distance between trees within a patch, and the distance between patches. As the distance between an attractive tree and a nonattacked neighboring tree increases, the proportion of beetles attacking the neighbor decreases. Attacks cease when this distance becomes too large. This phenomenon is conceptualized as a pheromone plume centered around those trees that are undergoing attack within the patch. The number of trees that can be potentially attacked by these spillover beetles depends on the area within this plume and the density of trees within the patch. The ease of infestation spreading to another patch depends on the area of the plume and the distance between patches.

The area of a specified pheromone concentration level can be determined utilizing results on pheromone dispersion by Fares et al. (1980). This area is a function of the local microclimate, including temperature, relative humidity, wind velocity, and the fraction of cloud cover. The geometry of the concentration isopleths derived by Fares et al. is approximated by a sector of a circle (pie slice). The radius for effective SPB attack under typical field conditions has been observed to be approximately 6 to 7.5 m (Gara and Coster 1968, Johnson and Coster 1978).

The allocation of southern pine beetles to neighboring trees depends not only on their presence within the pheromone plume, but also on their distance from the attractive tree. Johnson and Coster (1978) indicate that as the distance increases, the decrease in attacks follows a logarithmic function. This fact is combined with an approximation method given in Southwood (1978, p. 48) for the distance to the *i*th-nearest neighbor to obtain a function specifying the probability of SPB's attacking neighboring trees.

Calibration

A very accurate data set from the infestation of Plot 21 was available for calibration of the overall response. The initial conditions and the movement of the spot within the patchy environment are illustrated in figure 12. All trees attacked before Julian day 156 were used for initial conditions, and the model was run for 70 days. Figure 13 shows the resulting predictions and the data. The major unknown parameter was tree susceptibility. Susceptibility is defined here as the number of attacking SPB needed to consider a tree an active tree instead of a nonattacked neighbor. For Plot 21, susceptibility of 200 attacking SPB proved to give excellent results. The actual day-to-day dynamics agreed well, as can be seen from figure 13.

CONCLUSION

Preliminary testing, refinement, and validation of the emergence, reemergence, and oviposition models have reached the point where considerable confidence can be placed in their accuracy. The extensive biological mechanisms built into the mathematics allow for predictive powers over a wide range of environmental conditions. The overall integrated model gives very accurate response to the day-to-day infestation growth; however, considerable information is needed regarding the geometric description of the forest stand. When daily accuracy in

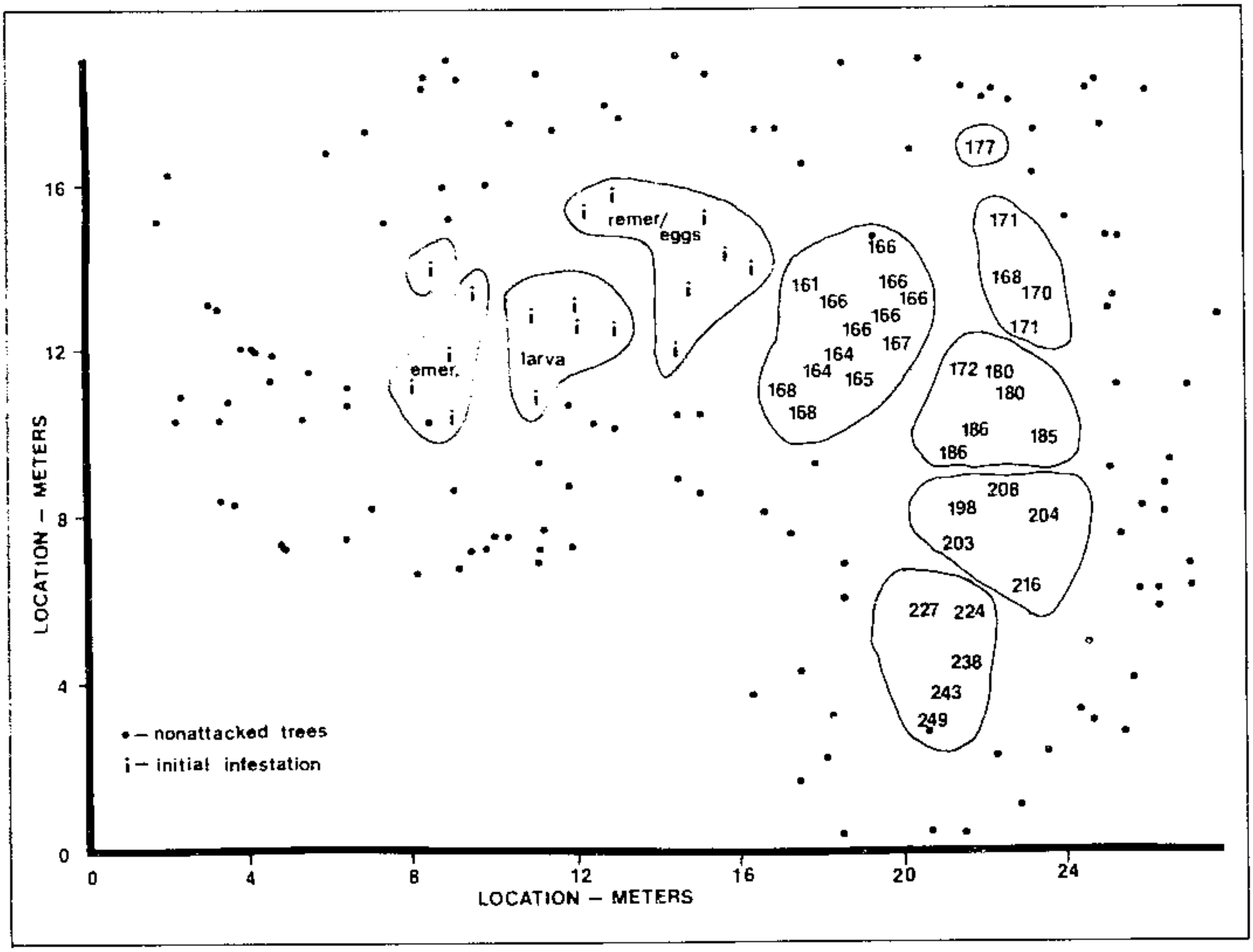


Figure 12.--Schematic from Coulson et al. showing movement and grouping for the attack dynamics in Plot 21.

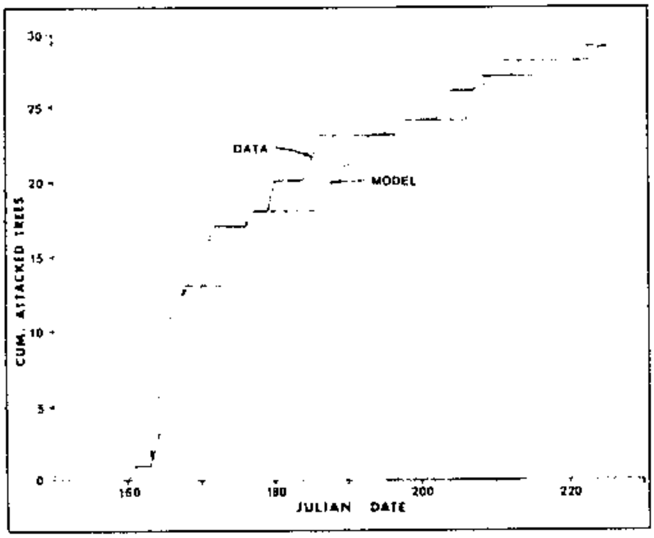


Figure 13.--Comparison of model predictions and field data for the number of cumulative attacked trees versus Julian date.

the predictions is needed, information about the stand patchiness is required. A simplistic method for measuring and describing stand patchiness would facilitate this use of TAMBEETLE. Tree susceptibility is a key parameter in establishing the rate of spot growth; however, it is not well understood biologically. The lack of biological quantification of this factor required numerical determination during model calibration. Work is needed to relate susceptibility to site/stand characteristics in order that TAMBEETLE will be applicable over a broad range of geographic regions.

In summary, the TAMBEETLE model of southern pine beetle infestation has been developed and preliminary calibration/validation of the model has been completed for 1977 east Texas data[2]. An ANSI standard FORTRAN package is under development for ease of distribution and should be executable at most computer installations. This FORTRAN code of TAMBEETLE is designed for use by the noncomputer specialist and includes the flexible input options discussed.

LITERATURE CITED

Coulson, R. N., P. E. Pulley, J. L. Foltz, and W. C. Martin. 1976. Procedural guide for quantitatively sampling within-tree populations of *Dendroctonus frontalis*. Texas Agric. Exp. Stn., Misc. Publ. 1267. College Station, Tex.

Coulson, R. N., P. E. Pulley, J. L. Foltz, W. C. Martin, and C. L. Kelley. 1977. Survival models for within-tree populations of *Dendroctonus frontalis* (Coleoptera:Scolytidae). Canad. Entomol. 109:1071-1077.

Coulson, R. N., W. S. Fargo, L. J. Edson, P. E. Pulley, and A. M. Bunting. 1979a. Procedural guide for conducting field investigations on the population dynamics of the southern pine beetle. Texas Agric. Exp. Stn., Misc. Publ. 1427. College Station, Tex.

Coulson, R. N., R. M. Feldman, W. S. Fargo, P.J.H. Sharpe, G. L. Curry, and P. E. Pulley. 1979b. Evaluating suppression tactics for *Dendroctonus frontalis* in infestations. *In* Evaluating control tactics for the southern pine beetle: symposium proceedings. [Many, La., Jan. 1979.] J. E. Coster and J. L. Searcy, eds. p. 27-44. U.S. Dep. Agric. For. Serv., Tech. Bull. 1613. Comb. For. Pest Res. Develop. Prog., Pineville, La.

Curry, G. L., R. M. Feldman, and P.J.H. Sharpe. 1978a. Foundations of stochastic development. J. Theor. Biol. 74:397-410.

Curry, G. L., R. M. Feldman, and K. C. Smith. 1978b. A stochastic model of a temperature dependent population. Theor. Pop. Biol. 13:197-213.

Fares, Y., P.J.H. Sharpe, and C. Magnuson. 1980. Pheromone dispersion in forests. J. Theor. Biology. [In press.]

Feldman, R. M., G. L. Curry, and R. N. Coulson. 1980. A population model for *Dendroctonus frontalis*. Working paper. Biosystems Research Division, Industrial Engineering Department, Texas A. & M. University.

Gagne, J. A., P.J.H. Sharpe, R. N. Coulson, and T. L. Wagner. 1980. Modeling southern pine beetle reemergence and emergence as functions of temperature. *In* Modeling southern pine beetle populations: symposium proceedings. [Asheville, N.C., Feb. 1980.] F. M. Stephen, J. L. Searcy, and G. D. Hertel, eds. U.S. Dep. Agric. For. Serv., Tech. Bull. 1630. Comb. For. Pest Res. Develop. Prog., Pineville, La.

Gara, R. I., and J. E. Coster. 1968. Studies on the attack behavior of the southern pine beetle. III: Sequence of tree infestation within stands. Contrib. Boyce Thompson Inst. 24:77-86.

Gutierrez, A. P., L. A. Falcon, W. Loew, P. A Leipzig, and R. Van den Bosch. 1975. An analysis of cotton production in California: a model for Acala cotton and the effects of defoliators on its yield. Environ. Entomol. 4:125-136.

Johnson, P. C., and J. E. Coster. 1978. Probability of attack by southern pine beetle in relation to distance from an attractive host tree. For. Sci. 24:574-580.

Sharpe, P.J.H., and D. W. DeMichele. 1977. Reaction kinetics of poikilotherm development. J. Theor. Biol. 64:649-670.

Sharpe, P.J.H., G. L. Curry, D. W. DeMichele, and C. L. Cole. 1977. Distribution model of organism development times. J. Theor. Biol. 66:21-38.

Southwood, T.R.E. 1978. Ecological methods Chapman and Hall, London.

---

[2] Subsequent to the presentation of this paper, further utilization of the data have allowed accurate validation without the need for a calibration step. A complete description of the resulting final models will be reported in a future publication.

Stephen, F. M., and H. A. Taha. 1979. Tree mortality, infested bark area, and beetle population measurements as components of treatment evaluation procedures on discrete forest management units. *In* Evaluating control tactics for the southern pine beetle: symposium proceedings. [Many, La., Jan. 1979.] J. E. Coster and J. L. Searcy, eds. p. 45-53. U.S. Dep. Agric. For. Serv., Tech. Bull. 1613. Comb. For. Pest Res. Develop. Prog., Pineville, La.

Wagner, T. L., R. M. Feldman, J. A. Gagne, and R. N. Coulson. 1980. Models describing gallery construction and oviposition by *Dendroctonus frontalis*. *In* Modeling southern pine beetle populations: symposium proceedings. [Asheville, N.C., Feb. 1980.] F. M. Stephen, J. L. Searcy, and G. D. Hertel, eds. U.S. Dep. Agric. For. Serv., Tech. Bull. 1630. Comb. For. Pest Res. Develop. Prog., Pineville, La.

Wang, Y., A. P. Gutierrez, G. Oster, and R. Daxl. 1977. A population model for plant growth and development: coupling cotton-herbivore interaction. Can. Entomol. 109: 1359-1374.

ACKNOWLEDGMENTS

The work herein reported was funded in part by a USDA-sponsored program entitled "The Expanded Southern Pine Beetle Research and Applications Program," Grant Number 89-106 (19-192), and in part by the Texas Agricultural Experiment Station, Texas A. & M. University.

The authors also wish to thank the many people of ESPBRAP who aided in this work through informal discussions. Data supplied by B. Hynum of the Texas Forest Service were very useful in parametric estimation. Particular thanks go to P.J.H. Sharpe, J. A. Gagne, T. L. Wagner, W. S. Fargo, P. E. Pulley, and D. N. Pope for their continual exchange of ideas within the TAMBEETLE program.

MODELING SOUTHERN PINE BEETLE REEMERGENCE AND EMERGENCE AS FUNCTIONS OF TEMPERATURE[1]

James A. Gagne, Peter J.H. Sharpe,
Robert N. Coulson, and Terence L. Wagner[2]

Abstract.--Two conditions have hindered modeling of southern pine beetle, *Dendroctonus frontalis* Zimmermann, reemergence and emergence as functions of temperature. First, entomologists have not gathered a comprehensive data base on the effects of temperature on these processes. Such a data base is now available. Second, models based on phenology, average temperature, or day-degrees gloss over the responses of reemergence and emergence to temperature, and thereby diminish our understanding of these responses. This diminished understanding ultimately decreases our ability to forecast reemergence and emergence.

A two-component model can describe reemergence and emergence as functions of temperature. The first component, based on absolute reaction rate theory, predicts rates of reemergence or emergence from temperature. The second component, an empirical cumulative density function, distributes the reemerging or emerging population over calendar time. The empirical density functions of both reemergence and emergence are independent of temperature. This finding suggests that there is an underlying order in the way beetle populations respond to temperature.

INTRODUCTION

Understanding of population dynamics is vital in a pest management program (Waters and Stark 1980). Forest entomologists have traditionally held that temperature plays a key role in bark-beetle population dynamics (Rudinsky 1962, Coulson 1979). Yet bark beetles are hard to rear and observe, so there are few data sets that permit the modeling of processes such as reemergence or emergence as functions of temperature. This statement is true even for a well-studied bark beetle like *Dendroctonus frontalis* Zimmermann.

Efforts to model processes such as reemergence and emergence yield three benefits. First, the modeling process calls for the acquisition of a comprehensive data base. This need challenges and enlarges our ability to handle and observe bark beetles under controlled conditions. Second, modeling forces us to state our concepts of how temperature affects reemergence and emergence and allows us to test these concepts with numerical predictions. In this way we increase our understanding. And third, a valid model for the effects of temperature on reemergence and emergence enables us to forecast events. This capability is needed for making control or management decisions. In this paper we discuss these benefits gained from modeling SPB reemergence and emergence.

EFFECTS OF TEMPERATURE

As mentioned, there is no single, comprehensive data set on the effects of temperature on southern pine beetle reemergence and emergence. But there are numerous field and laboratory studies that show parts of the relationship between the insect and temperature.

Thatcher and Pickard (1964, 1967) found that the beetle completed up to eight generations annually in southeast Texas. They stated that eggs required 3 to 21 days, larvae 13 to 63 days, and pupae 3 to 36 days to complete development. In total, a summer generation took as few as 26 days, whereas a winter generation took 110 days. These figures agree fairly well with estimates of 37 days' development time for SPB in trees infested in June and 140 days for beetles in November-infested trees (Billings and Kibbe 1978). Coulson et al. (1979) observed brood adults emerging 21 days

---

[1] This contribution is Texas Agricultural Experiment Station Paper No. 15841.

[2] The authors are, respectively, Graduate Research Assistant, Dept. of Entomology; Associate Professor of Bioengineering, Biosystems Research Division; Professor of Entomology, Dept. of Entomology; and Postdoctoral Fellow, Dept. of Entomology, Texas A. & M. University, College Station.

after attack from trees infested in June. Emergence peaked 29 days after initial attacks and lasted about 28 days.

The life cycle has been studied in other States besides Texas. Mizell and Nebeker (1978) measured development times throughout the year in Mississippi and related them to average temperature. Oviposition lasted 4 to 32 days, egg development required 8 to 27 days, larvae developed in 10 to 62 days, and pupae in 7 to 26 days. The average temperature for the coldest part of the year was 4°C and for the hottest part, 28°C (all temperatures herein are in Celsius). There were no detectable differences in development times of insects infesting different parts of the bole. In Georgia, Goldman and Franklin (1977) found that eggs hatched in 4 to 5 days and that larvae developed through four instars in 20 days.

Threshold and temperature extremes have also been measured. The threshold ambient air temperature for brood adult emergence is 14° to 15° (Thatcher 1967, Franklin 1970, Kinn 1978). Beal (1933) stated that brief exposure to -18° was lethal to pupae and adults and that larvae and pupae were killed by exposure to 44° for 1.5 hours. There also appears to be an adverse effect of high temperatures on larval development (Thatcher and Pickard 1964, 1967). During July and August, especially, larval development times increase and survival decreases. These phenomena were related to the number of days during the infestation when daily maxima exceeded 35° (Billings and Kibbe 1978). This decrease in survival of later-stage larvae was confirmed by Gagne et al. (1980).

Corresponding information on reemergence in the field is scarce. Thatcher and Pickard (1964, 1967) found that reemergence occurred 4 to 32 days after attack in east Texas. Beetles were capable of three reemergences. Coulson et al. (1978) also studied reemergence in east Texas. They determined that it began 4 days after the onset of attacks, peaked 3 days later, and continued for up to 14 days. Franklin (1970) noted a slightly different pattern for beetles reemerging from pines in the Georgia Piedmont. Beetles started reemerging 13 days after attacks began, and reemergence lasted 2 weeks, with a peak at 21 days postattack.

The above information on population processes in the field establishes realistic ranges to compare to laboratory results. Fronk (1947) studied beetle development in an insectary in Virginia. Eggs hatched in an average of 5.5 days (range 3 to 9 days). Larvae passed through four instars in 32 days (range 25 to 38 days). Brood adults emerged after an average pupal stage of 9.4 days (range 8 to 11 days). Thus, in Virginia, a generation required 47 days on the average (range 40 to 54 days).

Bremer (1967) has done the most comprehensive laboratory study on *D. frontalis* development to date. Insects completed development from egg to emergence in about 36 days at 21°, 24°, and 27° (range 32 to 49 days). However, at 29° development times increased to 51 days (range 46 to 56 days). In general, temperatures between 21° and 27° favored reproduction and development, although there was great variation in beetle size within this temperature range. Gaumer (1967) also studied the effects of temperature on beetle development. Development took 6 weeks at 15° and 4 weeks at temperatures up to 32°. A regime of 40° to 42° killed all stages in 12 days. Using the criteria of shortest development time and most progeny per parent, he concluded that temperatures of 20° to 22° with 50 to 60 percent relative humidity were optimum rearing conditions. Clark and Osgood (1964) stated that 22° to 27° with 40 to 60 percent relative humidity were the optimum conditions for mass rearing of the beetle. Covington (1969) found similar conditions to be optimal.

Some laboratory work on temperature thresholds and extremes has also been done. Palmer and Coster (1978) observed a precipitous decline in gallery length and eggs per centimeter of gallery when pairs were held at 30° or greater. Brood beetles exposed to 40°, 44°, and 48° were killed in 40, 16, and 8 hours, respectively. Surprisingly, larvae could tolerate hotter temperatures than could adults. White and Franklin (1976) studied low-temperature thresholds of beetle locomotion at constant temperatures. Beetles could move at 9°, climb at 12°, and take flight at 22°. Activity was inhibited at temperatures above 34°.

To our knowledge there are no reports on the effects of temperature on reemergence in the laboratory.

There is thus little doubt that more work on the relationship between *D. frontalis* and temperature is needed. This need is due to the following shortcomings. First, the full range of biologically meaningful temperatures has not been covered. Second, constant temperature thresholds have not been obtained for most of the life stages. Third, a key population process, reemergence, has not been studied at all. And fourth, the results of previous studies were neatly summarized as means, ranges, and standard deviations. Such summaries do not permit the reconstruction of the frequency distributions for the processes, and these frequency distributions are important in modeling reemergence and emergence.

MATERIALS AND METHODS

The aims of the experimental work were to develop techniques that permit the convenient, nondestructive observation of many insects in conditions that are as natural as possible.

Reemergence of Parent Adults

Adults emerging from naturally infested bark were collected in a table-top cage (Browne 1972). These beetles were held on ice and sexed. They were then introduced onto freshly cut 30-cm bolts of loblolly pine, *Pinus taeda* L., using the gelatin cap technique described by Wagner et al. (1980). During the experiment each bolt was held in a lard can fitted with a single pole blower to provide a small flow of fresh air. The can was held in a constant temperature chamber. Each lard can was checked at 24-hour intervals and reemerging beetles were collected, sexed, counted, and recorded.

Egg Development

Fresh bolts of *P. taeda* were cut into sections ca. 4 cm thick using a bandsaw. Vertical handsaw cuts, ca. 4 cm apart, were made through the bark to the xylem around the entire section. This process produced islands of intact bark that we call "wafers." Each loblolly section was then placed in a 21 × 31 × 9.5-cm plastic container with about 100 unsexed beetles. The sections were held in the laboratory for 48 hours.

Beetles readily paired off and attacked the sections along the handsaw cuts. Forty-eight hours after introduction of the beetles, the wafers were cut from the sections using a sharp knife. The small wafer size permitted separation of the phloem and xylem without destruction of the eggs. The eggs were then removed from their niches using the point of a dissection probe or microforceps and arranged on moist filter paper in petri dishes. Eggs were separated by a plexiglass template that was cut to fit snugly within the petri dish and drilled to accommodate 50 eggs. The petri dishes were then placed in a 14 × 28 × 8-cm plastic container, and the container was placed in a constant temperature chamber. Eggs were observed daily. About 24 hours before they hatch, larvae are visible through the egg shell (Fronk 1947). Once the first larva hatched, eggs were observed at 3-hour intervals until the last larva hatched. A larva was deemed hatched when it burst the chorion. Numbers of larvae hatching in each 3-hour interval were counted and recorded.

Larval, Pupal, and Callow Adult Development

We had difficulties in consistently rearing larvae and being able to observe them nondestructively. Some attempts using the following technique were successful. A straight, healthy loblolly pine 25 to 45 cm in d.b.h. was felled and bucked into 60-cm sections. Using a bandsaw, lab workers then cut these sections into bark-wood slabs 7.5 × 11 × 1.5 cm. Excess bark was removed from the slab sides to prevent curling, and loose bark scales were removed. Beetles were then introduced onto the slabs using techniques similar to those described by Wagner et al. (1980). The slabs were then held in plastic containers and placed in constant temperature chambers. They were radiographed at 24- or 48-hour intervals. The development of individual insects was followed and recorded.

Although it was not consistently possible to rear the insect from egg to adult using the above slab technique, it was possible to rear it from late larva to adult. Thus, trees infested with 2nd- or 3rd-instar larvae were felled and bucked into 60-cm sections. Slabs were made from these sections and held and observed as above. In this manner, it was possible to obtain development times of pupae and callow adults at constant temperatures.

Our inability to rear larvae consistently from 1st- to 4th-instar forced us to construct larval response to temperature in the following manner. First, we inspected the responses of egg, pupal, and callow adult development to temperature. Eggs were most sensitive to temperature. Larvae apparently developed normally from 1st to 4th instar at two temperatures, 15° and 25°. The ratio between larval and egg development times at 15° was 3.67, and the ratio between larval and egg development times at 25° was 3.57. Thus, an approximation of the larval response to temperature was constructed by multiplying the mean values for egg development times by 3.62. Next, the values for egg, larval, pupal, and callow adult times at the same temperature were added to give a total length of life cycle from egg to adult emergence. These values compared favorably with reports in the literature.

RESULTS AND DISCUSSION

Responses of Reemergence And Emergence to Temperature

Both reemergence and emergence responded to temperature, and they did so in a pattern that has often been observed for other processes (fig. 1). The mean values for reemergence are strictly from experimental results, but the mean values for emergence had to be constructed from data on egg, pupal, and callow adult development and an assumption about larval response.

Until now, there have been no reports of the response of reemergence rates to constant temperatures. The values obtained in the laboratory are in good agreement with reports from field studies (Thatcher and Pickard 1964, 1967; Franklin 1970; Coulson et al. 1978). Still, there were some surprising results. First, parent beetles reemerged at 10°, although this temperature is below the threshold for flight (Franklin 1970, White and Franklin 1976, Kinn 1978). Second, the maximum reemergence rate occurred at 25°, a relatively cool temperature during the east Texas summer. Also, temperatures above 25° slowed reemergence. Third, there was substantial variability in reemergence rates in replicated experiments. We feel that this variability was due to innate differences in the populations of beetles. This variability should be incorporated in models predicting rates as functions of temperature.

Emergence did not respond to temperature as one would expect from previous studies. First, emergence times were not essentially constant between 21° and 27°, as reported by Bremer (1967). Emergence was quite sensitive to temperatures in the 21° to 27° range. Second, fastest emergence took place at 30°, whereas Bremer (1967) found that emergence rates greatly decreased at 29° or above. In Bremer's 29° experiment, larval development rates decreased. Temperature may have caused this decrease, but blue-stain fungi could also have been involved (Barras 1970). The extreme susceptibility of larvae to temperature does not square with our observations on the response of eggs, pupae, and callow adults to temperature.

Models of Developmental Rates As Functions of Temperature

Many scientists have studied the response of development to temperature and proposed mathematical models to describe this response. Wigglesworth (1972) and Watt (1968) have ably reviewed the most important models. Watt made two criticisms of the extant models. First, few of the models have any theoretical basis. Second, few of the proposed models describe the response of development to temperature throughout the biological temperature range. After thorough evaluation of three models, Watt concluded that an absolute reaction rate model, based on the work of Eyring, came closest both to having a theoretical basis and describing the data adequately.

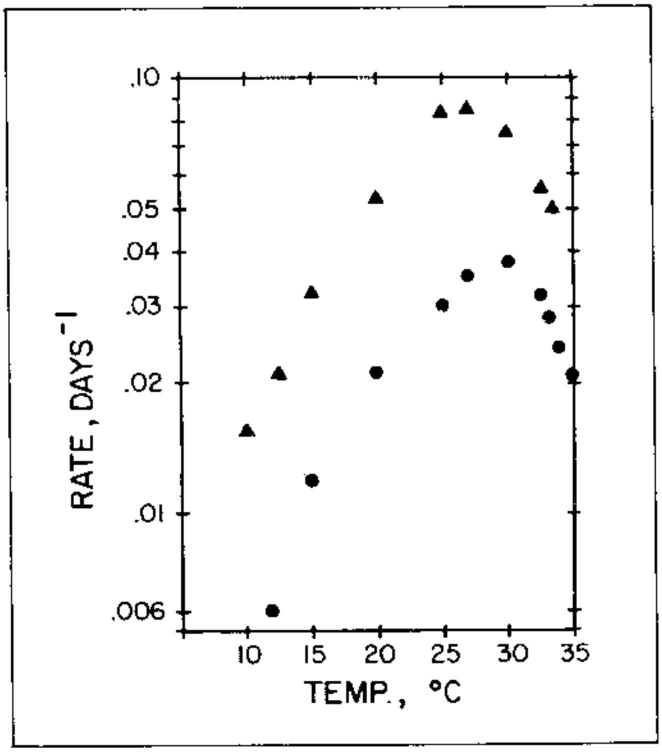


Figure 1.--The responses of reemergence (triangles) and emergence (circles) rates to various constant temperatures.

Recently Stinner, Gutierrez, and Butler (1974); Logan et al. (1976); and Sharpe and DeMichele (1977) have modeled temperature-dependent development. All three models have a theoretical basis, but the model of Sharpe and DeMichele is an extension of the work of Eyring. It therefore avoids the two criticisms voiced by Watt (1968). First, it has a theoretical basis, as it is derived from absolute reaction rate kinetics. Second, the model describes data on SPB reemergence and emergence (fig. 2). It has the form:

$$R_D = \frac{T\ e^{(\phi - \Delta H_A/T)/R}}{1 + e^{(\Delta S_L - \Delta H_L/T)/R} + e^{(\Delta S_H - \Delta H_H/T)/R}} \quad (1)$$

where R_D is the development rate at temperature T, R is the universal gas constant, and ϕ, ΔS_L, ΔH_L, ΔS_H, ΔH_H, and ΔH_A are thermodynamic constants of the process being studied. The subscripts

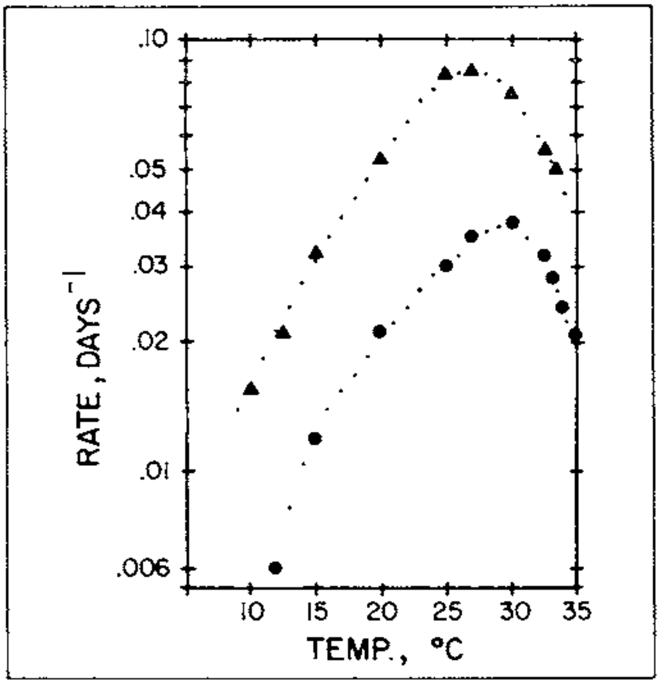


Figure 2.--The fits (smalls dots) of the developmental rate model to rates of reemergence (triangles) and emergence (circles).

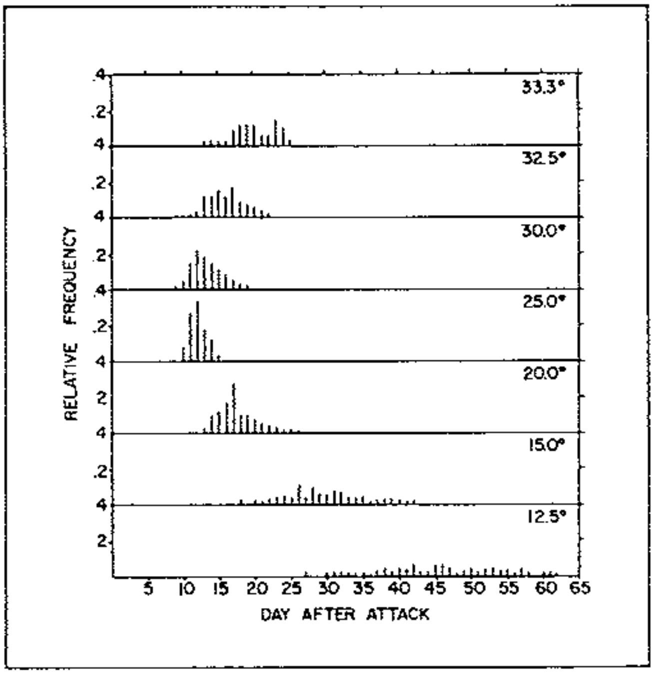


Figure 3.--Representative reemergence distributions for various constant temperature experiments.

L and H refer to the low and high extremes of temperature. The constants are estimated from constant temperature data using nonlinear regression.

Briefly, the model assumes that development is controlled by one rate-limiting enzyme. The enzyme can exist in three interchangeable forms: catalytically active, catalytically inactive due to low temperature, and catalytically inactive due to high temperature. Development rate is a function of temperature and the proportion of enzyme in the catalytically active state. Thus, in the midrange of temperatures the numerator of (1) predominates. As temperatures become too cold, the term with ΔS_L and ΔH_L gets large (i.e., more and more of the rate-controlling enzyme is inactive), so development slows. Similarly, as temperatures become too hot, the term with ΔS_H and ΔH_H becomes large and development slows.

Although the single control enzyme concept may not be literally correct, it is plausible, and economically accounts for the well-known response of insects to temperature. Because it has a theoretical basis, it is easy to apply to real-world data, as exemplified by the curves for reemergence and emergence in figure 2. Notice that rates of reemergence and emergence were inhibited above 25° and 30°, respectively. However, cold temperatures evidently did not inhibit reemergence. (Compare the shapes of the reemergence and emergence curves between 10° and 20°. Reemergence is linear, whereas emergence is curvilinear). Thus, the term with ΔS_L and ΔH_L was left out of the model fitted to reemergence but included in the model fitted to emergence. Here, a theoretical basis permitted a more accurate description of the data.

Models of the Distribution Of Development Times

The above rate model is deterministic in that it will always predict the same rate for a given temperature. But reemergence and emergence occur over a period of time even at constant temperatures. Figure 3 shows representative reemergence distributions for several constant temperature experiments. A mean time (or rate) does not fully represent the process. Also, figure 3 suggests that the distributions of development times were different at different constant temperatures.

Poikilotherm development models can incorporate this observed variability in two ways. One way is to use Monte Carlo techniques and to generate pseudorandom numbers for the development time of each organism (Kowal 1971, Hardman 1976). The other way is to use a probability density function based on a biological time scale (Stinner et al. 1975, Sharpe et al. 1977). Curry, Feldman, and Sharpe (1978) treated the general problem of using a probability density function based on biological time.

We first used the concepts developed by Sharpe et al. (1977). These authors hypothesized that the skew in development times is a consequence of a symmetric distribution of development rates, i.e. the rate-controlling enzyme. A consequence of this assumption is that distributions of rates at different constant temperatures will all have the same coefficient of variation. Also, over all temperatures, the distributions of development rates will be manifestations of the same distribution. The utility of this approach is that it gives one standard curve that can be used to distribute development times in constant and fluctuating temperature environments.

Sharpe et al. (1977) described the distribution of rates with the quadratic and normal probability density functions. In practice, the two distributions are quite similar and difficult to differentiate using Kolmogorov-Smirnov or χ^2 tests. Thus, the distributions of reemergence and emergence rates were compared with the normal distribution using the Kolmogorov-Smirnov test, and *t* tests on skewness and kurtosis. These tests forced us to reject the hypothesis that reemergence and emergence rates are normally distributed with a constant coefficient of variation. They also forced us to reject the hypothesis that the rate distributions are symmetric. Thus the model proposed by Sharpe et al. (1977) is not appropriate for SPB reemergence and emergence.

Having rejected this idea, we need to decide whether the reemergence and emergence distributions at different constant temperatures are manifestations of a single underlying distribution. If so, we need to estimate that distribution. The simplest hypothesis would be that temperature multiplies the times of one distribution by a constant, thereby yielding the distribution of another temperature. Physically this is analogous to having a single standard distribution sketched on latex. At cool temperatures the latex is stretched out; at warm temperatures it contracts. An empirical test of this hypothesis can be made as follows. First, define t1, t10, t20, ... t90, and t100 as the times when 1, 10, 20, ... 90, and, 100 percent of parent beetles reemerge at a given constant temperature. Further, define $\bar{t}$ as the average time to reemerge--the weighted mean of the frequency distribution. Now define the ratios R1 = t1/$\bar{t}$, R2 = t10/$\bar{t}$, R3 = t20/$\bar{t}$, ..., R10 = t90/$\bar{t}$, and R11 = t100/$\bar{t}$.

Table 1.--Coefficients of variation for the average shape ratios (R1-R11) of distributions of reemergence and emergence at constant temperatures (n = 19 reemergence distributions; n = 7 emergence distributions).

Ratio	Reemergence	Emergence
R1	12.9	4.5
R2	6.4	3.6
R3	6.0	3.9
R4	4.0	3.4
R5	3.5	2.2
R6	3.3	1.4
R7	2.8	1.5
R8	3.2	1.7
R9	4.6	3.0
R10	6.6	3.0
R11	12.7	3.1

If the hypothesis of a multiplicative effect of temperature holds, then R1, R2, ..., R11 should not vary much over temperature. A measure of the variability of the R's is their coefficient of variation. Means and coefficients of variation were calculated for R1, R2, ..., R11 of laboratory reemergence and emergence distributions. The coefficients of variation for both reemergence and emergence were modest (table 1). Also, the R's were independent of temperature. We therefore concluded that the reemergence and emergence distributions were manifestations of standard reemergence and emergence distributions that are independent of temperature.

As an additional check on this conclusion, we calculated R1, R2, ..., R11 for reemergence from 20 naturally infested trees, and for emergence from 18 naturally infested trees. Figures 4 and 5 show that the R's (shape ratios) of laboratory and field reemergence and emergence distributions were strikingly similar. This result suggests that reemergence at constant temperatures in the laboratory occurs in the same pattern as reemergence at fluctuating temperatures in the field. The same assertion appears to hold for emergence.

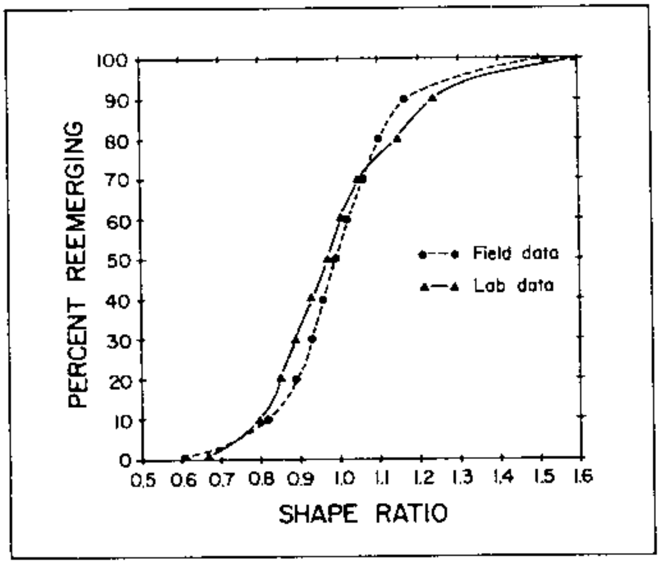


Figure 4.--Shape ratios (R1-R11) that give the standard cumulative reemergence distribution. This distribution is independent of temperature. Average shape ratios for 20 naturally infested trees from Cleveland, Tex., in 1978 are given for comparison.

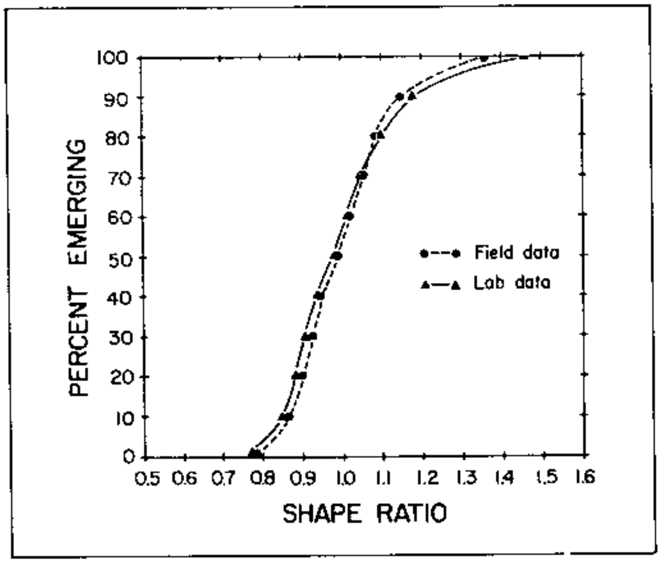


Figure 5.--Shape ratios (R1-R11) that give the standard cumulative emergence distribution. This distribution is independent of temperature. Average shape ratios for 18 naturally infested trees from Cleveland, Tex., in 1978 are given for comparison.

These shape ratios may be interpreted as follows. Suppose we obtain a mean for a frequency distribution of reemergence and then divide all reemergence times in that distribution by the mean. This forces the distribution to have a mean of 1.0. The shape ratios are the proportion of the average reemergence time (1.0) when 1 percent (R1), 10 percent (R2), ..., 100 percent (R11) of the beetles reemerge. This distribution can be linked directly with the development rate model. The rate model gives the fraction of development completed by the average insect per unit time spent at a given temperature. The fractions are added until R1 is reached (0.67 for reemergence, see fig. 5). At that time 1 percent of the population reemerges. When the fractions of development add to 1.6 (R11 for reemergence), 100 percent of the beetles have reemerged.

A Critique of Models of Development As a Function of Temperature

Interest in the effects of temperature on insects stems, in part, from a need to know when biological events will occur in the field. To this end, entomologists have used several methods to gage the timing of events. The simplest method employs phenological observations. However, this method would work best for univoltine insects that diapause. The SPB is multivoltine and develops without a diapause, at least in the South. Still, phenology might prove useful for gaging spring events in the northern parts of its range.

Some models describe development times as a function of average temperature. We feel that there are pitfalls in using average temperature. First, one does not know a priori the period over which temperature should be averaged. This dilemma could lead to the inclusion of temperatures occurring after development is complete in the average temperature. Second, if multiple observations on temperature are made per day, the average will quickly stabilize and become insensitive even to extreme temperatures. But development rates are sensitive to small changes in temperature, especially near the bends in the temperature-rate curve (for emergence the values are at 15° and 30°, fig. 1). Third, there are many combinations of temperatures that will have the same average. Insect response will depend on the magnitude of the temperature fluctuations and the location on the temperature-rate curve. And fourth, average temperatures are most commonly used to predict average times of development, thus ignoring the variablity in development times.

Other models describe development as a function of day-degrees. We also see several pitfalls in using day-degrees. First, day-degrees implicitly assume a linear response to temperature. This is a good assumption in some sections of the temperature-rate curve and a poor assumption in other sections. Departure from linearity can lead to serious error (Stinner et al. 1974). Figure 1 shows that, for much of the year in east Texas, the SPB is exposed to temperatures in the range where rates are nonlinear. Second, development takes different numbers of day-degress in experiments at different constant temperatures, even at temperatures within the linear response range. This result suggests that a day-degree at one temperature is not equal to a day-degree at another temperature.

There are also problems inherent in the models we have used, because we make four assumptions that are difficult to test and may be violated. First, changes in development rates are assumed to instantaneously follow changes in temperature. Development rates are probably more homeostatic and do not change instantaneously. Second, the responses of insects in the lab and field are assumed to be identical. But constant temperature thresholds are probably not equal to development thresholds at fluctuating temperatures in the field. Third, it is assumed that temperature extremes do not alter development rates, once temperatures return to the favorable zone. And fourth, development is assumed to be accumulative. We are currently unsure what the effects of violating these assumptions might be.

We have used the model to make predictions on reemergence and emergence in the field. The predictions were generated from laboratory rates and distributions and weather data from Houston International Airport. Predictions were compared to reemergence and emergence from trees infested in the summer of 1978 near Cleveland, Tex., about 60 mi from the airport. Representative results for four trees attacked on the same day will be presented.

Figure 6 shows the model prediction for reemergence and the patterns of reemergence for the four trees. There was substantial variation in reemergence from the four trees, and the model does not do well for two of the four reemergence patterns. It does do well for the other two patterns. Further, the prediction brackets the onset and termination of reemergence for all four trees.

Three model predictions are compared to emergence patterns from the four trees in figure 7. Three predictions were made because of our uncertainty about the relationship between high temperature thresholds in the lab and in the field. For the prediction closest to the y axis, development was allowed to continue up to 35°. Billings and Kibbe (1978) suggested that temperatures above 35° slowed larval development. For the middle prediction, development was allowed to continue up to 33°, the constant temperature threshold for egg development. Development was assumed to stop at 32° in the prediction farthest from the y axis. With a 33° threshold, the model not only bracketed the onset and termination of emergence, but also tracked the emergence patterns well.

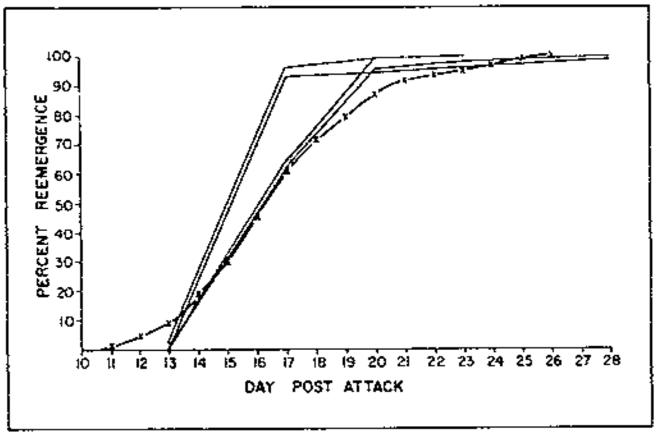


Figure 6.--Predicted (-x-) and actual (-o-) reemergence distributions for naturally infested trees near Cleveland, Tex., 1978. See text for details.

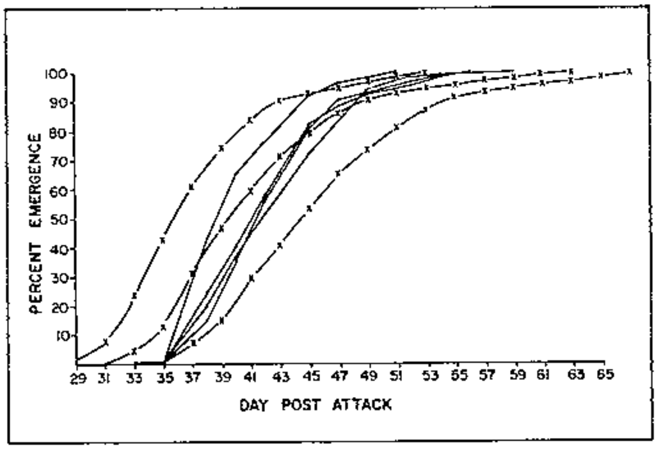


Figure 7.--Predicted (-x-) and actual (-o-) emergence distributions for naturally infested trees near Cleveland, Tex., 1978. See text for details.

CONCLUSIONS

We have gathered a data base on the effects of constant temperature on the rates of southern pine beetle reemergence and emergence. These two processes respond to temperature in patterns similar to those observed for other insects. A model, based on absolute reaction rate theory, can adequately describe the rates of reemergence and emergence as a function of temperature.

There was variability in reemergence and emergence times of insects held in identical conditions. We included this variability by empirically estimating the distributions of reemergence and emergence. The results of this empirical process suggest that there is a standard distribution for reemergence, and one for emergence, and that these standard distributions (shape ratios) are independent of temperature. This result may hold for other processes, environmental factors, or insects.

The rate and distribution models, fitted to laboratory data and driven by field temperatures, predicted reemergence and emergence in the field. These predictions are first approximations that can be refined by using more accurate temperature data and continuing research on threshold temperatures for development and reemergence.

LITERATURE CITED

Barras, S. J. 1970. Antagonism between *Dendroctonus frontalis* and the fungus *Ceratocystis minor*. Ann. Entomol. Soc. Amer. 63:1187-1190.

Beal, J. A. 1933. Temperature extremes as a factor in the ecology of the southern pine beetle. J. For. 31:329-336.

Billings, R. F., and C. A. Kibbe. 1978. Seasonal relationships between southern pine beetle brood development and loblolly pine foliage color in east Texas. Southwest. Entomol. 3:89-95.

Bremer, J. E. 1967. Laboratory studies on the biology and ecology of the southern pine beetle, *Dendroctonus frontalis* Zimm. M.S. thesis. Texas A. & M. University, College Station. 62 p.

Browne, L. E. 1972. An emergence cage and refrigerated collector for wood boring insects and their associates. J. Econ. Entomol. 65:1499.

Clark, E. W., and E. A. Osgood. 1964. Mass rearing the southern pine beetle and the coarse writing engraver. U.S. Dep. Agric. For. Serv., Res. Note SE-30. Southeast. For. Ext. Stn., Asheville, N.C.

Coulson, R. N. 1979. Population dynamics of bark beetles. Ann. Rev. Entomol. 24:417-447.

Coulson, R. N., W. S. Fargo, P. E. Pulley, J. L. Foltz, D. N. Pope, J. V. Richerson, and T. L. Payne. 1978. Evaluation of the reemergence process of parent adult *Dendroctonus frontalis* (Coleoptera:Scolytidae). Canad. Entomol. 110:475-486.

Coulson, R. N., W. S. Fargo, P. E. Pulley, D. N. Pope, J. L. Foltz, and A. M. Bunting. 1979. Spatial and temporal patterns of emergence for within-tree populations of *Dendroctonus frontalis* (Coleoptera:Scolytidae). Canad. Entomol. 111:273-287.

Covington, C. C. 1969. Laboratory rearing of the southern pine beetle, *Dendroctonus frontalis* Zimmermann, with emphasis on the production of virgin females. M.F. thesis. Stephen F. Austin State University, Nacogdoches, Tex. 38 p.

Curry, G. L., R. M. Feldman, and P.J.H. Sharpe. 1978. Foundations of stochastic development. J. Theor. Biol. 74:397-410.

Franklin, R. T. 1970. Southern pine beetle population behavior. J. Ga. Entomol. Soc. 5:175-182.

Fronk, W. D. 1947. The southern pine beetle--its life history. Va. Agric. Exp. Stn., Tech. Bull. 108. Blacksburg, Va.

Gagne, J. A., R. N. Coulson, J. L. Foltz, T. L. Wagner, and L. J. Edson. 1980. Attack and survival of *Dendroctonus frontalis* in relation to weather during 3 years in east Texas. Environ. Entomol. [In press.]

Gaumer, G. C. 1967. Effects of phloem temperature and moisture content on survival of southern pine beetle broods. M.F. thesis. Stephen F. Austin State Univ., Nacogdoches, Tex. 50 p.

Goldman, S. E., and R. T. Franklin. 1977. Development and feeding habits of southern pine beetle larvae. Ann. Entomol. Soc. Amer. 70:54-56.

Hardman, J. M. 1976. Deterministic and stochastic models simulating the growth of insect populations over a range of temperatures under Malthusian conditions. Canad. Entomol. 108:907-924.

Kinn, D. L. 1978. Diel emergence patterns of the southern pine beetle (*Dendroctonus frontalis* Zimm.). J. Ga. Entomol. Soc. 13:80-85.

Kowal, N. E. 1971. A rationale for modelling dynamic ecological systems. *In* Systems analysis and simulation in ecology I. B. C. Patten, ed. p. 123-196. Academic Press, New York.

Logan, J. A., D. J. Wollkind, S. C. Hoyt, and L. K. Tanigoshi. 1976. An analytic model for description of temperature dependent rate phenomena in arthropods. Environ. Entomol. 5:1133-1140.

Mizell, R. F., and T. E. Nebeker. 1978. Estimating the development time of the southern pine beetle *Dendroctonus frontalis* as a function of field temperatures. Environ. Entomol. 7:592-595.

Palmer, H. C., Jr., and J. E. Coster. 1978. Survival of southern pine beetles in felled and standing loblolly pines. J. Ga. Entomol. Soc. 13:1-7.

Rudinsky, J. A. 1962. Ecology of Scolytidae. Ann. Rev. Entomol. 7:327-348.

Sharpe, P.J.H., and D. W. DeMichele. 1977. Reaction kinetics of poikilotherm development. J. Theor. Biol. 64:649-6[illegible]0.

Sharpe, P. J. H., G. L. Curry, D. W. DeMichele, and C. L. Cole. 1977. Distribution model of organism development times. J. Theor. Biol. 66:21-38.

Stinner, R. E., A. P. Gutierrez, and G. D. Butler. 1974. An algorithm for temperature-dependent growth rate simulations. Canad. Entomol. 106: 519-524.

Stinner, R. E., G. D. Butler, Jr., J. S. Bacheler, and C. Tuttle. 1974. Simulation of temperature-dependent development in population dynamics models. Canad. Entomol. 107:1167-1174.

Thatcher, R. C. 1967. Winter brood development of the southern pine beetle in southeast Texas. J. Econ. Entomol. 60:599-600.

Thatcher, R. C., and L. S. Pickard. 1964. Seasonal variations in activity of the southern pine beetle in east Texas. J. Econ. Entomol. 57:840-842.

Thatcher, R. C., and L. S. Pickard. 1967. Seasonal development of the southern pine beetle in east Texas. J. Econ. Entomol. 60:656-658.

Wagner, T. L., R. M. Feldman, J. A. Gagne, and R. N. Coulson. 1980. Models describing gallery construction and oviposition by *Dendroctonus frontalis*. *In* Modeling of southern pine beetle populations: symposium proc. [Asheville, N.C., Feb. 1980.] F. M. Stephen and J. L. Searcy, eds. U.S. Dep. Agric. For. Serv., Tech. Bull.1630. Comb. For. Pest Res. Develop. Prog., Pineville, La.

Waters, W. C., and R. W. Stark. 1980. Forest pest management: concept and reality. Ann. Rev. Entomol. 25:479-509.

Watt, K.E.F. 1968. Ecology and resource management, a quantitative approach. 450 p. McGraw-Hill Book Co., New York.

White, R. A., Jr., and R. T. Franklin. 1976. Activity of southern pine beetle in response to temperature. J. Ga. Entomol. Soc. 11:370-372.

Wigglesworth, V. B. 1972. The principles of insect physiology. 7th ed. 827 p. Chapman and Hall, London.

ACKNOWLEDGMENTS

The work reported herein was supported in part by the National Science Foundation (NSF GB 34718) and the U.S. Department of Agriculture as part of the Expanded Southern Pine Beetle Research and Applications Program (CSRS 6163). Also, we thank Mr. John Wiley and Mr. Mark Hafernik of Champion Timberlands for their cooperation. The findings and opinions expressed herein are those of the authors and not necessarily those of the sponsoring agencies.

MODELS DESCRIBING GALLERY CONSTRUCTION AND OVIPOSTION BY *DENDROCTONUS FRONTALIS*[1]

Terence L. Wagner, Richard M. Feldman,
James A. Gagne, and Robert N. Coulson[2]

Abstract.--Models were developed that described the combined effects of constant temperature, density (pairs per dm^2), female size (weight times width), and type (month of emergence) on (1) total gallery and eggs per mating pair, and (2) cumulative proportion of total gallery and eggs through time for *Dendroctonus frontalis* Zimmermann. The models were consolidated to describe time-dependent gallery and eggs per mating pair. Variables influencing gallery construction and oviposition interacted in such a way that the effects of single variables could not be described independently. This result probably has far-reaching implications for modeling reproduction of insect species.

Models for total gallery and eggs fitted 39 of 41 experimental means within a 95 percent confidence interval. The model for total gallery adequately described field data, but prediction of total eggs underestimated egg niche counts from the field. Weibull and gamma functions provided good fits to cumulative proportional gallery and eggs through time, respectively. Model predictions of cumulative proportional gallery were similar for Weibull functions developed from field and laboratory data.

INTRODUCTION

Research conducted at Texas A. & M. University on population dynamics of *Dendroctonus frontalis* Zimmermann has concentrated on describing within-tree, between-tree, and within-stand population processes (Coulson 1979). Information from this research has been incorporated into a model describing infestation growth (Feldman et al. 1980).

Many components of the life system of the southern pine beetle have already been thoroughly studied, but reproduction is one important component that has not. Yet models describing population growth require information on the insect's reproductive response to different conditions.

Many variables influence reproduction in bark beetles (Berryman 1974). For the SPB, temperature (Bremer 1967, Palmer and Coster 1978), attack density (Coulson et al. 1976), female size, and phloem moisture (Clarke et al. 1979) have all been shown to influence reproduction. Nebeker et al. (1978) presented evidence also suggesting an effect of phloem thickness, and MacAndrews (1926) observed an effect of resin on gallery construction. To date, the simultaneous effects of these variables have not been examined.

Here we present models which describe the combined effects of constant temperature, density (mating pairs per dm^2), female size (oven dry weight times pronotal width), and type (month of adult emergence) on (1) total gallery and eggs, and (2) daily cumulative proportion of total gallery and eggs for the SPB. Consolidation of the above models described time-dependent gallery construction and oviposition per mating pair. These models answered the question "How much gallery and how many eggs will individual mating pairs produce in a certain amount of time under different conditions?"

EXPERIMENTAL MATERIALS AND METHODS

The following techniques permitted nondestructive daily observations on many mating pairs.

A straight loblolly pine (*Pinus taeda* L.), 25 to 30 cm d.b.h., was felled and cut into 60-cm bolts. All trees except one used at 10° C were taken from the same 0.5-ha plot. Bolts were cut into 7.5 × 11.0 × 1.5-cm bark slabs the day of felling (fig. 1). A lead identifying label was tacked on each of 27 slabs, and the xylem surface was coated with 1-percent aqueous $HgCl_2$

---

[1] This paper is TAES 15840.

[2] The authors are, respectively, Postdoctoral Fellow, Dept. of Entomology; Associate Professor, Dept. of Industrial Engineering, Biosystems Research Division; Graduate Research Assistant and Professor, Dept. of Entomology, Texas A. & M. University, College Station.

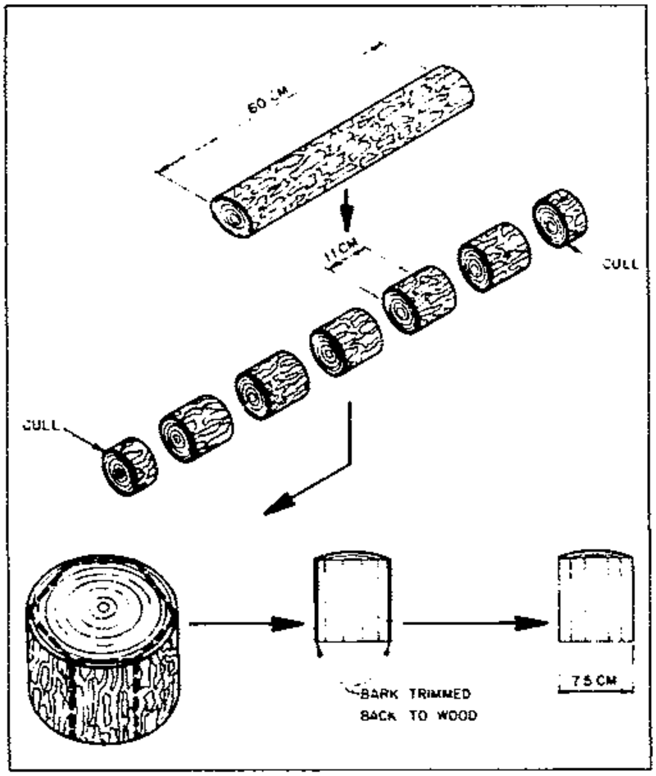


Figure 1.--A diagram showing the steps needed to make bark slabs from pine bolts.

solution (Barras 1972). Slabs were held on moist paper towels in sealed containers at 5° C until the next day, after which beetles were introduced.

Newly emerged *D. frontalis* adults were collected from naturally infested bark and introduced onto slabs as follows. Circular holes were cut into the bark with a #4 cork borer. A 1-mm diameter hole was drilled within each cork borer hole to give beetles access to the phloem. Gelatin capsules containing one female each were fitted into the cork-borer holes. Females not tunnelling after 19 hours were counted and discarded. Males were then introduced using gel caps. Males not tunnelling after 5 hours were counted and discarded, and radiographs were taken (Coulson et al. 1975). Radiographs were taken every 24 hours thereafter, and reemerged adults were collected, sexed, and counted.

During the experiment, slabs were held at a constant temperature in one of two plastic boxes, 29.0 × 25.4 × 15.0 cm. The upper box contained the 27 slabs that were held upright and separated by plastic dividers. Temperature was monitored hourly. The lower box contained an air pump and an open dish of H_2SO_4 solution prepared to maintain 75 percent relative humidity (Solomon 1951). Air moved between the boxes in 3-mm tubing.

After all beetles had reemerged, slabs were boiled in tapwater to loosen the phloem from the xylem. A knife was carefully worked between these tissues to remove the bark and phloem intact. Egg niches were exposed under a dissecting scope by slicing away thin sections of phloem with a scalpel. Daily gallery was identified on radiographs, and marked and measured to the nearest millimeter on slabs, permitting reconstruction of the ovipositional pattern.

These procedures were used to conduct nine experiments during a 12-month period from February 1978. Table 1 presents pertinent information related to each experiment. In all, 1,242 pairs were introduced, of which 73 percent initiated gallery and had an opportunity to mate. These pairs were considered successful whether they laid eggs or not. Occasionally beetles left the slabs on which they were introduced and initiated galleries the same day on other slabs. These pairs were also considered successful.

TOTAL GALLERY AND EGGS

Four factors influenced total gallery and eggs per mating pair: temperature *t*, female size *s* and type *i*, and density *d*. Size was calculated as the oven dry weight (mg) times pronotal width (mm); type was 1 for females emerging in February and 0 for those emerging at other times of the year; and density was the number of mating pairs per slab adjusted to a per-dm^2 basis. In the mathematical descriptions that follow, a subscript of 1 refers to gallery construction and 2 refers to oviposition.

Total gallery per mating pair, T_G, was

$$T_G = \begin{cases} f_1(t)h_1(s, i) & \text{for } T_G < 20/d, \text{ and} \\ (20/d) + [f_1(t)h_1(s, i) - 20/d]g_1(d, Z_1) & \text{for } T_G \geq 20/d \end{cases} \tag{1}$$

where $Z_1 = f_1(t)h_1(s, i)$ and f_1, h_1, and g_1 represented the temperature, size-type, and density functions, respectively. The amount of gallery produced under certain temperature and size-type conditions was small. Density effects could not be detected under these conditions; therefore, equation (1) has two functional forms. The term $g_1(d, Z_1)$ gave the reduction in total gallery due to density. The interactive term Z_1 in g_1 indicates that as temperature and size-type became more favorable to gallery construction, the effects of density increased. Thus

Table 1.--Pertinent information related to nine laboratory experiments on gallery construction and oviposition of D. frontalis

Exp. #	Month of emergence	Female size (wt × width)	Temp. (°C)	Starting densities (prs/slab)	Total mating. prs. intro.	Success intro. (%)
E-1	Sept.	0.873	10	4	108	58.3
E-2	Feb.	1.202	15	4	108	63.9
E-3	Feb.	1.378	20	4	108	82.4
E-4	Feb.	1.343	20	6	162	61.7
E-5	June	1.057	20	1 & 6	189	82.0
E-6	Feb.	1.387	25	6	162	69.8
E-7	June	1.254	25	1 & 6	189	85.2
E-8	May	0.877	25	4	108	87.0
E-9	May	0.909	30	4	108	57.4
					Total = 1242	$\bar{x}$ = 72.9

the function T_G was not separable, implying that the total effects of temperature, size-type, or density could not be expressed solely as a function of one variable. The function g_1 was such that $g_1(0, Z_1) = 1$.

Total oviposition per female, T_E, was

$$T_E = f_2(t)h_2(s, i)g_2(d, Z_1) \qquad (2)$$

where $g_2(0, Z_1) = 1$. Note that gallery construction influenced oviposition through the variable Z_1 in g_2, indicating a dependency of oviposition on gallery construction.

Functions describing the effects of temperature, size-type, and density on mean total gallery and eggs per mating pair were chosen and parameter values were fitted as follows. Total gallery and eggs in one bark slab were considered independent of that found in other slabs. At least two slabs held at a fixed temperature, size-type, and density allowed the establishment of confidence intervals (CI) around the experimental mean. Parameter values for each function in equations (1) and (2) were selected by maximizing the number of predicted values within a 95 percent CI. Adjustments of the parameter values were made so that the deviations between the model values and the corresponding experimental means were minimal. The final functions T_G and T_E fitted 39 of 41 mean values within the 95 percent CI.

Because of the interacting effects of temperature, size-type, and density, the effects of single factors could not be described independently. The effects of each factor were therefore described by examining a range of cases with regard to the other factors.

Effects of Constant Temperature

D. frontalis produced more gallery per mating pair at 15° C than at other temperatures, while least gallery was produced at 30° C. Gallery lengths were similar at 10°, 20°, and 25° C. The unimodel response to temperature was described by a discrete function, f_1 from equation (1), given as

t	10°	15°	20°	25°	30°	
$f_1(t)$	9.5	16.1	9.6	8.8	5.9	(3)

A discrete function was used because the exact temperature of maximum gallery production was undefined.

More eggs were deposited at 15° C than at other temperatures, but unlike the phenomenon observed for gallery production, fewest eggs occurred at 10° C. The temperature function for total eggs, f_2 from equation (2), was

t	10°	15°	20°	25°	30°	
$f_2(t)$	9.2	28.6	19.0	16.2	8.3	(4)

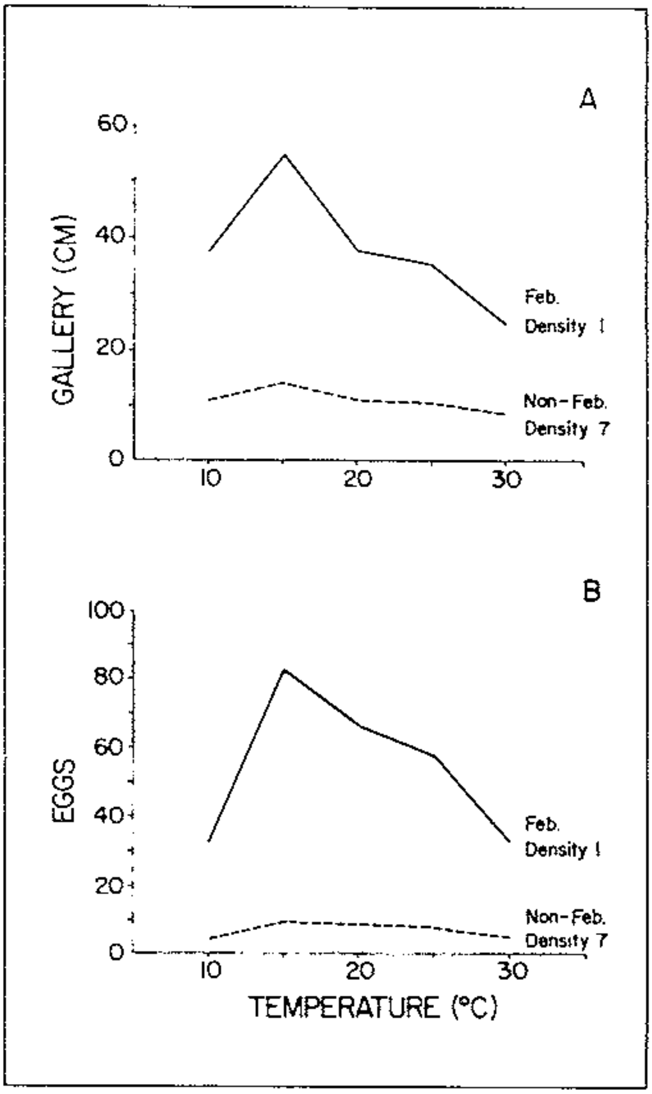


Figure 2.--Prediction of total (A) gallery and (B) eggs per mating pair from equations (1) and (2), respectively, at different constant temperatures. Solid and dashed lines represent production by females of sizes 1.387 and 0.873, respectively.

Figures 2A and B illustrate the effects of temperature on total gallery and eggs per mating pair, respectively, at two extremes in reproductive capacity. By examining equation (4), one might believe that fewer eggs were deposited at 30° than at 10° C, while in fact just the opposite was found, as shown in figure 2B. This apparent inconsistency was due to the interaction of gallery construction on oviposition through the term Z_1 in g_2. More gallery per mating pair was produced at 10° than at 30° C (fig. 2A), indicating that the density and temperature functions in equation (2) interacted in such a way that fewer total eggs were predicted at 10° than at 30° C.

Effects of Female Size-Type

Beetles emerging in February produced more gallery and deposited more eggs than beetles emerging at other times of the year. We examined data on female size and phloem thickness in an effort to provide an explanation for these relationships.

Females emerging in February were large (table 1), a fact that may explain their greater reproductive capacity. At 25° C, the females emerging in June of experiment 7 (E-7) were also large, but they produced less total gallery and eggs than February beetles (E-6). More gallery and eggs were found for E-7 than E-8 beetles, implicating size as important, but not the only factor affecting reproductive capacity. We continued by examining phloem thickness but found no relationship with reproductive capacity. Although we were unable to identify all the agents responsible for the seasonal variation in gallery construction and oviposition, we were able to quantify their combined effects.

A linear function described the effects of female size on total gallery and eggs per mating pair, with larger beetles having greater reproductive capacity. The reproductive capacity of February beetles (type i = 1) was greater than non-February beetles (type i = 0). The size-type function for total gallery, h_1 from equation (1), was

$$h_1(s, i) = 1.58s + 1.5i + 0.4 \qquad (5)$$
$$\text{for } 0.87 \leq s \leq 1.4 \text{ and } i=0, 1$$

The size-type function for total eggs, h_2 from equation (2), was

$$h_2(s, i) = 1.58s + 2.4i - 0.47 \qquad (6)$$
$$\text{for } 0.87 \leq s \leq 1.4 \text{ and } i=0, 1.$$

Figures 3A and B illustrate the effects of female size-type on total gallery and eggs per mating pair, respectively, for extremes in reproductive capacity. We were unable to detect any difference in the effect of size on total gallery *v.* eggs; thus, the predicted slopes for the size component of equations (5) and (6) were the same. We did detect a difference in the effect of type on total gallery *v.* eggs, such that eggs were influenced more strongly by type than gallery. The effects of both size and type were greater for conditions favoring gallery and egg production, e.g., at 15° C and density 1 (figs. 3A and B).

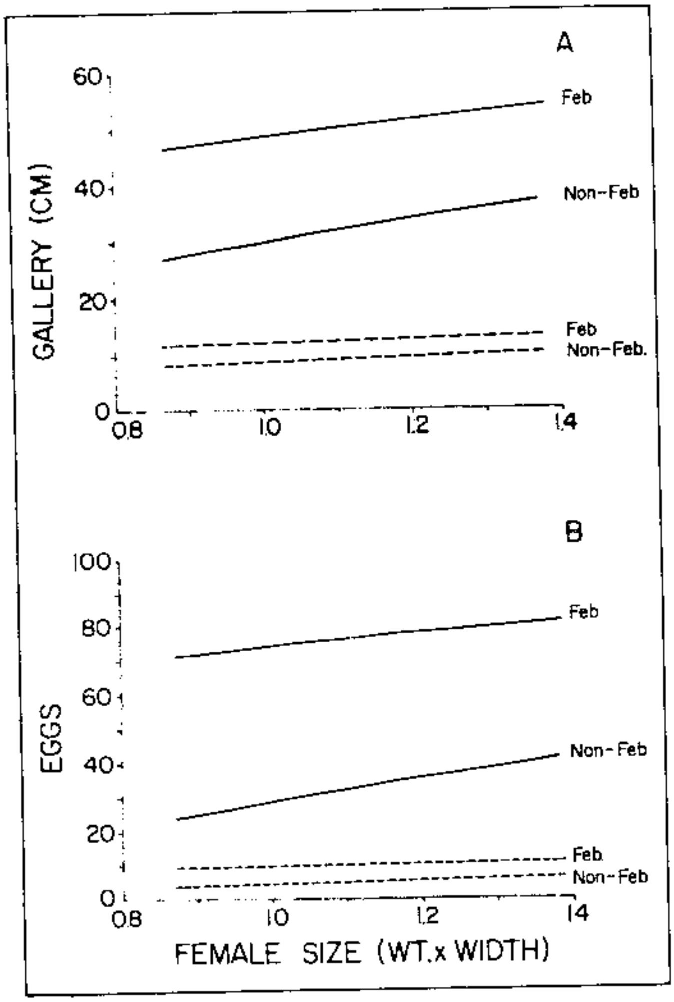


Figure 3.--Prediction of total (A) gallery and (B) eggs per mating pair from equations (1) and (2), respectively, for females of different sizes and types. Solid lines represent production at 15° C and density 1, while dashed lines represent 30° C (gallery) and 10° C (eggs) and density 7.

Effects of Density

Coulson et al. (1976) first proposed resource utilization for the southern pine beetle based on field data from east Texas. They found that gallery construction per beetle pair decreased exponentially with increasing pairs per unit area of phloem. From this relationship they hypothesized the same effect on eggs using the 1.59 eggs per centimeter gallery length constant described by Foltz et al. (1976). We hoped to confirm their results, and at the same time expand our understanding of the beetle's response to density. As it turned out, the beetle's response to density was more complex than its response to temperature, size, or type. The following biological information was used to develop the density function.

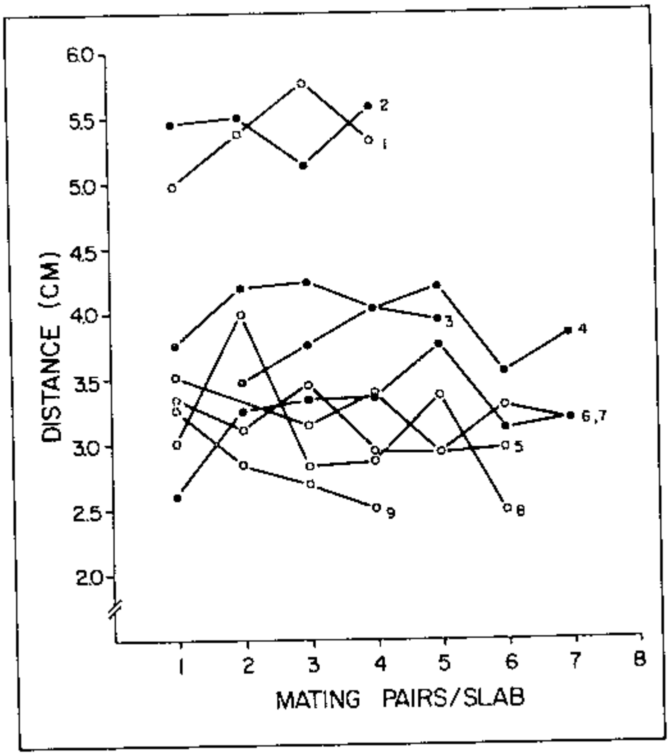


Figure 4.--The mean distance from the gallery origin to the first egg at different densities per slab for each of nine experiments. Closed and open circles represent February and non-February beetles, respectively.

During gallery construction females avoided other galleries as much as possible. As more phloem was utilized, however, avoidance became difficult and galleries occasionally intersected. This behavior results in the characteristic serpentine gallery pattern of the beetle.

This information suggested that the first part of the gallery should be free from density effects, since initially beetles will not compete for phloem resource. To test this hypothesis, we examined the mean distance from the gallery origin to the first egg (fig. 4). The trend across densities was erratic, indicating that this distance was not strongly affected by density.

We also observed that the effects of density were not the same under all conditions of temperature and female size-type. The effects of density were greatest for conditions favoring gallery construction, and least for conditions limiting gallery construction, e.g., at 15° C for February beetles and at 30° C for non-February beetles, respectively.

With this information we developed a function describing the effects of density on total gallery and eggs per mating pair. The general exponential

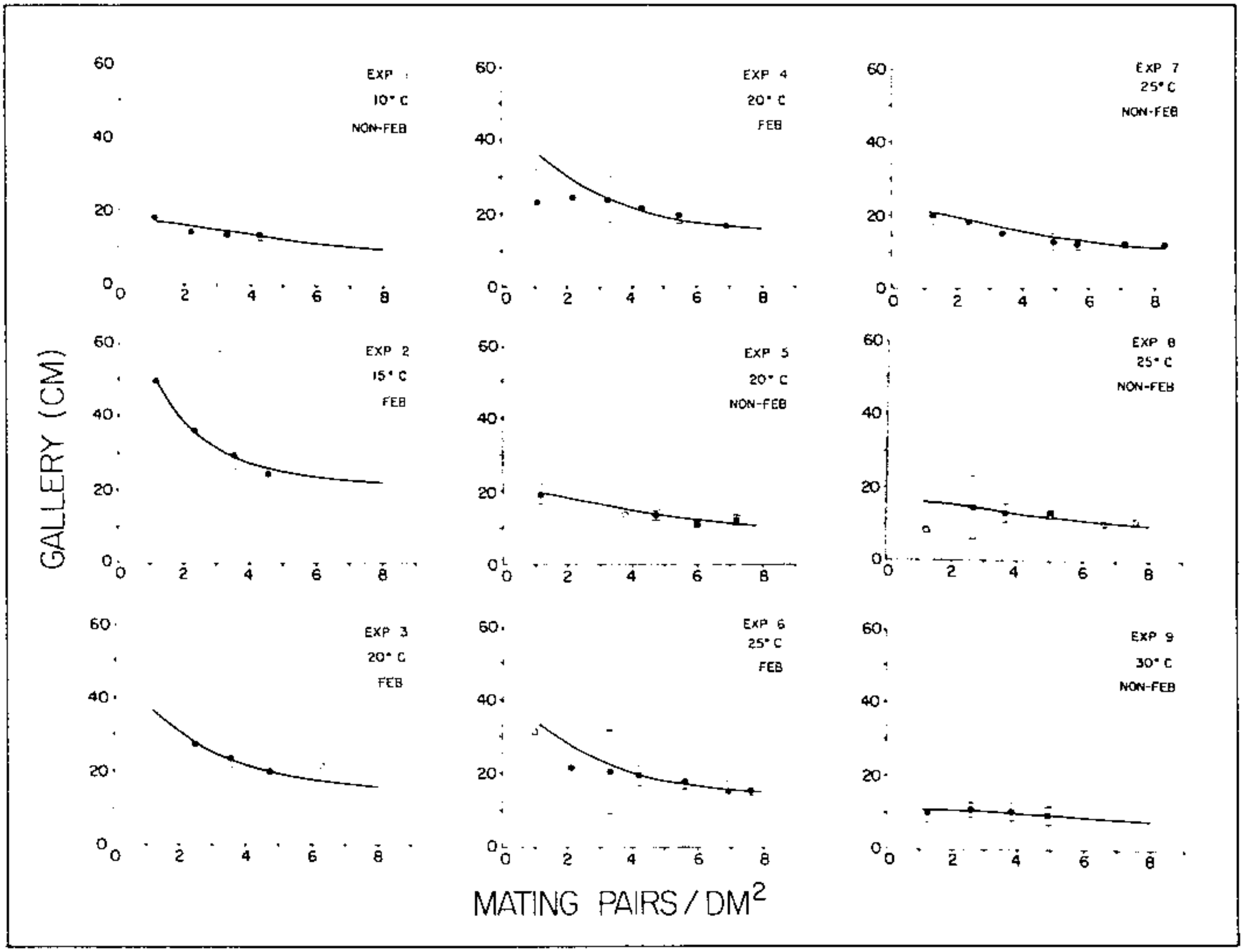


Figure 5.--Prediction of total gallery per mating pair from equation (1) at different densities for each of nine experiments. Closed circles represent observed gallery per pair ($\bar{x}$ ± 95 percent CI). Open circles represent mean gallery for densities having only one slab.

function proposed by Coulson et al. (1976) was modifed as follows: (1) The first 20 cm of gallery per dm^2 were excluded from exponential decay, i.e., this section of gallery was held free of density effects. (2) The slope of the decay curve was steeper for conditions favoring gallery construction, such as at 15° C and February beetles, while the slope was flatter for conditions suppressing gallery construction, such as at the temperature extremes and non-February beetles. (3) The decay curve had an asymptote above zero.

The density function for total gallery, g_1 from equation (1), was

$$g_1(d, Z_1) = \begin{cases} 1.0 & \text{for } dZ_1 < 20, \text{ and} \\ 0.33 + 0.67\exp\{-0.011(dZ_1-20)\} & \text{for } dZ_1 \geq 20, \end{cases} \quad (7)$$

where $Z_1 = f_1(t)h_1(s, i)$.

The density function for total eggs, g_2 from equation (2), was

$$g_2(d, Z_1) = \begin{cases} 1.0 & \text{for } dZ_1 < 20, \text{ and} \\ 0.25 + 0.75\exp\{-0.011(dZ_1-20)\} & \text{for } dZ_1 \geq 20. \end{cases} \quad (8)$$

It can be seen by solving equations (7) and (8) that density had a greater effect on eggs than gallery. Eggs were affected more than gallery because the proportion of egg-bearing to total gallery decreased with increasing density.

Evaluation of Models For Total Gallery and Eggs

Models describing total gallery and eggs were evaluated by (1) comparing predicted values from equations (1) and (2) with observed values, and (2) comparing predicted values with data col-

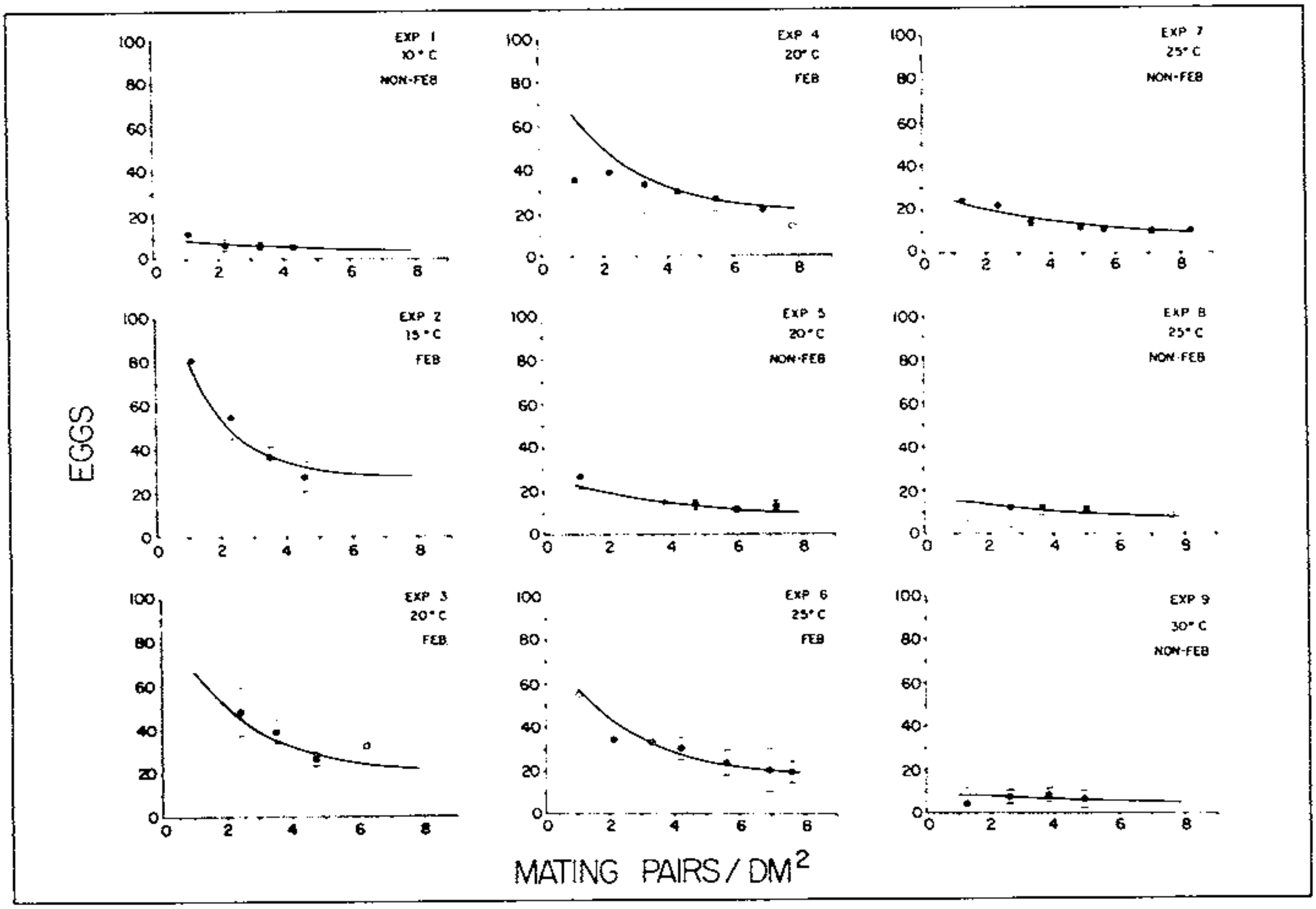


Figure 6.--Prediction of total eggs per female from equation (2) at different densities for each of nine experiments. Closed circles represent observed eggs per female ($\bar{x}$ ± 95 percent CI). Open circles represent mean eggs for densities having only one slab.

lected in the field. Figures 5 and 6 show how well the models fitted the experimental data. Note that each model fitted 39 of 41 mean values within a 95 percent CI. These figures also illustrate the three modifications of the Coulson et al. (1976) decay function mentioned in the preceding section.

Further evaluation of equation (1) was accomplished by determining peak gallery length and number of beetles per dm^2 for each of 113 trees sampled in east Texas between 1972 and 1974. Gallery lengths were classed and averaged by density to the nearest beetle per dm^2, and compared with model values (fig. 7). These comparisons show that gallery lengths per pair were similar at all densities except those below two pairs per dm^2. At these low densities, predicted values underestimated the field data.

The same procedures were used to evaluate equation (2) for total eggs; however, less field data on actual egg niche counts were available. Data from 15 trees sampled in east Texas during 1973 and 1977 were classed and averaged as before, and compared to model predictions (fig. 8). Clearly, the model did not do as well for eggs as for gallery, especially at the lower densities.

Confining beetles within a fixed area of phloem will limit total gallery and eggs per mating pair. The outcome of this confinement will be most evident at the lower densities, as seen in figures 7 and 8. As beetles constructed gallery, they avoided the edges of slabs; thus the edges acted as a density-limiting factor. Proportionally, the number of times beetles contacted the edges, compared to the number of times they contacted other galleries, was probably greater at the low densities than high densities. Consequently, the effect of the edges on reducing total gallery and eggs would be greater at the lower densities. Further-

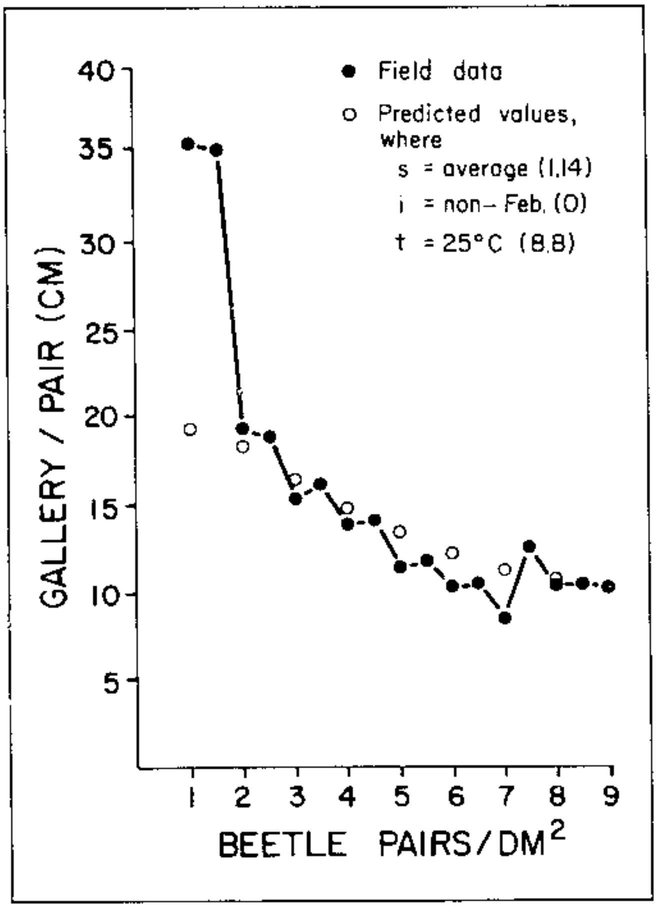


Figure 7.--Prediction of total gallery per pair from equation (1) at different densities (open circles), compared to classed and averaged gallery from 113 trees sampled in east Texas during 1972-1974 (closed circles).

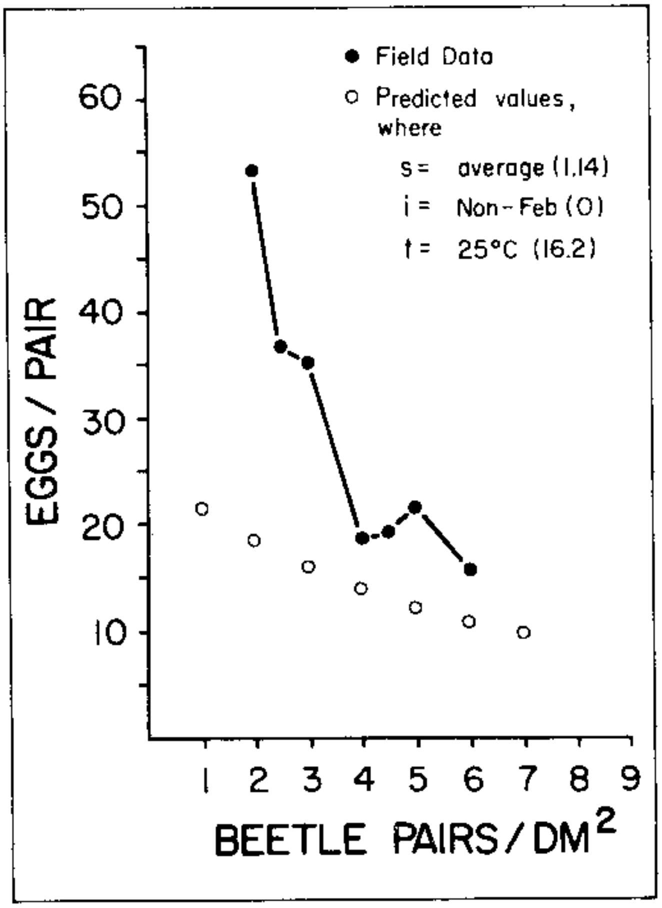


Figure 8.--Prediction of total eggs per pair from equation (2) at different densities (open circles), compared to classed and averaged egg niche counts from 15 trees sampled in east Texas during 1973 and 1977 (closed circles).

more, the initial and terminal egg-free sections of gallery were not affected by density. Thus, the slab edges had a stronger limiting influence on eggs than gallery.

DAILY CUMULATIVE PROPORTION OF GALLERY AND EGGS

Functions were developed to describe the cumulative proportion of total gallery and eggs through time. These functions were called profiles and were similar to cumulative distribution functions. Although size had no apparent effect on the profiles, temperature, density, and type did. For a fixed type, the influence of temperature and density on daily fractional reproduction was described by a single profile using normalizing constants to adjust the time scale (*x* axis). Greater details of these analytical procedures were given by Curry, Feldman, and Sharpe (1978, p. 405) and Curry, Feldman, and Smith (1978, Section 5).

The normalized gallery profile for a type i female was denoted by $p_1(i, \cdot)$, where $p_1(i, y)$ was the cumulative fractional gallery up to normalized time y. For a given temperature and density, chronological time x was transformed to normalized time y by multiplying the chronological time by normalizing constants, thus

$$y_1 = x\hat{r}_1(t)\tilde{r}_1(i, d) \qquad (9)$$

where $\hat{r}_1$ and $\tilde{r}_1$ were the temperature- and density-normalizing functions, respectively.

Separate functions p_2, $\hat{r}_2$, and $\tilde{r}_2$ were likewise formulated for the ovipositional process, so that

$$y_2 = x\hat{r}_2(t)\tilde{r}_2(i, d) \qquad (10)$$

Effects of Constant Temperatures

Cumulative gallery profiles for different temperatures but similar densities were superimposed by adjusting their time scales (*x* axis). The constants used to normalize the profiles increased with increasing temperature from 10° to 25° C, but thereafter decreased slightly to 30° C. This relationship was described by the discrete function $\hat{r}_1$ from equation (9), where

t	10°	15°	20°	25°	30°
$\hat{r}_1(t)$	0.313	0.532	1.00	1.342	1.305

(11)

The 20° C constant was set as the standard, i.e., 1.0, thereby allowing easy assessment of the relative effects of temperature on process time. It should be noted that the normalizing constants were obtained by visually alining entire profiles using an interactive graphics program. Consequently, the proportional relationship of the constants is similar to, but not exactly the same as, the proportional relationship of the average duration of the process.

Using the normalizing procedure, we determined that temperature did not dramatically influence the shape of the gallery profiles, except at 10° C. Relative to the profiles at other temperatures, those at 10° C were steeper at the beginning of the normalized process, and flatter at the end. This result was most pronounced at four mating pairs per dm^2.

The constants used to normalize the cumulative oviposition profiles also increased with increasing temperature from 10° to 25° C but remained the same at 30° C. This relationship was described by $\hat{r}_2$ from equation (10), as

t	10°	15°	20°	25°	30°
$\hat{r}_2(t)$	0.365	0.559	1.00	1.508	1.508

(12)

Cumulative oviposition profiles for different temperatures but similar densities were alike when normalized using these constants. That is, temperature did not influence the shape of the normalized curves.

Effects of Density

Density influenced process time and thus the constants used to normalize the cumulative gallery profiles. However, unlike what we observed for temperature, single profiles could not be obtained for both types. That is, beetles emerging in February (i = 1) responded differently than those emerging at other times (i = 0). This relationship was described by the function $\tilde{r}_1$ from equation (9), given as

d	1	2	3	4	5	6	7
$\tilde{r}_1(1, d)$	0.800	0.833	0.935	1.00	1.053	1.176	1.250

(13)

for February beetles, and

d	1	2	3	4	5	6	7
$\tilde{r}_1(0, d)$	0.926	0.952	1.00	1.00	1.031	1.031	1.031

(14)

for non-February beetles. These constants indicate that process time took ca. 36 percent longer at the lowest density compared to the highest density for beetles emerging in February, but only ca. 10 percent longer for non-February beetles.

Density also influenced process time for the cumulative oviposition profiles, but to a greater degree than observed for gallery. The normalizing constants given by the function $\tilde{r}_2$ from equation (10) were

d	1	2	3	4	5	6	7
$\tilde{r}_2(1, d)$	0.741	0.833	0.980	1.00	1.111	1.212	1.299

(15)

for February beetles, and

d	1	2	3	4	5	6	7
$\tilde{r}_2(0, d)$	0.870	0.909	0.980	1.00	1.053	1.111	1.176

(16)

for non-February beetles. Based on the normalizing constants, process times for beetles emerging in February were ca. 43 percent longer at density 1 than at density 7. For non-February beetles, a similar change in density increased the process time by 26 percent.

Effects of Female Size-Type

There was no discernible difference in the cumulative gallery profiles produced by females of different sizes. That is, size alone had no apparent effect on the timing or shape of the profiles. However, gallery profiles were different for each type, such that a single profile could not be obtained for both. After removing the effects of temperature and density on the profiles using equation (9), only a cumulative distribution function describing the normalized profile for each type was needed to determine time-dependent gallery construction. A

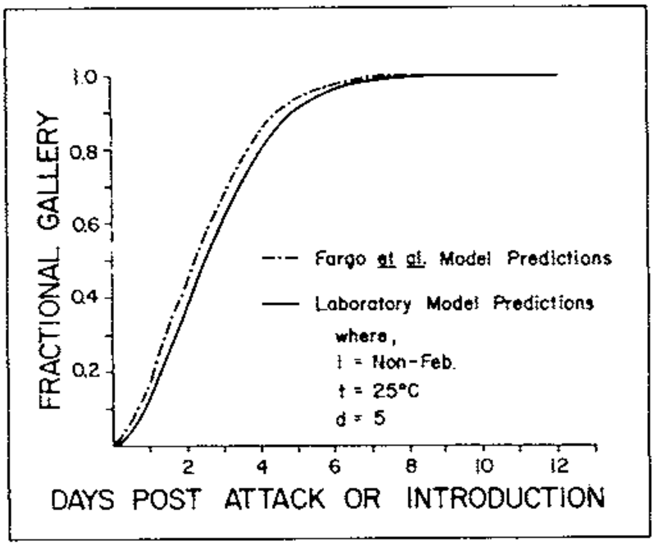


Figure 9.--A comparison of predicted cumulative gallery curves from two independent Weibull functions. The solid line represents the profile given by equation (18), while the dashed line represents the profile given by Y = 1-exp{-15.04x1.65} from Fargo et al. (1978) for field data. Average daily temperature during the field study was 26.8° C (determined from a nearby weather station), and average attack density was 9 beetles/dm^2.

Weibull function provided a good description of the normalized gallery profiles, with equations for February (i = 1) and non-February (i = 0) beetles, respectively, given as

$$p_1(1,\ y) = 1\text{-}\exp\{-(y/5.19)^{1.6}\} \text{ for } y > 0. \qquad (17)$$

and

$$p_1(0,\ y) = 1\text{-}\exp\{-(y/4.27)^{1.8}\} \text{ for } y > 0. \qquad (18)$$

Fargo et al. (1978) also used a Weibull function to describe cumulative gallery per dm^2 occurring in six trees in east Texas during the summer of 1975. We used their Weibull function to evaluate equation (18) by comparing the predicted curves for each function, as given in figure 9. This figure shows the similarity of the two profiles and indicates that the model developed from laboratory data provides a good description of proportional cumulative gallery observed in the field.

Like gallery, size had no apparent effect on the cumulative oviposition profiles, but type did. A gamma function provided a good description of the oviposition profiles, such that the equations for February and non-February beetles, respectively, were

$$p_2(1,\ y) = 0.034\int_0^y x^{4.2}\exp\{-x/0.98\}dx \text{ for } y>0, \qquad (19)$$

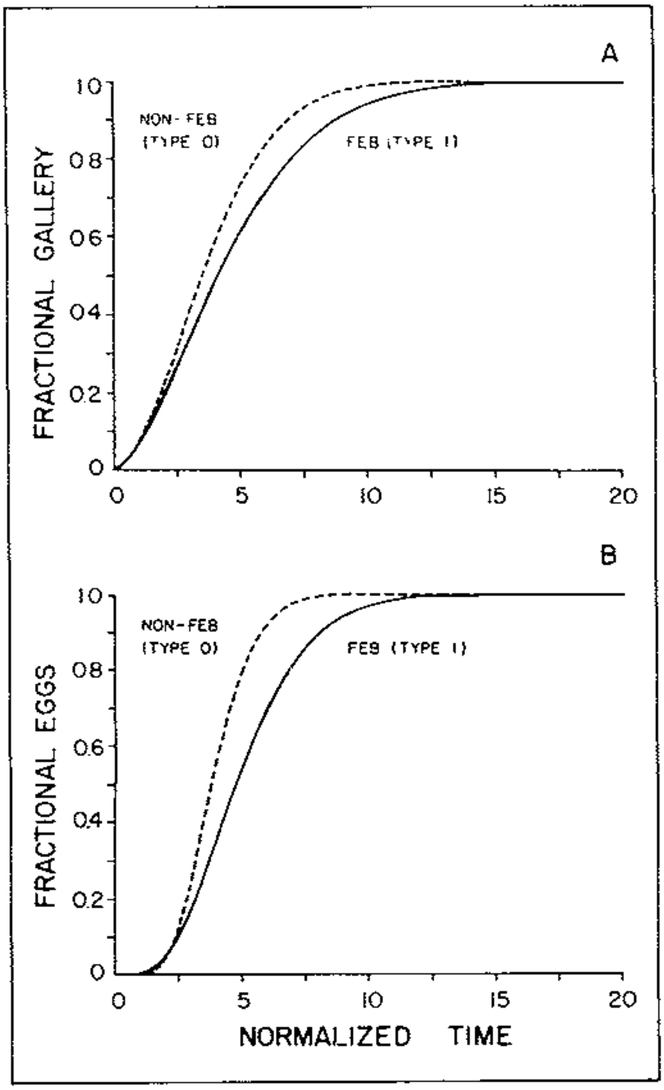


Figure 10.--The normalized (A) gallery and (B) egg profiles for February and non-February beetles.

and

$$p_2(0,\ y) = 0.04\int_0^y x^8\exp\{-x/0.44\}dx \text{ for } y>0. \qquad (20)$$

The normalized profiles described by equations (17) to (20) were flatter for February than non-February beetles (figs. 10A and B).

TIME-DEPENDENT PRODUCTION OF GALLERY AND EGGS

Consolidation of the models developed in the preceding sections allowed us to predict time-dependent gallery construction and oviposition under a range of conditions. These models were developed as follows.

Cumulative gallery produced in the first x days, G(x), for a type *i* female

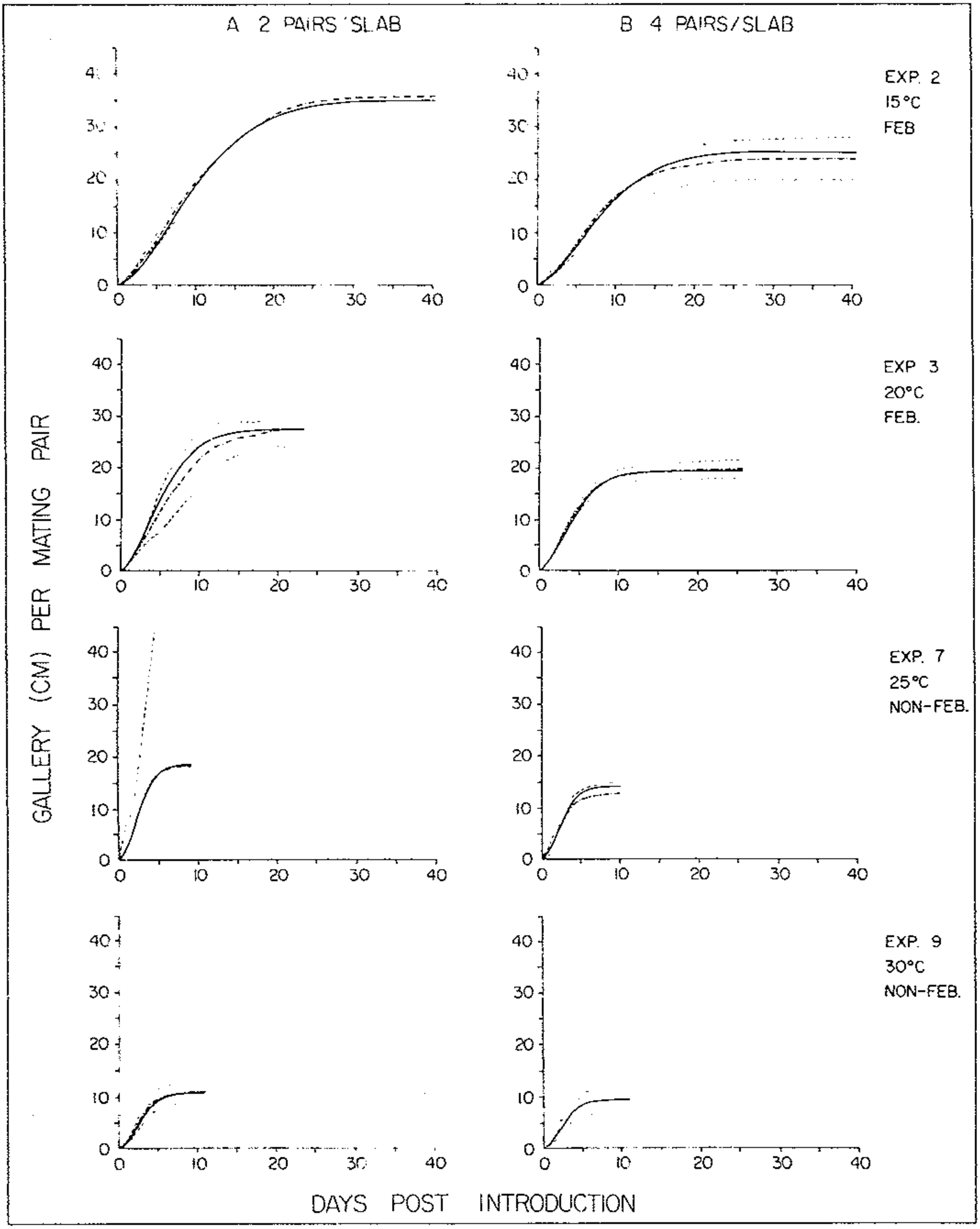


Figure 11.--Daily cumulative gallery per mating pair for February and non-February beetles held under different temperatures and densities. Dashed lines represent observed oviposition (± 95 percent CI), and solid lines represent predicted oviposition from equation (22).

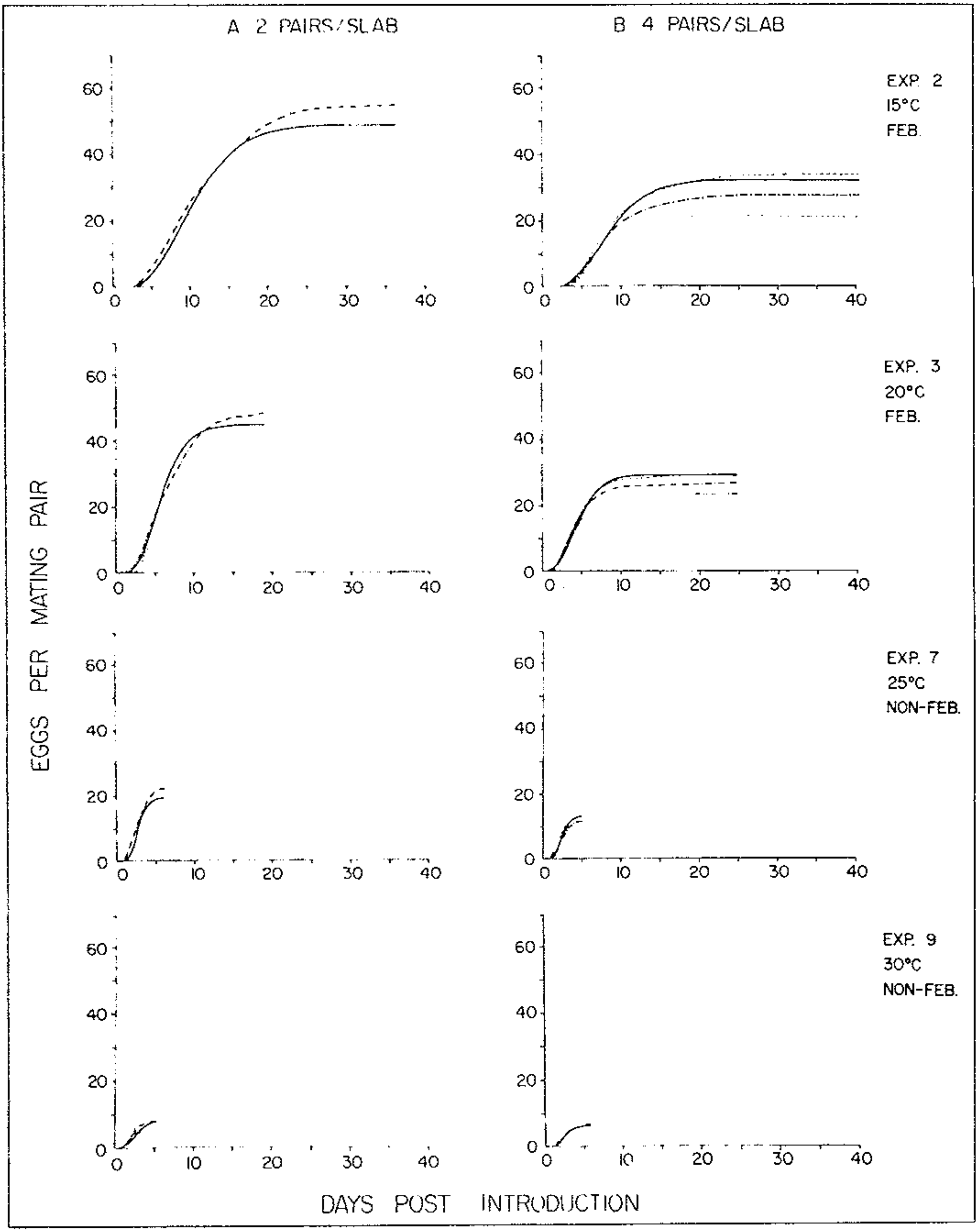


Figure 12.--Daily cumulative oviposition per mating pair for February and non-February beetles held under different temperatures and densities. Dashed lines represent observed oviposition (± 95 percent CI), and solid lines represent predicted oviposition from equation (22).

held at a constant temperature and density was

$$G(x) = T_G p_1(i, y_1) \qquad (21)$$

where T_G was total gallery per mating pair from equation (1), y_1 was normalized time corresponding to chronological time *x* from equation (9), and $p_1(i, y_1)$ was the normalized gallery profile for a type *i* female from equations (17) and (18).

In a similar manner, cumulative eggs deposited in the first *x* days, E(x), for type *i* female held at a constant temperature and density was

$$E(x) = T_E p_2(i, y_2) \qquad (22)$$

where T_E was total eggs per female from equation (2), y_2 was normalized time corresponding to chronological time *x* from equation (10), and $p_2(i, y_2)$ was the normalized oviposition profile for a type *i* female from equations (19) and (20).

Figures 11 and 12 illustrate how well equations (21) and (22) described daily cumulative gallery construction and oviposition, respectively.

CONCLUSIONS

Our results, interpreted in the context of information on population dynamics, suggest different seasonal reproductive strategies by the southern pine beetle. During winter months population numbers are low. Population centers are found in isolated trees scattered throughout the forest. During late winter and early spring, the reproductive contribution of individual females is important because few adults are present. At this time, conditions of temperature, density, size, and type all favor reproduction. Females remain active for greater periods of time, and deposit more of their total complement of eggs in single hosts. It is advantageous to stay in one host because unpredictable weather limits attacks on new hosts.

Infestations begin to grow as weather conditions become more favorable during the spring. Newly attacked trees are colonized rapidly by more adults in the population. Thereafter, a continuous supply of adults is needed for infestation growth, since beetles must overcome healthy trees by mass attack to permit successful brood development. At midyear, when adults are abundant, the reproductive contribution of individual females in single hosts is less important, whereas attacks on new hosts are more important. Laboratory data suggest that females spend less time, and deposit fewer eggs, in single trees at this time of the year.

LITERATURE CITED

Barras, S. J. 1972. Improved White's solution for surface sterilization of pupae of *Dendroctonus frontalis*. J. Econ. Entomol. 65:1504.

Berryman, A. A. 1974. Dynamics of bark beetle populations: towards a general productivity model. Environ. Entomol. 2:579-585.

Bremer, J. E. 1967. Laboratory studies on the biology and ecology of the southern pine beetle, *Dendroctonus frontalis* Zimm. Unpubl. M.S. thesis, Texas A. & M. Univ. 62 p.

Clarke, A. L., J. W. Webb, and R. T. Franklin. 1979. Fecundity of the southern pine beetle in laboratory pine bolts. Ann. Entomol. Soc. Am. 72:229-231.

Coulson, R. N. 1979. Population dynamics of bark beetles. Ann. Rev. Entomol. 24:417-447.

Coulson, R. N., F. P. Hain, J. L. Foltz, and A. M. Mayyasi. 1975. Procedures for sampling southern pine beetle populations. 20 p. Texas Agric. Exp. Stn., Misc. Publ. 1184. College Station.

Coulson, R. N., A. M. Mayyasi, J. L. Foltz, F. P. Hain, and W. C. Martin. 1976. Resource utilization by the southern pine beetle, *Dendroctonus frontalis*. Can. Entomol. 108:353-362.

Curry, G. L., R. M. Feldman, and P. L. Sharpe. 1978. Foundations of stochastic development. J. Theor. Biol. 74:397-410.

Curry, G. L., R. M. Feldman, and K. C. Smith. 1978. A stochastic model of a temperature-dependent population. J. Theor. Pop. Biol. 13: 197-212.

Fargo, W. S., R. N. Coulson, P. E. Pulley, D. N. Pope, and C. L. Kelley. 1978. Spatial and temporal patterns of within-tree colonization by *Dendroctonus frontalis* (Coleoptera:Scolytidae). Can. Entomol. 110:1213-1232.

Feldman, R. M., G. L. Curry, and R. N. Couslon. 1980. The use and structure of the TAMBEETLE spot dynamics model. *In* Modeling of southern pine beetle populations: symposium proceedings. [Asheville, N.C., Feb. 1980.] F. M. Stephen, J. L. Searcy, and G. D. Hertel, eds. U.S. Dep. Agric. For. Serv., Tech Bull. 1630. Comb. For. Pest Res. Develop. Prog., Pineville, La.

Foltz, J. L., A. M. Mayyasi, F. P. Hain, R. N. Coulson, and W. C. Martin. 1976. Egg-gallery length relationship and within-tree analyses for the southern pine beetle, *Dendroctonus frontalis*. Can. Entomol. 108:341-352.

MacAndrews, A. H. 1926. The biology of the southern pine beetle. Unpubl. M.S. thesis. N.Y. State Col. For., Syracuse. 103 p.

Nebeker, T. E., R. R. Hocking, O. P. Hackney, and J. H. Lashomb. 1978. A comparison of non-linear and linear models for describing gallery length distribution of *Dendroctonus frontalis* attacking shortleaf pine. Environ. Entomol. 7:636-640.

Palmer, H. C., and J. E. Coster. 1978. Survival of southern pine beetles in felled and standing loblolly pines. J. Ga. Entomol. Soc. 13:1-7.

Solomon, M. E. 1951. Control of humidity with potassium hydroxide, sulphuric acid, or other solutions. Bull. Entomol. Res. 42:543-554.

ACKNOWLEDGMENTS

The authors wish to thank Drs. G. L. Curry and P. E. Pulley for modeling and analytical assistance. Thanks are also extended to J. Schmaltz, A. Gibson, A. Bunting, and P. Hennier for technical assistance.

The work reported herein was supported by the USDA-sponsored project entitled "The Expanded Southern Pine Beetle Research and Applications Program," (TEXO 6163-G), and the Texas Agricultural Experiment Station (TEX 6009). The findings and opinions are those of the authors and not necessarily those of the sponsoring agencies.

DYNAMICS OF BARK BEETLE-FUNGUS SYMBIOSIS

I. Pine Tree Anatomy and Fungus Growth Pattern

Youhanna Fares, John D. Goeschl, and Peter J.H. Sharpe[1]

Abstract.--The fungus *Ceratocystis minor* is introduced in the inner bark of pines by the southern pine beetle. Via the woodrays, the fungi spread in a three-dimensional pattern in the tangential, radial, and longitudinal directions in the ratio 1:2:7 to 1:4:15 respectively.

Water blockage in infested stems is due to aspiration when fungal hyphae penetrate the tracheids through the pits, and due to the presence of resin globules released by destruction of the epithelial tissues. The fungi cause reduction of water content of infested trees to the degree necessary for beetle brood development and the rapid death of the pine tree.

OBJECTIVES

Our research team has planned a series of three papers dealing with bark beetle dynamics in relation to host habitat and the environment, and two of these studies are completed. The first, entitled "Pine Tree Anatomy and Fungus Growth Pattern," serves as an introduction and explains why and how the fungus blocks water flow in the tree, leading to the tree drying. The second study, the "Pine Tree Drying Model," is a biomathematical formulation that relates the rate of drying of the pine tree to the physiology of the tree and of the fungus and to the environmental conditions. The third study will deal with the correlation of the degree of tree drying to the extent of brood development and beetle emergence time. Taken together, these studies serve to input to any mechanistic spot dynamics model, determine timber salvage tactics, and project the history (age) of the infestation.

INTRODUCTION

The blue-staining fungus *Ceratocystis minor* (Hedge) Hunt is introduced into the inner bark of pines by the southern pine beetle, *Dendroctonus frontalis* Zimm. (Craighead 1928, Caird 1935, Bramble and Holst 1940, Dixon and Osgood 1961, Franklin 1970). Functionally similar blue-staining fungi are introduced by bark beetles in the western United States, Canada, and Mexico (Von Schrenk 1903, Lindgren 1942). Extensive research since 1928 has established that it is the blue-staining fungus which plays the key role in killing living pines (Craighead 1928, Nelson and Beal 1929, Grossman 1930, Rumbold 1931, Nelson 1934, Caird 1935, Bramble and Holst 1940). The relationship among beetles, fungi, and host tree is not, however, completely understood, as pointed out by Hodges, Barras, and Mauldin (1968).

Craighead (1928) observed the rapid killing of pines by the bark beetles and suggested that the fungus destroys or clogs the tracheids, either by toxic secretions or rapidly developing hyphae. He also suggested that the fungus conditioned the host so that the physical habitat becomes suitable for the development of the bark beetle brood and may possibly provide food requirements. What Craighead postulated was thus a true symbiotic relationship between the beetle and the fungus.

Nelson and Beal (1929) found the tangential spread of the fungus beyond beetle galleries to be slight. The fungus appeared able to move only radially and longitudinally. Tangential spread of infection seemed to result from beetle inoculation along the egg galleries.

Recent studies have indicated that a complex physiological interdependence exists between bark beetles and blue-stain fungi. Barras (1973) found that removal of fungi reduced beetle progeny to less than 20 percent of that observed in beetles with fungi, and development of surviving progeny was delayed by nearly 30 days. Removal of blue-stain fungus *Ceratocystis ips* from *Ips* bark beetles in pine bolts was also found to be detrimental (Yearian 1967).

---

[1] The authors are, respectively, Senior Research Scientist, Senior Research Scientist, and Associate Professor, Biosystems Research Division, Dept. of Industrial Engineering, Texas A. & M. University, College Station.

Barras (1973) points out that such a decrease in beetle reproduction and delay in development would be helpful in efforts to decrease SPB-caused economic losses if a practical method could be devised to manipulate this phenomenon. Besides the immediate effect on progeny survival, the delay in brood development would allow more time for detection and salvage of infested trees.

MANIPULATION OF MOISTURE AS A POTENTIAL CONTROL MEASURE

Recent evidence tends to support the hypothesis of Nelson (1934) that the fungus brings about a reduction in the water content of the infested tree. Moisture has been suggested as a major host-related mortality factor in beetle population dynamics (Thatcher 1960), as the cause of poor and erratic success in rearing the beetle in the laboratory (Clark and Osgood 1964), and as a mechanism in the effect of cacodylic acid on brood development (Williamson 1970). Studies of the influence of phloem moisture on brood development by Gaumer and Gara (1967), Webb and Franklin (1978), and Wagner et al. (1979) suggest that high phloem moisture is associated with the formation of long larval mines, instead of feeding chambers. This phenomenon, in turn, led to lower survival of early larvae. Conversely, the emergence of survivors was positively correlated with phloem moisture, suggesting that high moisture was beneficial to late larvae and pupae in the bark. Since adequate moisutre appears to be important for pupal survival, the blue-stain fungus may have a complex role of reducing moisture in the early larval period while increasing the bark moisture content in the late larval and pupal period.

The importance of moisture is implied in the various within-tree control measures tested over the past 80 years or so. These control measures include topping (Caird 1935, Webb and Franklin 1978); cut-and-top, cut-and-leave (Thatcher 1960); and cacodylic acid treatment (Williamson 1970). Successful implementation of these control techniques has been limited by our inadequate understanding of the internal processes that were affected and how these processes were influenced by the prevailing physical environment.

Along somewhat the same line of thought, Webb and Franklin (1978) suggest that phloem moisture may be an important factor determining the expansion or decline of bark beetle infestations. These investigators call for the study of the relationship of phloem moisture to various site and stand characteristics as well as an analysis of the relationship among moisture, beetles, and microorganisms in the infested tree.

It is important to recognize the dynamic nature of the water relations of the stem of an infested tree. These relations are the result of complex biological and physical interaction of fungus, host tree, and beetles. This interaction is a hidden process: it is visible only by desiccation of the foliage, loss of bark from the tree, or relative reduction in yield of emerging beetle brood. A computer model is therefore practically the only means by which to follow water relationships as a function of the biological and physical driving forces.

Knowledge of the tree drying period from beetle attack to visible foliage desiccation (or tree fade, as it is often termed) may be of interest in the interpretation of aerial reconnaissance information. Such knowledge could be used to remove some of the bias inherent in observations of fade frequency or rate of spot growth. During cool, moist conditions, spots will go virtually unnoted, whereas during hot, dry conditions, old and new infestations will suddenly become visible, which can be extremely misleading both for the forester and the applications entomologist. Scheduling of salvage operations thus becomes dependent upon climatic conditions rather than apparent infestation frequency. Knowledge of the tree-drying period also has implications for behavioral chemical control procedures, which will be discussed in later sections of this analysis.

As the tree drying process is complex, we analyze it as a sequence of theoretical studies oriented toward the assessment of various practical control methods based upon the manipulation of stem water relations of infested trees. This paper describes the dynamics of fungal penetration of the xylem of infested trees. The interactions between xylem and phloem moisture levels will be discussed in a subsequent analysis.

THE DIRECTIONAL GROWTH OF FUNGUS IN THE WOOD

The symbiotic relationship between the beetle and the fungi involves alteration of the resin environment as well as moisture. Barras (1970) points out that once the beetle overcomes the inital force of the oleoresin exudation pressure, it is the growth of the fungi through the resin ducts that reduces or stops the tree's subsequent production of oleoresin. Thus beetle development can proceed without the resinous flooding of egg and larval galleries.

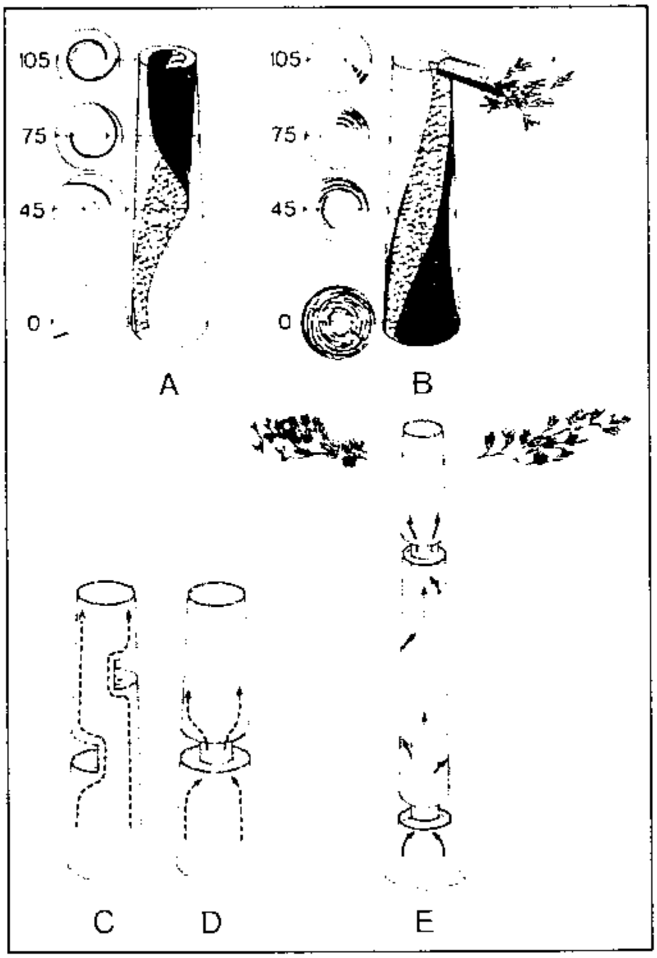


Figure 1.--*A* and *B*: the path of water flow in a normal pine tree. Numbers indicate the heights of cross section in centimeters above the base. *C-E*: the path of water flow when portions of the xylem are cut. (After Vité 1961).

The beetle in turn provides transport and entry to the xylem, where the fungus colonizes the nutritious ray parenchyma (Barras 1970). Attempts to inoculate trees by means other than bark beetles have generally been poor and erratic. When introduced under intact healthy bark, *C. minor* is able to penetrate only a short distance tengentially along the stem. Nelson (1934) found that when successful inoculation on all sides was not achieved, leaving a continuous band of sapwood uninfested, the tree continued to live (fig. 1). This band probably is a result of the lack of tengential ray and resin ducts, necessitating beetle inoculation at all positions around the circumference of the tree at the cambium-wood interface (fig. 2A).

In addition it appears that the beetle gallery is necessary to provide the fungi access to air at the surface of the xylem. Lagerberg, Lundberg, and Melin (1927) found that *C. minor* could grow in wood if a slightly dry surface existed, with access to air.

The hyphae of blue-stain fungi are initiated from spores deposited by beetles in their egg galleries in the phloem-cambium tissues between the bark and wood. The hyphae enter the wood primarily by way of the wood rays; thus their initial growth is radially inward.

The highest density and diameter of hyphal growth occurs in the parenchyma cells of the rays and the parenchyma and epithelial cells that surround the resin ducts (fig. 2B). These tissues supply essentially all of the necessary nutrients for growth (e.g., carbohydrates and nitrogen compounds). We do not know how fully the fungi utilize components of the resin ducts per se. However, Lagerberg et al. (1927) point out that the hyphae in the epithelial tissues around the resin ducts attain unusually large diameters (e.g., 10 to 15 μm, compared to 3 to 5 μm in other tissues).

The spread of the fungus through these tissues requires that the hyphae dissolve and digest the cross walls (Scheffer and Lindgren 1940). They noted that "rays so affected commonly are reduced to large open channels with hardly more than a vestige of their former cellular structure." But the vertical resin ducts do intersect with the horizontal (radial) resin ducts and with the uniserate rays (Münch 1908, Howard and Manwiller 1969; *see also* Lagerberg et al. 1927). Thus the interconnected ray-resin duct tissues (constituting 8 to 10 percent of the wood volume) contribute to the radial, vertical, and tangential spread of the fungus, (fig. 3).

Once the fungus is introduced into the ray system, branching of the hyphae also leads to penetration into the tracheids, which comprise the remaining 90 percent of tissues in pine wood. Intrusion into these cells is almost entirely through the pits, which connect the vertical tracheids with ray tracheids (Lagerberg 1927, Scheffer and Lindgren 1940) (fig. 4).

The tracheids, of course, have no cytoplasmic contents, and the blue-staining fungi, especially *C. minor*, do not appreciably digest the tracheid cell walls. As a result these branches obtain little or no nutritive value and are probably fed by transport of nutrients from the main feeding branches in the ray-resin duct tissues. This scenario is reflected

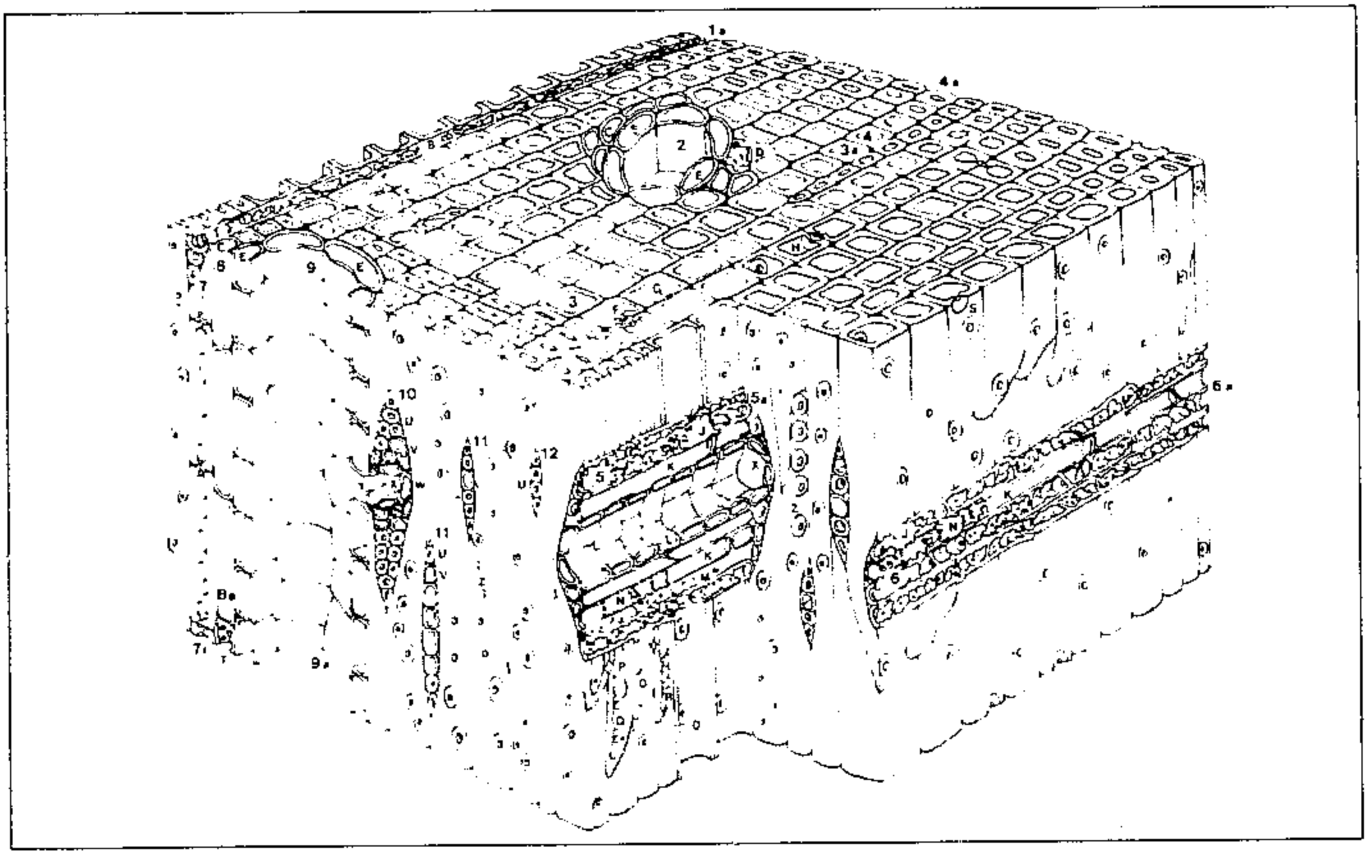


Figure 2A.--Schematic drawing of typical southern pine wood. Of importance are the vertical resin ducts (2 and 9-9a), which are lined with thin-walled epithelial cells (E), and the radial or horizontal ducts (x and 4), also lined with epithelial cells (L and 3). The radial ducts are components of the multiserate rays (10 and 5-5a), which include parenchyma cells (K,N, and 2) and ray tracheids (J,M, and 1). There are a much larger number of uniserate rays (11, 12, and 6-6a). Note the connection (Y) of vertical and horizontal ducts. (From Howard and Manwiller 1969.)

in the small diameter (i.e., 3 μm v. 10 to 15 μm in epithelial tissue) and rapid longitudinal growth of hyphal branches in the tracheids. Continued fungal spread in the wood results from branching of these hyphae, especially in the vicinity of the pits that connect the tracheids. Since there are pits connecting to ray tracheids, the hyphae can reenter nutritive parenchyma tissues after having elongated rapidly through the tracheids.

While the greatest biomass of fungus may arise in the ray-resin duct tissues, the rate of fungal spread may be most rapid through the tracheary portion of the wood. Vertical growth is most rapid because the lumen of the tracheids, which are about 200 times longer than they are wide, offer least mechanical resistance in the vertical direction. Radial spread is second fastest because most pits are oriented radially (i.e., through the tangential walls of radially adjacent tracheids). Finally, the slowest rate of spread is tangential since there are fewer pits in that direction (fig. 2A).

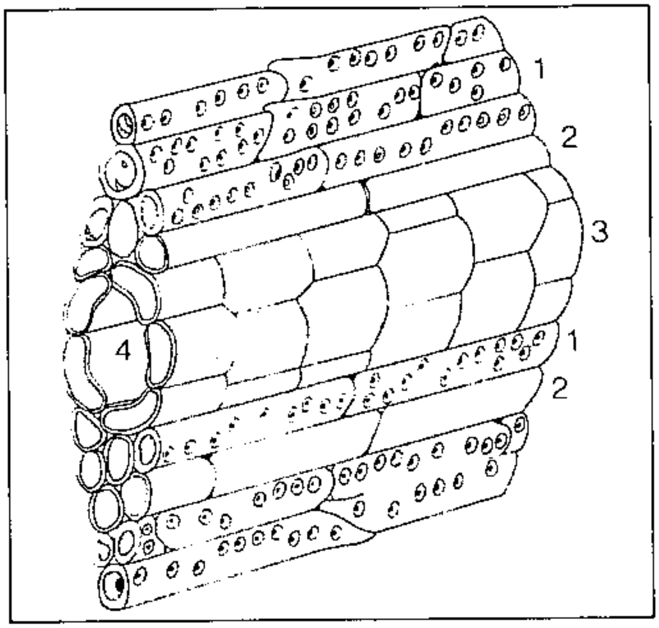


Figure 2B.--Enlarged example of a radial resin duct. (From Howard and Manwiller 1969.)

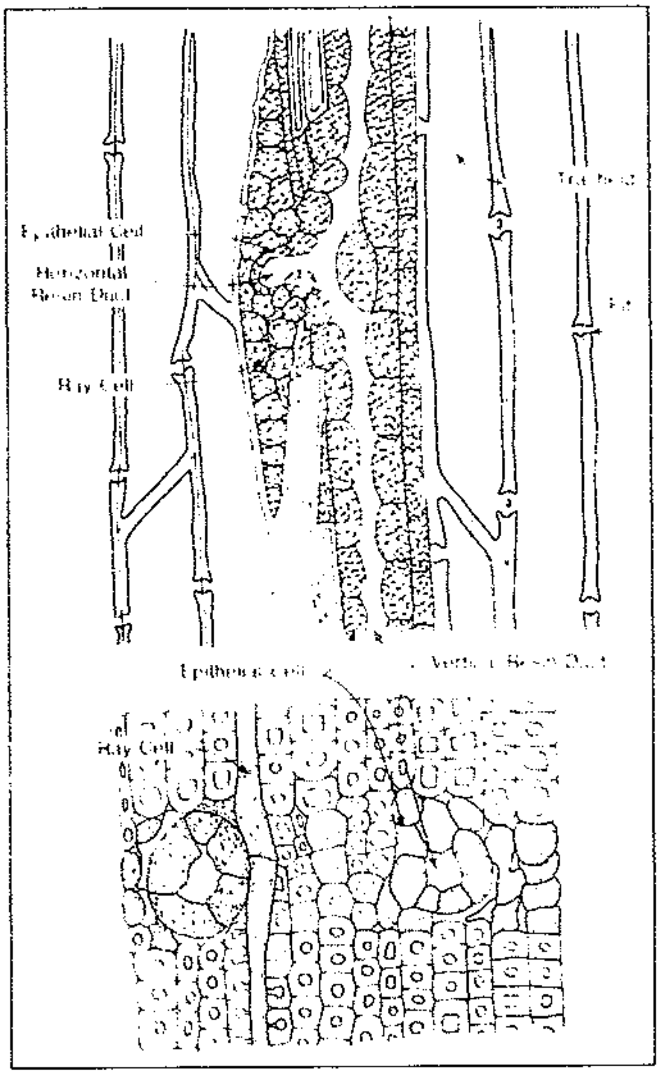


Figure 3.--*Top*:Tangential section through a vertical resin duct, where it intersects with a ray and horizontal (radial) resin duct. *Bottom*: Cross section (looking downward) of vertical resin ducts, where one of them intersects some ray parenchyma cells. In both cases the stippled cells are alive and contain cytoplasm, which is the primary food source for the fungi.

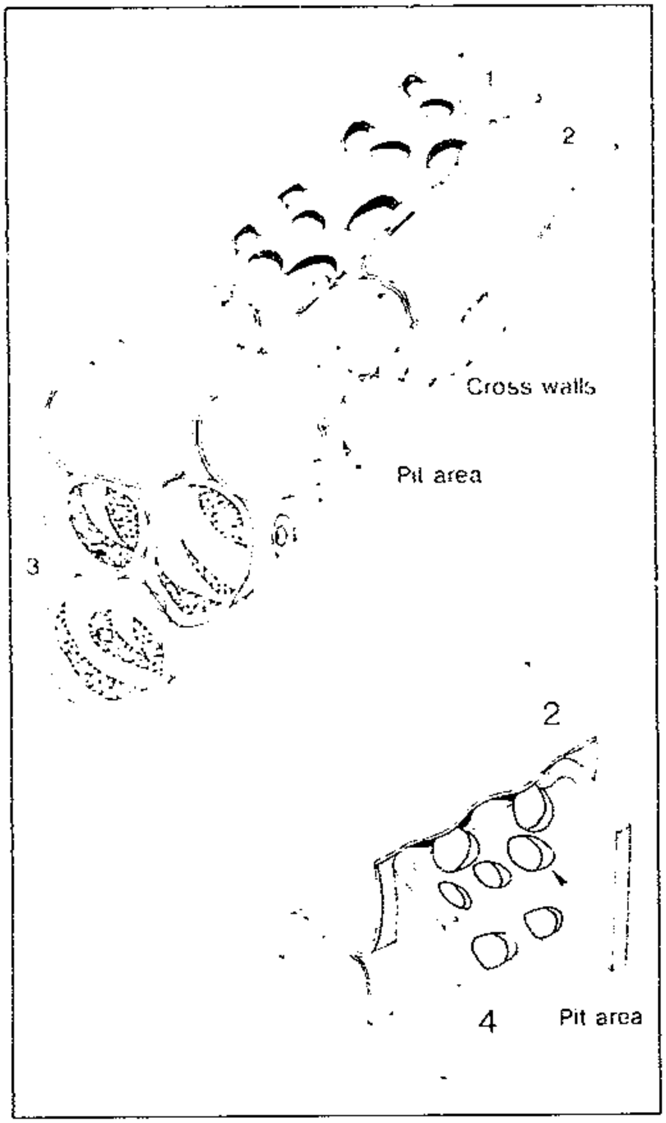


Figure 4.--*Top*: Diagram of ray cells including thick walled parenchyma (1) and ray tracheids (3). *Bottom*: Relationship between ray parenchyma cells and vertical tracheid (4). Note cross walls and wall areas (adjacent to pits), which fungi must digest to pass from one cell to another.

The combined properties of the wood tissues, then, explain the experimentally observed rates of penetration in the tangential, radial, and longitudinal directions, which vary from 1:2:7 to 1:4:15 respectively. As pointed out by Scheffer and Lindgren (1940), there is less variation in these ratios among species of fungi than might be expected. They likewise conclude that the anatomical-mechanical properties of the wood are the controlling factor. Indeed it might be possible to predict these ratios from the hydraulic conductivity of the wood in the three directions.

THE MECHANISM OF WATER BLOCKAGE

The mechanism of water blockage has been studied by Nelson (1934) and Bramble and Holst (1940). Stem drying by transpiration was compared with that of stems infested by fungi. In the fungal-infested stems, globules of resin were present in the lumina of the tracheids. These globules were absent from the wood of stems dried by transpiration. The globules, presumably released by destruction of the epithelial tissues (as described above), may block the flow of water or dye solutions (Caird 1935). We also point out that the resin acids are known to crystallize on contact with moisture, and the fine mesh structure of pit membranes make an excellent surface for the formation of microcrystals.

In addition to blockage by substances in the vicinity of damaged resin ducts, it is clear from published photographs (e.g., Lagerberg et al. 1927, Scheffer and Lindgren 1940) that hyphal penetration of tracheids plays a major role in the reduction of water conduction. Specifically, the water in each tracheid is under tension load (sometimes referred to as "suction force") and is thus aspirated when a fungal hypha penetrates through a pit and allows air at atmospheric pressure to enter. Generally air is prevented from entering the adjacent tracheids because the pressure differential causes closure of the pits by the torus (a small plug normally suspended away from the pit aperture by a thin fibrous membrane) (fig. 4).

Once bulk water is aspirated from a given tracheid, the hypha grows rapidly through the lumen. Branches from this hypha tend to penetrate the plugged pits into adjacent tracheids, causing additional aspiration of water from these elements. All trachеary elements so aspirated are lost as conductors of water through the xylem. The rapid rate of fungal spread through the tracheids probably contributes most to the blockage of water flow.

Combining the two effects of the fungi on water conduction--aspiration and blockage by resin residues--it can be concluded that any three-dimensional area of xylem occupied by the fungus is no longer capable of conducting water. However, it should be noted that the xylem is a complex, three-dimensional network. A characteristic of such networks is that substantial percentages of the network can be cut or blocked with only modest reductions of flow through the system. This is borne out by experiments where various portions of the xylem of living pine trees have been cut (see fig. 1).

Thus, to stop or reduce the flow of water enough to cause fading or death of a tree, it is probably necessary that the sapwood be blocked by a nearly continuous, circumferential band of fungus. Such a band would result when the wedge-shaped patches of fungus, introduced at various levels and positions around the bole, spread sufficiently to overlap (fig. 5). In early spring, when water demand is low, it is likely that essentially the entire cross section of sapwood be blocked before fading or tree death occurs. In summer, however, less than total blockage is necessary. But in either case, blockage or aspiration of the peripheral sapwood by the fungus probably suffices to isolate the phloem-cambium layer from the bulk water supply of the xylem. The resultant drying and ventilation of this peripheral layer allows beetle brood development.

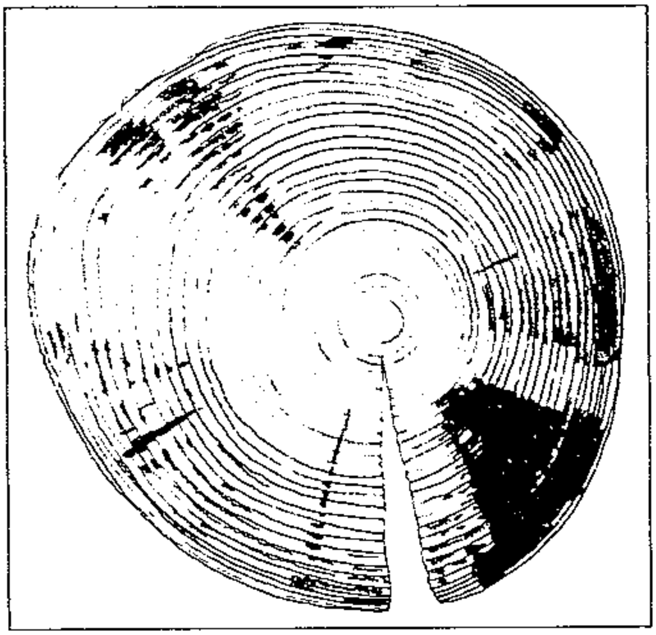


Figure 5.--Cross section of pine bole showing typical distribution of blue stain.

LITERATURE CITED

Barras, S. J. 1970. Antagonism between *Dendroctonus frontalis* and the fungus *Ceratocystis minor*. Ann. Entomol. Soc. Am. 63:1187-1190.

Barras, S. J. 1973. Reduction of progeny and development in the southern pine beetle following removal of symbiotic fungi. Can. Entomol. 105:1295-1299.

Bramble, W. C., and E. C. Holst. 1940. Fungi associated with *Dendroctonus frontalis* in killing shortleaf pine and their effect on conduction. Phytopathol. 30:811-889.

Caird, R. W. 1935. Physiology of pines infested with bark beetles. Bot. Gaz. 96:709-733.

Clark, E. W., and E. A. Osgood, Jr. 1964. Mass rearing of the southern pine beetle and the coarse writing engraver. 4 p. U.S. Dep. Agric. For. Serv., Res. Note SE-30. Southeast. For. Exp. Stn., Asheville, N.C.

Craighead, F. C. 1928. Interrelation of tree-killing bark beetles (*Dendroctonus*) and blue stain. J. For. 26:836-837.

Dixon, J. C., and E. A. Osgood. 1961. Southern pine beetle, a review of present knowledge. 34 p. U.S. Dep. Agric. For. Serv., Res. Pap. SE-128. Southeast. For. Exp. Stn., Asheville, N.C.

Franklin, R. T. 1970. Observations on the blue stain-southern pine beetle relationship. J. Ga. Entomol. Soc. 5:53-57.

Gaumer, G. C., and R. I. Gara. 1967. Effects of phloem temperature and moisture content on the development of the southern pine beetle. Contrib. Boyce Thompson Inst. 23(11):373-378.

Grosmann, H. 1930. Beitrage zur kenntnis der lebensgemeinschaft zwischen Borkenkafern und pilzen. Z. parasit. 3:56-102.

Hodges, J. D., S. J. Barras, and J. K. Mauldin. 1968. Amino acids in inner bark of loblolly pine, as affected by southern pine beetle and associated microorganisms. Can. J. Bot. 46:1467-1472.

Howard, E. T., and F. G. Manwiller. 1969. Anatomical characteristics of southern pine stem wood. Wood Sci. 2:77-86.

Lagerberg, T., G. Lundberg, and E. Melin. 1927. Biological and practical researches into blueing in pine and spruce. Svenska Skagsvardsfor. Tidsk. Haft II:145-272.

Lindgren, R. M. 1942. Temperature, moisture, and penetration studies of wood-staining Ceratostamellae in relation to their control. U.S. Dep. Agric., Tech. Bull. 807. U.S. Dep. Agric., Washington, D.C.

Münch, E. 1908. Die Blufaüle des Nadelholzes. Naturwiss. Zertschr. für Forstu. Landwirtsch. 6:297-323.

Nelson, R. M. 1934. Effect of blue stain fungi on southern pines attacked by bark beetles. Phytopathol. 7:327-353.

Nelson, R. M., and J. A. Beal. 1929. Experiments with blue stain fungi in southern pines. Phytopathol. 9:1101-1106.

Rumbold, C. T. 1931. Two blue-staining fungi associated with bark beetle infestation of pines. J. Agric. Res. 43:845-873.

Scheffer, T. C., and R. M. Lindgren. 1940. Stains of sapwood products and their control. 123 p. U.S. Dep. Agric., Tech. Bull. 714. U.S. Dep. Agric., Washington, D.C.

Thatcher, R. C. 1960. Bark beetles affecting southern pines: a review of current knowledge. 25 p. U.S. Dep. Agric. For. Serv., South. For. Exp. Stn., Occas. Pap. 180. [Discontinued South. Stn. series.]

Vité, J. P. 1961. The influence of water supply on oleoresin exudation pressure and resistance to bark beetle attack in *Pinus ponderosa*. Contrib. Boyce Thompson Inst. 21: 37-66.

Von Schrenk, H. 1903. The blueing and red rot of western yellow pine with special reference to the Black Hills forest reserve. 40 p. U.S. Dep. Agric., Bull. 36.

Wagner, T. L., J. A. Gagne, P. C. Doraiswamy, R. N. Coulson, and K. W. Brown. 1979. Development time and mortality of *Dendroctonus frontalis* in relation to changes in tree moisture and xylem water potential. Environ. Entomol. 8:1129-1138.

Webb, J. W., and R. T. Franklin. 1978. Influence of phloem moisture on brood development of the southern pine beetle (Coleoptera:Scolytidae). Environ. Entomol. 7:405-410.

Williamson, D. L. 1970. A pest management system for the southern pine beetle, *Dendroctonus frontalis* Zimm., in east Texas. Ph.D. dissertation. Texas A. & M. Univ., College Station. 108 p.

Yearian, W. C., Jr. 1967. Relations of the blue stain fungus, *Ceratocystis ips* (Rumbold) C. Morean, to *Ips* bark beetles (Coleoptera:Scolytidae) occurring in Florida. Diss. Abstr. 27:3356-3413.

DYNAMICS OF BARK BEETLE-FUNGUS SYMBIOSIS

II. Pine Tree Drying Model

Youhanna Fares, Charles E. Magnuson, Paul C. Doraiswamy, and Peter J.H. Sharpe[1]

Abstract.--A Fungus Growth Tree Drying Environment model is formulated. The model calculates the rate of drying of the fungus-infested pine tree as a function of environmental and tree physiological variables. The rate of drying determines the degree of brood development, which in turn determines the time of beetle emergence. The model also can determine the age of the infestation for control and forest management.

INTRODUCTION

The southern pine beetle, *Dendroctonus frontalis* Zimm., from here on denoted SPB, is a particularly destructive insect in the pine forests of the South. Three factors--the constant presence of blue-stain fungi in trees successfully attacked by the SPB; the fact that blue-stain is found in the water-conducting tissues of the xylem, whereas the beetles are chiefly confined to the phloem and cambium regions; and the extremely rapid death of infested trees, apparently due to water deficiency--have focused attention on the possible role of these staining fungi in the death of trees (Nelson and Beal 1929, Nelson 1934).

The development of the southern pine beetle in loblolly pines (*Pinus taeda* L.) represents a classical case of symbiosis between insects and associated fungi on a coniferous host, resulting in rapid death of the tree. Because of the close association between larval development and fungi in the phloem, Barras (1973) found that the number of progeny and the time of emergence is highly dependent on fungal development.

Gaumer and Gara (1967) studied the effect of phloem temperature and moisture content on the development of southern pine beetles. They came to the conclusion that it is possible, at the onset of the beetle attack, that somewhat lower phloem temperatures and higher moistures are more favorable to egg survival and early eclosion. If moisture content is maintained beyond a certain point in the early development of a brood, it is detrimental.

The theory that beetles carry blue-stain into trees is strongly supported by the evidence obtained through the examination of entrance tunnels, from cultures obtained from beetles taken from unstained galleries, and by the phenomenon of specificity found independently by Nelson and Beal (1929) and Rumbold (1931). So far as is known, blue-stain appears in the sapwood of all trees that have been successfully attacked by bark beetles. Blue-stain appears in the vicinity of the tunnels (galleries) within a week or less after trees become infested with SPB. The areas of infestation vary greatly in size and shape, depending upon age; but as a rule their length considerably exceeds the width. They frequently coalesce to form particles of considerable size. The cross section of an infested stem area appears as irregularly wedge-shaped sectors extending from the periphery to the hardwood, due to the hyphae growing from the outside toward the center along the medullary rays. Inoculation experiments demonstrated that these fungi will grow with considerable rapidity in the sapwood of living pine, and if the entire cross section of the trunk becomes stained, death invariably follows.

Experiments on water relations of pines demonstrated great differences in moisture content between trees attacked by the beetle and unattacked trees. Most noticeable is the fact that the moisture content of SPB-attacked trees was highest at the base and decreased with increase in the height. This is the reverse of conditions found in normal trees. The lowered water content of attacked trees can be attributed chiefly to two causes. Either the water is lost through the beetles' tunnels or it is prevented from passing upward into the tree by the blued zone in the sapwood in the lower part of the bole.

---

[1] Drs. Fares, Magnuson, and Sharpe are, respectively, Senior Research Scientist, Senior Research Scientist, and Associate Professor, Biosystems Research Division, Dept. of Industrial Engineering, Texas A. & M. University, College Station, Tex. Dr. Doraiswamy is Senior Scientist, Lockheed JSC, Houston, Tex.

Caird (1935) and Vité (1959) used dye solutions to study conduction and distribution of moisture in healthy and infested pines. The changes occurring when the beetles infest the healthy tree are marked. The outer rings fail to conduct dye solution, drying takes place in the outer rings, and various fungi enter the wood. Examinations during the second and third days after attack show light-colored patches in the wood along beetle galleries, caused by the accumulation of air in the cells as drying takes place. As the outer rings become nonconducting on about the fourth day after attack, the transpiration stream is carried in rings which are closer and closer to the center of the tree. Researchers found that in the later stages of the disease no dye reaches the top, owing to the stoppage of conduction at midstem. (The pattern of fungus growth and mechanism of water blockage is explained in detail in Part I of this series, entitled "Pine Tree Anatomy and Fungus Growth Pattern".) The moisture content of the diseased tree soon falls below that of a healthy tree (225 percent to 100 percent) and the drying progresses from the surface of the wood toward the center. Drying does not continue indefinitely but reaches a minimum moisture content at about 30 percent. After 25 to 30 days, the entire trunk is usually dry except for the base. During subsequent decay the tree may become moist again.

Bramble and Holst (1940) studied water conduction in fungus-infested pines and identified the major fungi associated with *D. frontalis* and their effect on conduction. This team arrived at important and similar conclusions to those of Nelson and Caird. They determined that certain organisms later found in the sapwood during early stages of attack were carried on and in the bodies of the beetles. Thus the presence of the fungi may be ascribed to direct inoculation by beetles.

Role of *Ceratocystis Minor*

In the first stage of infestation (1 to 7 days after attack), initial invasion of the sapwood takes place. Foliage of the attacked tree remains green, however. During the second stage (8 to 14 days after attack), when the foliage begins to turn yellow, some fungi reach the heartwood of the stems 4 to 6 inches in diameter. The third stage includes the period 15 to 30 days after attack, during which time the foliage turns from yellow to reddish-brown.

It is during the period of 1 to 14 days after attack that complete primary infection of the sapwood takes place and stoppage of conduction is first noticed. The fungi infecting the sapwood during this period are considered most important. The effect of inoculation made with individual fungi in the period of June and July showed that *Ceratocystis minor* was the only fungus able to cause the death of trees from 2 to 6 inches in d.b.h. Only stems inoculated with *C. minor* became unable to conduct dye through the sapwood to the crown within a 2-month period.

As has been pointed out by Nelson (1934), the death of inoculated trees occurred only when successful inoculation was secured on all sides of the tree. If a continuous band of sapwood remained uninfested, the tree continued to live (*see* Vité 1959, his fig. 4). In general, *C. minor* is able to penetrate tangentially but only a short distance under intact, healthy bark.

According to Lagerberg, Lundberg, and Melin (1927), *C. minor* can grow in wood that dries slightly provided the fungus has an immediate access to air at the surface of the wood. Sapwood of the outer growth rings of shortleaf pines averages about 110 to 175 percent moisture on a dry-weight basis, so that with some drying due to exposure when stems are inoculated, *C. minor* should be able to grow in the wood.

TREE-DRYING MODEL

It is obvious from the above discussion that tree drying as a result of SPB-introduced fungus infestation influences to a great degree (1) the fate of the tree and its timber value, and (2) more importantly the SPB brood development, the number of progeny, and the time of emergence. It is important then to develop a tree drying model that can predict the time-drying and time-brood development relationships and could be integrated with spot dynamic models.

Model Assumptions

A simple model for tree drying following infestation by the southern pine beetle has been formulated. The concepts of the model are based on the following assumptions:

(1) The tree is assumed to be a conducting system, whose conductivity is directly proportional to the noninfested cross-sectional area.

(2) When the tree is attacked by the beetle, it simultaneously introduces

the fungus *C. minor*, which gradually reduces the effective water-conducting system of the tree as the fungi grow toward the center of the bole.

(3) As the ratio of the effective conducting area to the original conducting area of the healthy tree decreases over time, a threshold is reached beyond which the sapwood dries to a lethal level (see fig. 1).

(4) Although the drying process is a time-dependent change within the tree, the water balance of the tree as a whole is in a steady state with the environment. We can then apply the equation of conservation and continuity of mass:

> The Rate of water loss from the tree crown + Rate of water uptake of the tree from the soil + Rate of change of water content of the tree = zero. (1)

Components of the Model

As can be seen from these basic assumptions of the model, the concepts and approach are simple. However, because of interdependencies of the variables involved in the formulation, we must define the various terms and their interdependencies. These relationships are given in tables 1 and 2.

The Rate of Water Loss From Tree Crown

The rate of water loss from tree crown, dM/dt, is proportional to the difference in leaf (needle) water vapor density, ρ_L, and that of the ambient air, ρ_a, at the given ambient temperature, T_a, and to the effective evaporative area of the leaves, S. Also, dM/dt is inversely proportional to the leaf resistance to water vapor diffusion, R_L. The rate of water loss from the tree crown is then given by

$$\frac{dM}{dt} = \frac{D}{\delta}(\rho_L - \rho_a) \cdot S$$

i.e.,

$$\frac{dM}{dt} = \frac{(\rho_L - \rho_a) \cdot S}{R_L} \qquad (2)$$

where M is the mass of water lost from the crown in grams, and

$$R_L = 1/\frac{D}{\delta} = \frac{\delta}{D} \quad \text{sec cm}^{-1}.$$

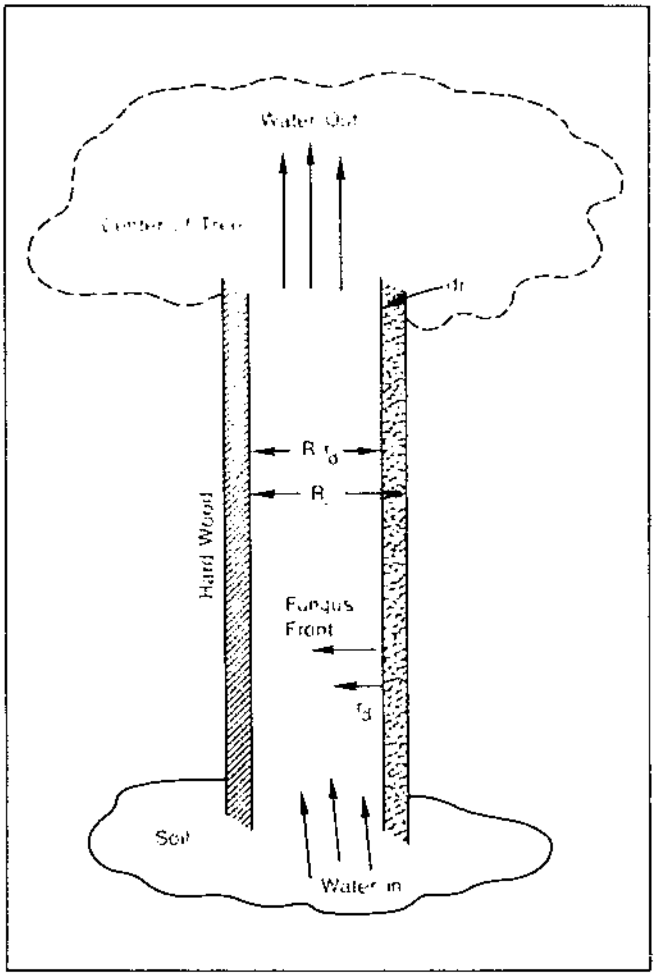


Figure 1.--Schematic representation of the tree drying model.

On introducing the functional dependence of the various parameters, equation (2) reads

$$\frac{dM}{dt} = \frac{\rho_L(T_a) - \rho_a(T_a)}{R_L(\psi_L, N_s)} \cdot S(\text{DBH}, N_s) \qquad (3)$$

Since $\rho_L(T_a)$ is usually taken to be the saturated water vapor density of air, ρ_{sa}, at T_a, equation (3) becomes

$$\frac{dM}{dt} = \frac{\rho_{sa}(T_a) - \rho_a(T_a)}{R_L(\psi_L, N_s)} \cdot S(\text{DBH}, N_s) \qquad (4)$$

S is usually related to the tree's d.b.h. by means of a simple polynomial. Kinerson and Fritschen (1971) developed a double-normalized model by normalizing total needle surface area per branch position with respect to the maximum foliage surface area and position in the crown. A third-order polynomial of the form

$$S = 8.0201 - 0.397x + 0.199x^2 + 0.004x^3$$

where x is the d.b.h. in centimeters and S, the needle surface area in square centimeters.

Table 1.--Definition of various parameters in the tree drying model.

ρ_{as}	Saturated water vapor density of air in gm cm^{-3}
Ψ_s	Soil water potential in bars
Ψ_L	Leaf water potential in bars
Ψ_f	Infested tree (bole) water potential in bars
Ψ_{nf}	Noninfested tree (bole) water potential in bars
θ_f	Infested tree percent moisture content
θ_{nf}	Noninfested tree percent moisture content
T_a	Ambient air temperature in degrees Kelvin
T_t	Tree (bole) temperature in degrees Kelvin
ρ_a	Ambient air water vapor density in gm cm^{-3}
ρ_L	Leaf water vapor density in gm cm^{-3}
W_T	Total water content of tree bole in gm
S	Effective evaporative surface area in cm^2
G_f	Fungus growth rate in cm sec^{-1}
r_f	Radius of fungal front in cm
F	Number of fungus wedges (related to the number of attacking beetles or beetle attack density) in cm^{-2}
L_w	Hydraulic water conductivity of the tree in gm cm^{-2} sec^{-1} bar^{-2}
D	Effective diffusion coefficient of water in the leaf in cm^2 sec^{-1}
N_s	Number of stomata per unit area of leaf surface cm^{-2}
DBH	Tree diameter at breast height in cm
δ	The thickness of the unstirred air layer on the leaf surface + the thickness of leaf layer across which water diffuses in units of cm
R_L	Leaf resistance to water diffusion sec cm^{-1}
R_f	Infested tree (bole) water resistance in sec cm^{-1}
A_T	Tree cross section in cm^2
A_f	Fungus-infested area (bole) (nonconducting area) in cm^2
L_T	Tree height in cm
A_c	Conducting surface area (bole) in cm^2
r	Healthy tree radius in cm
t	time

Table 2.--Dependent and independent variables in the tree drying model.

Dependent variables		Independent variables
ρ_a = $f(T_a)$ or f (water vapor press, P_{wv}, at T_a)	$G_f = f(T_t, \theta_f)$	T_a
	$r_f = f(T_t, G_f, t)$	L_w (taken as constant)
ρ_L = $f(T_a)$ (usually taken as saturated water vapor density at T_a) i.e., $\rho_{as}(T_a)$)	$W_t = f(\theta, r)$	Ψ_s
	$R_f = f(\Psi_f, A_c, L_w)$	D
T_t = $f(T_a)$	$R_L = f(\Psi_L, \Psi_s)$	
	$A_f = f(G_f)$	
Ψ_f = $f(\theta_f)$	$A_c = f(G_f)$ $[A_c = A_T - A_c]$	
Ψ_{nf} = $f(\theta_{nf})$	$S = f(\text{DBH}, N_s)$	
Ψ_L = $f(\theta_l, \Psi_s)$		

R_L is strongly dependent on the leaf water potential ψ_L, the stomatal frequency N_s, and soil water potential ψ_s. The latter term is approximated with a constant for a given stand site and soil water condition. The functional relationship between R_L and ψ_L and N_s is obtained from the work of DeMichele and Sharpe (1973 and 1974). These authors derived a detailed model of guard cell motion and made a parametric analysis of the anatomy and physiology of the stomata. The relationship between R_L and ψ_L and N_s is given here, in simplified form, in terms of needle stomatal parameters:

$$R_L = K + \frac{A}{B+C\psi_L}$$

where

$$K = \frac{\eta}{4L_o\,\theta\,N_s}$$

$$A = (48\,E\,I\,H_o)/(L_o^4\,\theta\,N_s)$$

$$B = H_1(L_1 - L_2)\,\Phi_G - H_o L \Phi_s$$

$$C = H_1(L_1 - L_2) - H_o L$$

where

L_o = semicircumference of stomatal pore

H_o = thickness of guard cell

I = the moment of inertia about the neutral axis of the guard cell

E = cell wall modulus of elasticity

Φ_G, Φ_s = guard cell and epidermal cell osmotic potential, respectively

H_1 = the interior thickness of the guard cell

L_1, L_2 = the interior length of the dorsal wall and ventral wall, respectively

L = the exterior circumference of the guard cell

These parameters are well known for the pine needle.

Water Uptake From The Soil

The rate of water uptake, dW_{in}/dt, by the tree from the soil is proportional to the water potential gradient, to the conducting cross-section area of the tree, A_c, and to the hydraulic conductivity of the tree bole, L_W, such that

$$\frac{dW_{in}}{db} = \frac{(\psi_L(\theta_{AV}) - \psi_s)}{L_T}\;L_T A_c L_W \qquad (5)$$

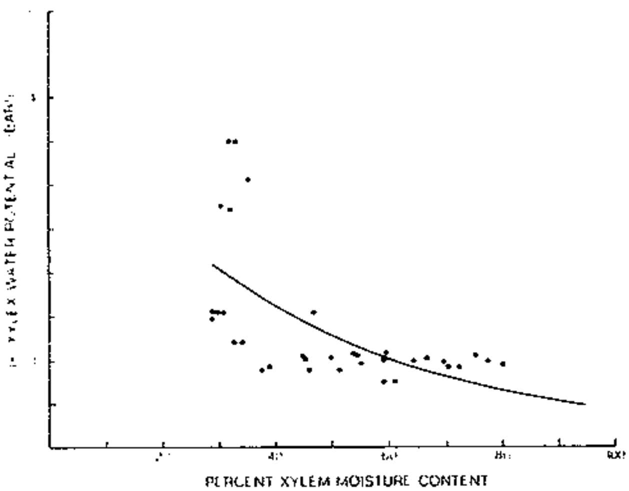


Figure 2.--The change of xylem moisture content of the pine tree with water potential after infestation. (+) represents data points, and the solid line is the fitted model.

which may be written as

$$\frac{dW_{in}}{dt} = \Delta\psi(\theta_{AV})\,A_c\,L_W \qquad (5')$$

For a given site over the short period during which the tree is drying, ψ_s is considered constant. ψ_L and moisture content, θ, are strongly related. In whole cells or tissue segments the various forces retaining water interact continuously to produce a general relationship between relative water content and water potential. When relative water content (θ) is plotted *v.* water potential (ψ), curves are produced which are effectively sorption isotherms for the tissue segments concerned and are similar in form to the $\psi(\theta)$ curves for soils and pinewood (Slayter 1967). The progressive change in ψ, with decreasing water content, can be analytically expressed as an exponentially decaying function or a simple second- or third-order polynomial.

The decrease in water content of a loblolly pine tree could be induced by subjecting the tree to progressively increasing water stress or infesting the tree with blue fungus via SPB (as shown above). Field data collected from infested pine trees (Wagner et al. 1979) indicate that the general relationship of ψ_L to water content θ_f is as suggested by Slayter. Therefore, we will use the simple exponential expression to describe the dependence of leaf water potential of the infested pine tree on the relative water content such that (fig. 2),

$$\psi_L = a\,e^{-b\theta_f} \qquad (6)$$

where *a* and *b* are species characteristic contants to be determined experimentally.

The conducting area of the tree stem, A_c, is that portion of the stem cross section that has its xylem intact, i.e., not yet infested with the fungus. This area decreses with time from infestation of the tree and can be expressed as the difference between A_T and A_f, i.e.,

$$A_c = A_T - A_f \qquad (7)$$

However, A_f is a function of several variables. It is a function of successful beetle attack density F, if we assume that each infesting beetle inoculates the tree with the fungus and starts a fungal hypha where it enters (Nelson and Beal 1929, Nelson 1934, Craighead 1928, Münch 1908, and McCallum 1922). A_f is also a strong function of fungus growth rate G_f, which in turn is dependent on bole temperature T_t, and moisture content after infestation θ_f and time from inoculation *t* (Gaumer and Gara 1967, Münch 1908, Nelson 1934, and Rumbold 1931). That is,

$$A_f = f(F, G_f(T_t, \theta), t) \qquad (8)$$

and

$$A_c = A_T(DBH) - A_f(F, G_f(T_t, \theta), t) \qquad (9)$$

EFFECT OF TEMPERATURE ON FUNGUS RATE OF GROWTH

It has long been recognized that organism growth and development as a function of temperature follows the Arrhenius hypothesis and Eyring equation in the midtemperature region (see, for example, Precht et al., [1973], Laudien [1973], and Sizer [1943]). Recently Sharpe and DeMichele (1977) developed a stochastic thermodynamic model of poikilotherm development from the Erying equation, assuming multiple activity states of the underlying developmental control enzymes. Data on the growth of *C. minor* as a function of temperature is found in the work of Bramble and Holst 1940. The analysis of these data shows a poikilotherm behavior as developed by Sharpe and DeMichele (1977) that follows this relationship:

$$G_f(T) = \frac{\frac{\varepsilon_c kT}{h}\, e^{(\Delta S_A^{+} - \Delta H_A^{+}/T)/R}}{1 + e^{(\Delta S_L - \Delta H_L/T)/R} + e^{(\Delta S_H - \Delta H_H/T)/R}} \qquad (10)$$

where k, h, R are the Boltzmann constant, Planck's constant, and the gas constant, respectively. ΔS_A^{+} is entropy of activation, ε_c is relative concentration, and ΔS_L represents the difference in entropy of activation between low temperature and midtemperature states of the controlling enzyme. Similarly, ΔH_L represents the difference in enthalpy of activation between these two states. ΔS_H and ΔH_H represent the difference of entropy and enthalpy of activation between high-temperature and midtemperature states, respectively. ΔS_A^{+}, ΔH_A^{+}, ΔS_L, ΔH_L, ΔS_H, and ΔH_H are thermodynamic constants characteristic of the organism control enzyme system, which is assumed to control development. Analysis of the data from Bramble and Holst (1940) and Lindgren (1942) on the relation of temperature to growth rate enabled us to evaluate these thermodynamic contants as listed in table 3. Figure 3 shows how closely the poikilotherm approach describes the growth temperature behavior of such a biophysical system.

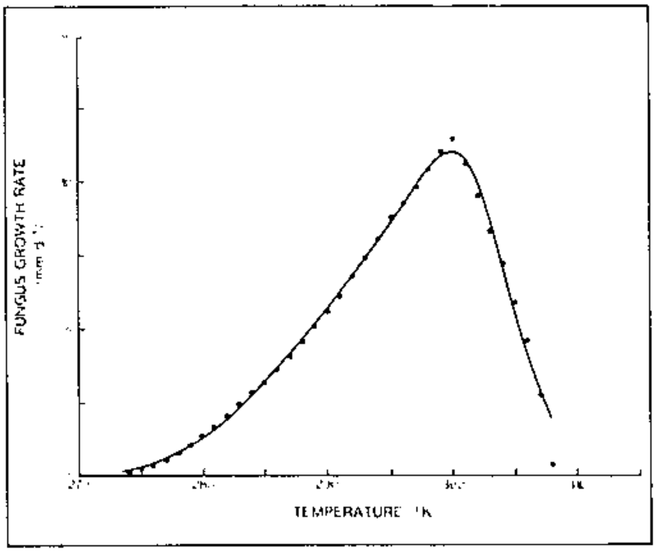


Figure 3.--The poikilotherm behavior of *C. minor* growth rate as a function of temperature. (+) represents data points, and the solid line is fitted poikilotherm equation. (Data from Bramble and Holst 1940.)

Similar studies on other ceratostomellae, conducted by Lindgren (1942), indicate that their growth response to different temperatures was in general the same on wood surfaces as on agar.

The relationship between fungus growth rate and moisture content of wood could be elucidated in two ways--directly, by analyzing fungus growth rate-moisture content data, or indirectly, from growth rate-water potential studies. The former data is available in the work of Lindgren (1942), Colley and Rumbold (1930), and Snell (1929). The later information could be obtained by analyzing the data published by Kidd, Reid, and Davidson (1977), utilizing the relationship between ψ and θ developed above.

Table 3.--Main components and constants in the tree drying model.

Component	Relationship	Constant
1. Fungus area growth rate G_f as a function of water potential Ψ_L, i.e., $G_f(\Psi_L)$	$G_f(\Psi_L) = A\ e^{-B\Psi_L}$	$A = 22.24\ mm^2\ d^{-1}$ $B = 0.171\ bar^{-1}$ $B' = BR(\bar{R} = \text{gas constant})$
2. Xylem (or leaf water potential) as a function of moisture content of infested tree, $G_f(\%)$, i.e., $\Psi_L(\theta_f)$	$\Psi_L(\theta_f) = a\ e^{-b\theta_f}$	$a = 39.93$ bar $b = 0.02242$
3. Ψ_L as a function of time from day of infestation, i.e., $\Psi_L(t)$	$\Psi_L(t) = a' + b'\ t^m$	$a' = 9.601$ bar $b' = 10^{-5}$ bar $m = 3.332$
4. Xylem moisture content θ_f (%) as a function of time from day of infestation.	$\theta_f(t) = k\ e^{a'' + b''t + c''t^2}$	$k = 80.48$ $a'' = -0.106$ $b'' = 0.026\ d^{-1}$ $c'' = -0.002\ d^{-2}$
5. Fungus area growth rate G_f, as a function of time <u>t</u>, from day of infestation, i.e., $G_f(E)$	$G_f(t) = \dfrac{\alpha t}{\beta + \gamma t}$	$\alpha = 1.028\ mm^2\ d^{-1}$ $\beta = 8.332$ d $\gamma = 1.165$

Continued

Table 3.-- Continued

Component	Relationship	Constant
6. G_f as a function of temperature $\underline{T}$, i.e., $G_f(T)$	$G_f(T) = \dfrac{\varepsilon_c \frac{kT}{h} e^{(\Delta S_A^{\neq} - \Delta H_A^{\neq}/T)/R}}{1 + e^{(\Delta S_L - \Delta H_L/T)/R} + e^{(\Delta S_H - \Delta H_H/T)/R}}$ i.e., $G_f(T) = \varepsilon_c \frac{kT}{h} e^{(\Delta S_A^{\neq} - \Delta H_A^{\neq}/T)/R} \quad P_2.$	k, h, R are the Boltzmann's constant, Planck's constant and the gas constant respectively $\Delta S_A^{\neq}$ = entropy of activation = 25.69 cal/mole °K ΔH^+ = enthalpy of activation = 12770 cal/mole ΔS_L = difference in entropy of activation between low and midtemperature states = -165.5 cal/mole °K ΔS_H = difference in entropy of activation between high and midtemperature states = 319.1 cal/mole °K ΔH_L = difference in enthalpy of activation between low temperature and midtemperature states = -46320 cal/mole ΔH_H = difference in enthalpy of activation between high temperature and midtemperature states = 96790 cal/mole ε_c = Relative concentration = 10^{-8} $\Omega = (\omega) \frac{d^2}{mm^2} \cdot (\varepsilon_c \frac{k}{h}) \ d^{-1}.$ $(\alpha)\ mm^2\ d^{-1}\ (A)$ $mm^2\ d^{-1}. \quad (2\pi rh) mm^2$ $= mm^4\ d^{-1}$

Lindgren studied the development of *C. pilifera* in small inoculated blocks of *Pinus echinata* sapwood maintained for 10 days at different moisture contents at 25° C. His results indicate that below 24 percent moisture content of blocks (oven-dry basis), there was no surface or interior growth of the fungus. At moisture contents between 24 and 25 percent, hyaline filaments were well distributed through the wood rays and tracheids. Above 27 percent, the blocks contained mature, brown hyphae and were usually visibly stained by the end of 10 days of incubation.

Colley and Rumbold's (1930) studies are in agreement with Lindgren (1942), that a moisture content in the region of 24 percent is the lower limit for staining of wood caused by *C. pilifera*. Such a limit is considered reasonable even though minimum moisture contents for stain development undoubtedly vary to some extent for different organisms and for woods with different fiber-saturation points.

Snell (1929) reported that for southern pine sap of sp. gr. 0.44, the upper limit of moisture content for optimum growth of blue-staining fungi is 100 percent, while inhibition takes place at 145 to 150 percent of moisture. For southern yellow pine, of sp. gr. 0.70, the limits are 50 percent and 75 to 80 percent, respectively.

On the basis of Kidd's data using *C. monita*, the area growth rate of the fungus as a function of water potential is given by

$$G_f(\psi) = A\, e^{-B\psi} \qquad (11)$$

Taking the logarithm of (10), we obtain

$$\ln G_f = \ln A - B\psi \qquad (12)$$

Substituting for Ψ from equation (6), we get

$$\ln G_f = \ln A - B\, a\, e^{-b\theta_f} \qquad (13)$$

That is,

$$\ln G_f = \ln A - c\, e^{-b\theta_f} \qquad (14)$$

where

$$c = a\,B.$$

Data for the longitudinal penetration of *Trichoderma lignorum* into sapwood of *P. taeda* (Spradling 1936) show an optimum growth rate around 100 percent moisture. Development data (less defined than penetration or growth rate) of *C. pilifera* in small inoculated blocks of *P. echinata* sapwood at different moisture contents indicate that after the establishment of the spores the growth rate reaches maximum above 24 percent moisture content (Lindgren 1942). The longitudinal penetration of *T. lignorum* in *P. taeda* averaged 4.41 mm a day over a moisture content range of 77 to 118.4 percent (oven-dry basis). In the final formulation of the model equation, all the components will be expressed either in terms of water potential or moisture content, which are related via equation (6). Figure 4 shows the relation between fungus growth rate and water potential, based on the data of Kidd et al. (1977).

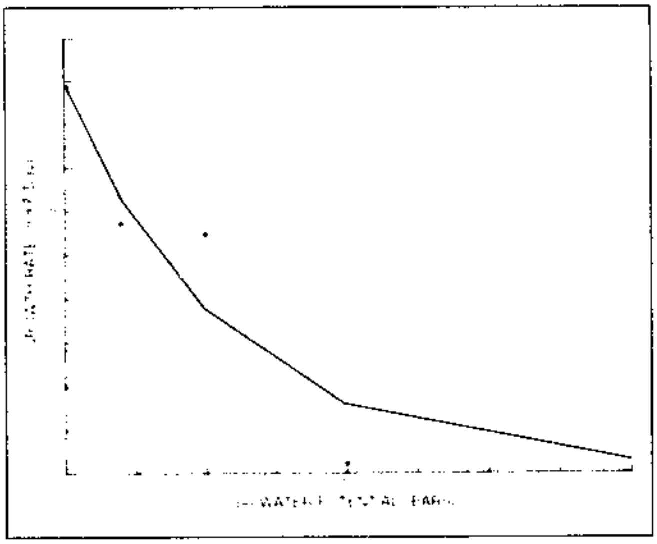


Figure 4.--Area growth rate of *C. monita* as a function of tree water potential. (+) represents data points, and solid line is the fitted model. (Data from Kidd et al. 1977.)

Growth Rate as a Function Of Physiological Time

For a given set of conditions (e.g., temperature T_t, moisture content θ, and/or water potential Ψ), the rate of growth of several fungi was studied (Lindgren 1942, Kidd et al. 1977, and Snell 1929). We analyzed the data published by these authors in order to understand the biophysical basis of the growth rate of the fungus as a function of physiological time, i.e., $G_f = f(t)$.

The changes in the growth-temperature relations with time have been reported for several groups of fungi (Scheffer and Lindgren 1940). If the factor of time is important, its effect should be particularly evident in comparing growth of wood-staining organisms for short periods on agar against decay of wood during periods of several months. In such cases, however, we must acknowledge the possible effect of differences in substrate, as well as time. Humphrey and Siggers (1933) reported that for 7 of 21 fungi studied, the optimum temperature for growth on agar shifted to lower points with increase of inoculation periods. This change suggested that the optimum temperature for decay of wood over long periods might be lower than those indicated by the agar tests of short duration.

Lindgren (1942) noted that for one of three fungi studied there was a slight reduction in growth on agar and decay of wood with time at the higher temperatures. In his study with *C. pilifera* there was no definite periodicity in growth rate, as suggested by Lagerberg et al. (1927). Furthermore, there was no apparent shifting downward of optimum and maximum temperatures for growth on agar or in wood with increase in time of incubation. The rapid development of most staining fungi on wood, as well as on agar, would make the factor of time less significant than it might be for many other wood-attacking organisms.

Information on the rate of penetration of staining fungi into wood has been limited largely to general indications yielded by studies affecting stain development. Münch (1907, 1908) reported an average longitudinal growth of *C. minor* of 5 to 10 mm/day. Lagerberg et al. (1927) present some general figures that indicate daily radial rates of penetration on the magnitude of 2 to 2.5 mm for *C. minor*, under favorable or semi-favorable growth conditions. Greatly reduced rates of penetration were indicated as moisture, oxygen, and other conditions affecting growth become less favorable.

Bramble and Holst (1940) indicate that during the growing season, 14 days after initial attack, when the foliage begins to turn yellow, *C. minor* reaches the heart of the wood of stems 4 to 6 inches in diameter, representing an average penetration rate of 4.5 mm/day. Cultures taken from the phloem surrounding the beetle tunnels and from underlying sapwood to a depth of 1 mm (one or two growth rings) yielded *C. minor*, *Dacryomyce* spp., and *Z. minor* (Bramble and Holst 1940). Such early penetration indicates that infection precedes any considerable drying of sapwood through loss of moisture from beetle tunnels but does not preclude the possibility that a certain slight drop in mositure may be necessary for penetration into the outer rings. The ability of fungi to penetrate into the sapwood shortly after initial entrance by beetles is perhaps a significant feature in connection with their effect on the attacked tree.

Lindgren's (1942) experiments on the penetration of *C. pilifera* into wood blocks as a function of time under controlled conditions of temperature and relative humidity represent one of the rare quantitative studies of this type. The average moisture contents of the blocks after several incubation periods, based on six specimens in each case, were 104, 98, 106, 105, and 100 percent under conditions of 90 percent relative humidity; and 106, 107, 96, 102, and 96 percent at 60 percent relative humidity. He measured the tangential, radial, and longitudinal daily penetration of the fungus. On the basis of his data, a ratio of 1:2:9 for the rates in three directions of penetration is obtained. The rate of penetration of the fungus in any direction shows an enzyme-controlled type of behavior. If we consider the fraction of the stem's cross-section area covered daily by the fungus (i.e., tangential penetration × radial, it shows a behavior (*see* fig. 5) that can be described by an analytical expression of the type

$$G_f(t) = \frac{\alpha t}{\beta + \gamma t} \qquad (15)$$

where α, β and γ are constants to be determined.

We can now write a final expression for A_c as a function of temperature T, time t, and xylem water potential Ψ, assuming A_T to be constant during the short period while the tree is drying:

$$A_c = A_T - \omega \frac{\varepsilon_c kT}{h} \cdot e^{(\Delta S_A^{+} - \Delta H_A^{+}/T)/R} \cdot Ae^{-B\Psi} \cdot P_2 \cdot \frac{\alpha t}{\beta + \gamma t} \cdot 2\pi rHF \qquad (16)$$

$2\pi rHF$ is dimensionless, *H* being the length of the tree bole first attacked by the beetle; therefore, the proportionality constant ω has units time area^{-1}. If we consider $2\pi rHF$ a constant, then we can lump all coefficients into Ω which will have units of area time. The expression becomes

$$A_c = A_T - \Omega \frac{\varepsilon_c kT}{h} e^{(\Delta S_A^{+} - \Delta H_A^{+}/T)/R} \cdot P_2 \cdot e^{-B\Psi} \cdot \frac{1}{\beta + \gamma t} \qquad (17)$$

where $\Omega = \omega \cdot A \cdot \alpha \cdot 2\pi rHF$.

We note here that for long times, equation (15) reduces to a constant. That is, as t becomes large,

$$G_f(t) = \frac{\alpha}{\frac{\beta}{t} + \gamma} \simeq \frac{\alpha}{\gamma} = \text{constant}$$

Equation (17) can be rewritten as follows

$$A_c = A_T - \Omega \frac{\varepsilon_c kT}{h} e^{(\Delta S_A^+ - \Delta H_A^+/T)/R}$$

$$\cdot P_2 \cdot e^{-B\Psi} \cdot \frac{1}{\beta + \gamma t}$$

$$= A_T - \Omega e^{\ln\left(\frac{\varepsilon_c kTt}{h}\right)} e^{(\Delta S_A^+ - \Delta H_A^+/T)/R}$$

$$\cdot P_2 \cdot e^{-B\Psi} \cdot \frac{1}{\beta + \gamma t} \qquad (18)$$

If we define

$$\phi = \Delta S_A^+ + R \ln \left(\frac{\varepsilon_c kTt}{h}\right) \quad \text{cal mole}^{-1} \text{ deg}^{-1} \qquad (19)$$

and

$$B' = RB \qquad \text{cal mole}^{-1} \text{ deg}^{-1} \text{ bar}^{-1}$$

then equation (18) becomes

$$A_c = A_T - \Omega e^{(\phi - B'\Psi - \Delta H_A^+/T)/R} \cdot P_2 \cdot \frac{1}{\beta + \gamma t} \qquad (20)$$

One may be interested in the fraction of the stem cross section that is covered with the fungus over a certain period of time, which is given by

$$\text{Fraction} = \frac{A_c}{A_T} = 1 - \frac{\Omega}{A_T} e^{(\phi - B'\Psi - \Delta H_A^+/T)/R}$$

$$\cdot P_2 \cdot \frac{1}{\beta + \gamma t} \qquad (21)$$

The final expression for dW_{in}/dt should then be

$$\frac{dW_{in}}{dt} = \Delta\Psi_{L,s} \cdot L_w(A_T - \Omega e^{(\phi - B'\Psi - \Delta H_A^+/T)R}$$

$$\cdot P_2 \cdot \frac{1}{\beta + \gamma t})$$

or

$$\frac{dW_{in}}{dt} = L_w(\Psi_L - \Psi_S) \cdot (A_T - \Omega e^{(\phi - B'\Psi - \Delta H_A^+/T)R}$$

$$\cdot P_2 \cdot \frac{1}{\beta + \gamma t}) \qquad (22)$$

It should be noted that Ψ is a function of water content θ and time *t*. The relationship between Ψ and θ is given in equation (6). However, the variation of Ψ with the physiological time of fungus growth is believed to be dependent on the fungus species and its water requirement for growth. For a given set of conditions (site and environmental demands), the negative water potential is approximately constant. When the beetle inoculates the tree with fungi, their water demand will result in an increasing water stress. It seems reasonable then to assume that the time dependence of Ψ can be represented by the expression

$$\Psi = a + bt^m \qquad (23)$$

where the constant *a* is the water potential of the noninfested tree and *b* and *m* are dependent on the fungus water demands, which should be species dependent. Recent data (see Wagner et al. 1979) seem to validate the concept represented by equation (23) and give the values of *a*, *b*, and *m*. Figure 6 shows a plot of Ψ *v*. time of their data.

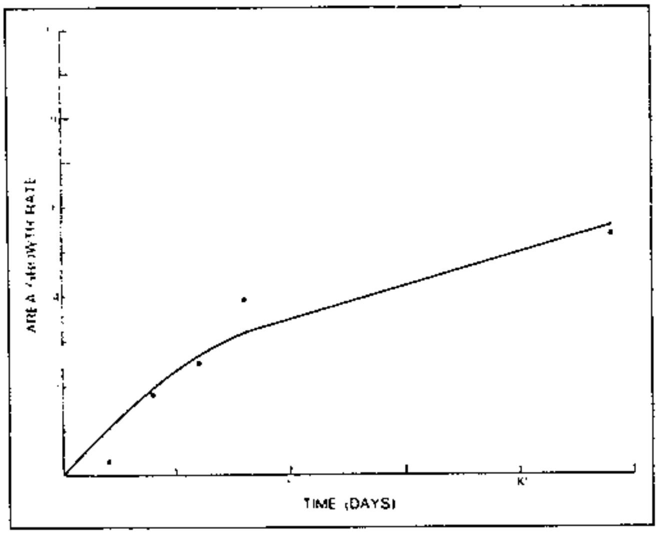


Figure 5.--*C. pilifera* growth rate as a function of time. (+) represents data points from Lindgren (1942), and the solid line is the fitted model.

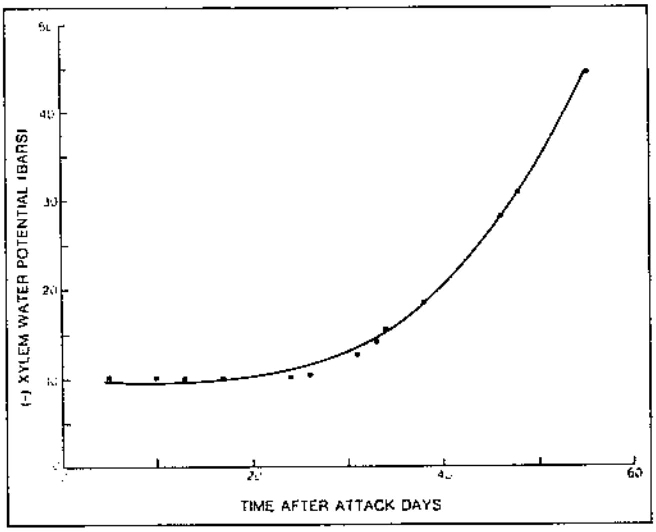


Figure 6.--The change of xylem water potential with time after beetle attack. (+) represents data points from Wagner et al. (1970). The solid line represents the model.

For purposes of computation, the dependence of Ψ on ϕ and t, [i.e., $\Psi = f(\phi, t)$] may be expressed in the following fashion using equations (6) and (22)

$$\Psi(\phi,t) = ke^{C\theta}(a + bt^{m})$$

i.e.,

$$\Psi(\phi,t) = ake^{C\theta} + bkt^{m}e^{C\theta} \qquad (24)$$

And if we define $ak = k'$ and $bk = k''$, then

$$\Psi(\phi,t) = k'e^{C\theta} + k''t^{m}e^{C\theta} \qquad (25)$$

However, equations (17) and/or (21) can be expressed directly in terms of moisture content if the growth rate of the fungus as a function of time is known as well as the variation of moisture contnet with time.

As mentioned earlier, when the fungus is introduced in the attacked tissue there is a 10 to 15 percent reduction in xylem moisture content over a short period of time. After this initial period the xylem moisture content decreases very slowly. The rapid drop of moisture content in the initial period of infestation seems to provide the fungus with the proper medium for growth. At a later time after infestation the moisture content may increase. This phenomenon is probably of little bearing on the tree drying in relationship to the brood since the brood would have emerged. However, the increase is of great importance in relation to the timber value. Gaumer and Gara (1967) reported similar observations on the phloem water content of infested boles. This type of behavior is described by an expression of the form

$$\theta(t) = ke^{a''+b''t+c''t^{2}} \qquad (26)$$

Again, the data obtained by Wagner et al. (1979) seem to validate this expression, as shown in figure 7, and provide values of the models constant. However, it is normally easier to measure Ψ in the field than θ, and equations (17) and (21) can be directly utilized.

Rate of Change Of the Tree Water Content

dW_c/dt is dependent on the tree volume, $V_T = A_T L_T$, the specific water loss of the tree, $d\theta_f/dt$ (i.e., the weight of water loss per unit weight of tissue per unit time after infestation). It is also dependent on the specific water content of the tree, ρ (i.e., water content mass/unit volume of tissue). Therefore, we have

$$\frac{dW_c}{dt} = A_T L_T \rho \frac{d\theta}{dt} \qquad (27)$$

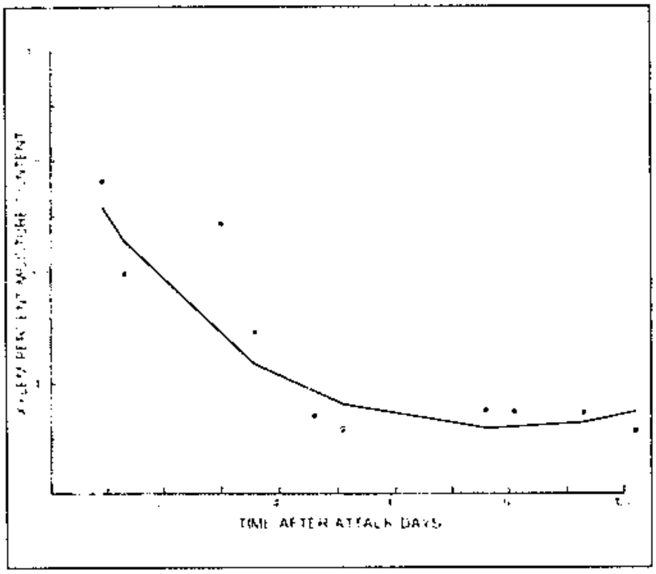


Figure 7.--The change of xylem moisture content with time after beetle attack. (+) represents data points from Wagner et al. (1979), and the solid line is the fitted model.

On differentiating equation (26), we obtain

$$\frac{d\theta}{dt} = k(b''+2c''t)\, e^{a''+b''t+c''t^{2}}$$

or

$$\frac{d\theta}{dt} = (b''\theta + 2c''t\theta) \qquad (28)$$

Therefore,

$$\frac{dW_c}{dt} = \rho\, V_T\, (b''\theta + 2c''t\theta) \qquad (29)$$

or

$$\frac{dW_c}{dt} = \rho\, V_T(b^{+}\, e^{a''+b''t+c''t^{2}} + 2c^{+}t\;\; e^{a''+b''t+c''t^{2}}) \qquad (30)$$

where

$$b^{+} = kb'' \text{ and } c^{+} = kc''.$$

Not much is known about $d\theta_f/dt$ after infestation; however, some insight of the change in θ_f with time was obtained from the data collected by Wagner et al. (1979). These data were also used in the validation of equation (27).

The Final Expression of the Model

From equation (1) we write the general expression as

$$\frac{dW_c}{dt} = \frac{dw_{in}}{dt} - \frac{dM}{dt} \qquad (31)$$

From (31) we can write the equivalent expression

$$\frac{d\theta_f}{dt} = \frac{1}{V_T}\left[\frac{dW_{in}}{\rho dt} - \frac{dM}{dt}\right] \qquad (32)$$

making use of equation (27). Note that equation (31) gives the change of total water of the tree with time, while equation (32) gives the change in the moisture content of xylem with time after infestation. From equations (28) and (29) one can obtain an independent expression for $d\theta/dt$ and dW_c/dt, respectively, as a function of θ and t only. When the expressions for all the interdependencies are substituted in equations (31) and (32), they become

$$\frac{dW_c}{dt} = (a\,e^{-b\theta_f} - \Psi_s) \cdot \left\{A_I - \left[\Omega\,e^{(\phi - B'\Psi - \Delta H_A^{\ddagger}/T)/R} \cdot P_2 \cdot \frac{1}{\beta + \gamma t}\right]\right\} - \frac{[\rho_{sa}(T_a) - \rho_a(T_a)](B + C\Psi_L)S}{A + BK + CK\Psi_L} \qquad (33)$$

and

$$\frac{d\theta_f}{dt} = \frac{1}{\rho V_T}\,\frac{dW_c}{dt} \qquad (34)$$

respectively. Each term in equation (33) and the constants obtained from model component validation are given in table 2 together with an expression for the model component validated.

Equation (33) and/or (34) relate the rate of drying to (1) environmental conditions, and (2) the changes in the physiological properties of the tree, resulting from pine bark beetles and the effects of fungus growth within the tree bole.

On integrating equations (33) and (34), one simply obtains expressions of the form

$$W_c = f\,(G_f, T, \Psi, t) \qquad (35)$$

and

$$\theta_f = f\,(G_f, T, \Psi, t) \qquad (36)$$

respectively. If G_f, T, and Ψ are known, measured, or calculated from model components, then experimental measurement of θ_f at any time enables one to calculate t, the time from beetle attack. This serves as a dating technique in relation to timber salvage and gives vital information on infestation age. When t, the time from infestation, is known together with Ψ and the daily temperature range over a period of time, t, it is then possible to predict the degree of development of the brood and time of emergence of the beetle, an important input to any mechanistic spot dynamics model. (We will address the degree of drying in relation to brood development in a future communication.)

Although the model components have been validated, the overall model has not yet been validated due to lack of data that deal with all the variables incorporated in the model.

CONCLUSION

This paper has presented a model describing the quantitative interaction of the pine tree, the blue-stain fungus, and the environment. We identified the physiological factors of the tree, their relationships to the environment, and their influence on the fungus growth rate and incorporated them in the model formulation. The interdependencies--tree physiology, tree environment, and fungal growth--have been analyzed and quantitatively integrated into a fungus tree environment model. This model gives a time course description of the pine tree drying that relates to the degree of brood development and beetle emergence time as well as to the age of the spot and its obvious implications for forest management.

LITERATURE CITED

Barras, S. J. 1973. Reduction of progeny and development in the southern pine beetle following removal of symbiotic fungi. Can. Entomol. 105:1295-1299.

Bramble, W. D., and E. C. Holst. 1940. Fungi associated with *Dendroctonus frontalis* in killing short leaf pines and their effect on conduction. Phytopathology 30:881-889.

Caird, R. W. 1935. Physiology of pines infested with bark beetles. Bot. Gaz. 96:709-733.

Colley, R. H., and C. T. Rumbold. 1930. Relation between moisture content of the wood and blue stain in loblolly pine. J. Agric. Res. 41(5): 389-399.

Craighead, F. C. 1928. Interrelations of tree-killing bark beetles (*Dendroctonus*) and blue stain. J. For. 26: 836-837.

DeMichele, D. W., and P.J.H. Sharpe. 1973. An analysis of the mechanism of guard cell motion. J. Theor. Biol. 41:77-96.

DeMichele, D. W., and P.J.H. Sharpe. 1974. A parametric analysis of the anatomy and physiology of the stomata. Agric. Meteorol. 14:229-241.

Gaumer, G. C., and R. I. Gara. 1967. Effects of phloem temperature and moisture content on the development of the southern pine beetles. Contrib. Poyce Thompson Inst. 23(11): 373-378.

Humphrey, C. J., and P. V. Siggers. 1933. Temperature relations of wood destroying fungi. J. Agric. Res. 47(12):947-1008.

Kidd, F. A., C.P.P. Reid, and R. W. Davidson. 1974. Cultural growth inhibition of *Ceratocystis monita* by induced water stress. Mycologia 69:615-618.

Finerson, R., Jr., and L. J. Fritschen. 1971. Modeling a coniferous forest canopy. Agric. Meteorol. 8:439-445.

Lagerberg, T., G. Lundberg, and E. Melin. 1927. Biological and practical researches into blueing in pine and spruce. Svenska Skogsvardsfor. Tidsk Haft II:145-272.

Laudien, H. 1973. Temperature and life. p.355-399. H. Precht, J. Christopherson, H. Hensel, and W. Larcher, eds. Springer-Verlag, Berlin and Heidelberg.

Lindgren, R. M. 1942. Temperature, moisture, and penetration studies of wood-staining Ceratostamellae in relation to their control. U.S. Dep. Agric., Tech. Bull. 807.

MacCallum, B. D. 1922. Some wood staining fungi. Trans. Bi. Myc. Soc. 7:231-236.

Münch, E. 1907. Die Blaufaüle des Nadelholzes. Naturwiss. Zeitschr. für Forstu. Landwirtsch. 5:531-573.

Münch, E. 1908. Die Blaufaüle des Nadelholzes. Naturwiss. Zeitschr. für Forstu. Landwirtsch. 6:297-323.

Nelson, R. M. 1934. Effect of blue stain fungi on southern pines attacked by bark beetles. Phytopath. Z. Bd. 7 Heft 4, 23.

Nelson, R. M., and J. A. Beal. 1929. Experiments with blue stain fungi in southern pines. Phytopathology 19:1101-1106.

Precht, H., J. Christopherson, H. Hensel, and W. Larcher. 1973. Temperature and Life. 779 p. Springer-Verlag, Berlin and Heidelberg.

Rumbold, C. T. 1931. Two blue staining fungi associated with bark beetle infestation of pines. J. Agric. Res. 43:847-873.

Scheffer, T. C., and R. M. Lindgren. 1940. Stains of sapwood products and their control. 123 p. U.S. Dep. Agric., Tech. Bull. 714.

Sharpe, P.J.H., and D. W. DeMichele. 1977. Reaction kinetics of poikilotherm development. J. Theor. Biol. 64:649-670.

Sizer, J. W. 1943. Effects of temperature on enzyme kinetics. Adv. Enzymol. 3:35-63.

Slayter, R. O. 1967. Plant water relationships. Chapter 5 and references therein. Academic Press, London.

Snell, W. H. 1929. The relation of the moisture contents of wood to its decay III. Am. J. Bot. 16:543-545.

Spradling, M. 1936. Penetration of *Trichoderma lignorum* in sapwood of pine. J. Agric. Res. 52(7):541-546.

Vité, J. P. 1959. Observations on the movement of injected dyes in *Pinus ponderosa* and *Abies concolor*. Contrib. Boyce Thompson Inst. 20:7-38.

Wagner, T. L., J. A. Gagne, P. C. Doraiswamy, R. N. Coulson, and K. W. Brown. 1979. Development time and mortality of *Dendroctonus frontalis* in relation to changes in tree moisture and xylem water potential. Environ. Entomol. 8:1129-1138.

PHEROMONE DISPERSION IN A FORESTED ECOSYSTEM

Youhanna Fares, Peter J.H. Sharpe, and Charles E. Magnuson[1]

Abstract.--In this paper we present a simple generic model for the dispersion of pheromones in a forested ecosystem. We also describe methods for the calculation of various concentration-related parameters and discuss the influence of different micrometeorological conditions on concentration profiles. Two separate studies from two different geographical locations lend support to the predictions of the dispersion model. For two different species of *Dendroctonus* beetles, aggregration behavior correlates with meteorological condition resulting from inversion profiles. Finally, we propose a technology transfer scheme for the utilization of the model in forest management.

INTRODUCTION

Recently, the olfactory response systems of insects have received a great deal of attention (Kaissling 1971). Although we now know a great deal about the chemistry and electrophysiology of pheromone receptors, we have a lot to learn about how these pheromones are transmitted between organisms. Vité, Gara, and von Scheller (1964) demonstrated the importance of pheromones in regulating flight, population aggregation, and attack behavior of the southern pine beetle (SPB). Vité's team found that insect activity and response to likely pheromone sources was strongly affected by seasonal weather conditions. Many of Vité's observations can be explained in terms of the meteorological conditions characterizing either lapse or inversion profiles within the forest. With the prospect of behavioral chemical control for management of forest insects in the future, it is imperative that the micrometeorology of olfactory communication be understood and quantitatively described. We simply will not be able to assess the potential value of behavioral chemicals unless we understand the influence of weather in dispersing them.

This study attempts to lay a theoretical foundation for pheromone dispersion within natural ecosystems. We are concerned here with pheromone dispersion in a forested area in general and in particular with regard to the aggregation and flight patterns of the southern pine beetle (*D. frontalis* Zimm.) and mountain pine beetle (*D. ponderosae* Hopk.). The model, however, is generic and should also be applicable to other insect ecosystems.

The general approach has been to draw upon meteorological models already developed and currently in use in pollution studies. It is obvious that Fickian diffusion--even for large rates of pheromone emmission and low sensory thresholds--cannot provide a mechanism for the range of olfactory communication distances observed. For olfactory communication to have more than a very limited range, it must rely upon the turbulence of the wind. In any perceptible wind, a turbulent diffusivity, often called eddy diffusivity, overwhelms the diffusion properties of a given medium, with the resultant diffusivity constants becoming properties of the wind structure, boundary surfaces, and ambient micrometeorology. (Relevant terms are defined in the Appendix.)

MECHANICS OF DISPERSION

There have been two basic approaches to describing the role of Earth's lower atmosphere in redistributing and diluting the concentration of emmitted particles. The first, based on Fickian diffusion, was developed by Roberts (1923) and extended to a general three-dimensional case independently by Richardson (1926) and Schmidt (1925). In Sutton's (1953) variation on this approach, C_z and C_y are diffusion constants determined by the wind profile and n is a third, arbitrary constant. Sutton's formulation was utilized by Bossert and Wilson (1963).

---

[1] The authors are, respectively, Senior Research Scientist, Associate Professor, and Senior Research Scientist, Biosystems Research Division, Dept. of Industrial Engineering, Texas A. & M. University, College Station. The work herein reported was funded in part by a USDA-sponsored program entitled "The Expanded Southern Pine Beetle Research and Applications Program", Grant Number 89-106 (19-258).

But more recently, field studies by the U.S. Army Electronic Command, ECOM-3 (1970), on the dispersion of air tracers into and within forested areas have shown that Sutton's equation is generally unreliable for predicting special concentration patterns. Only with night time releases in an open clearing did the Sutton equation, modified for deposition, provide reasonable estimates.

The alternative approach is the statistical theory of fluid turbulence, which began with the investigation of turbulent diffusion by Taylor (1921). This approach is widely applied in many areas ranging from oceanography to cosmology. In the statistical approach, one studies the histories of motion of individual fluid particles, trying to determine from these the statistical properties necessary to describe the underlying dispersal process.

The most widely accepted distribution for describing particulate dispersion in space is the probability density function, i.e., the Gaussian function (Batchelor 1949, 1950; Barad and Haugen 1959). The underlying principle is that the Gaussian function provides a general description of the dispersion of the three-dimensional plume of the average pheromone concentration because of the essentially random nature of dispersion. Lin and Reid (1963) point out that for very small dispersal times, the spatial distribution of particles should take the same form as the wind-fluctuation distribution since the particle trajectories coincide with the instantaneous windspeed vector. In the atmosphere this approximates a Gaussian distribution (G.D.) fairly closely. The advantage of the G.D. is its simplicity. Only two dispersion parameters are required--σ_y and σ_z--and most field studies are currently reported in terms of these parameters of plume spread.

There are five underlying assumptions in the application of an atmospheric Gaussian distribution model to pheromone dispersion.

(1) Pheromone release is from a continuous point source.

(2) A continuous plume is composed of an infinite number of puffs released sequentially with a vanishingly small time interval between puffs. Initially each puff moves in the wind direction at the moment of release (this simplifies the calculations).

(3) The expected concentration distribution perpendicular to the axis of the plume resembles a normal or Gaussian distribution around the centerline.

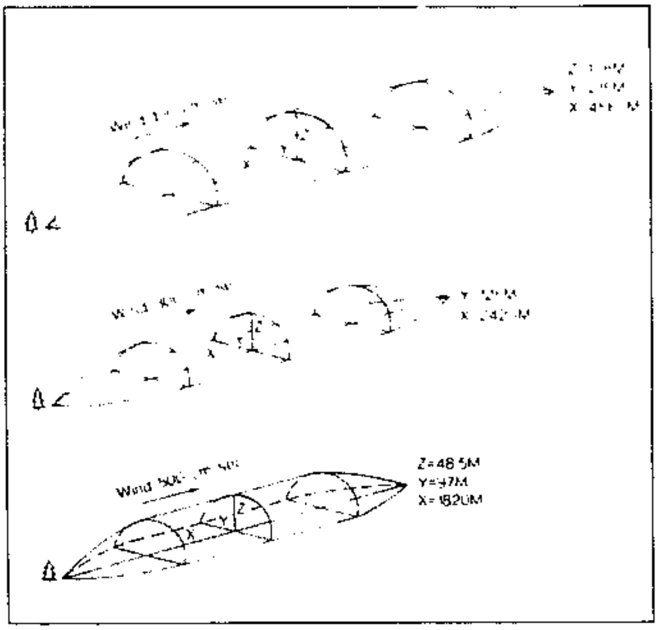


Figure 1.--The threshold volume of sex attractants from a single female gypsy moth at various wind velocities (Bossert and Wilson 1963).

(4) The rate at which the centerline concentration decreases varies with the atmospheric stability, i.e., with the magnitude and scale of turbulence. It is also important to recognize that wind fluctuations that are larger than the plume dimensions tend to transport the plume intact, whereas those that are smaller tend to tear it apart.

(5) The turbulent structure of the atmosphere is intimately related to the vertical temperature structure, and the latter is an index to the former.

The significant difference between the Gaussian plume model and that utilized by Bossert and Wilson (1963) can be seen in figures 1 and 2. Figure 1 shows Bossert and Wilson's plume shape, which maintains a constant width. The Gaussian plume model shown in figure 2 expands both laterally and vertically with downwind distance from the source. Because the plume cross section is usually close to the Gaussian distribution function, the linear dimensions of the plume perpendicular to plume axis can be given in terms of the standard deviation of the concentration distribution.

GAUSSIAN PLUME MODEL

Pheromone dispersal occurs in three-dimensional space, which can be located in a Cartesian coordinate system (x,y,z) as shown in figure 3. In this sytem, the origin (0,0,0) is fixed at ground level, at or beneath the source of emission. The x axis extends horizontally in the direction of the wind, the y axis is located in the horizontal plane perpendicular to the x axis, and the z axis extends vertically. The plume travels along or parallel to the x axis. This coordinate system and origin location will be used throughout this analysis.

The Gaussian model describes the dispersal of gases, vapors, or aerosols where the molecule or particle size is less than 20μ. It therefore includes almost all known gaseous pheromones, which generally have molecular weights in the range of 100 to 300 daltons. The concentration C of pheromone molecules at any given point x,y,z, resulting from a continuous emmission at effective height H, is given by:

$$C\,(x,y,z;\,H) = \frac{Q}{2\pi\sigma_y(x)\,\sigma_z(x)\,u}\left[\exp -\tfrac{1}{2}\left(\frac{y}{\sigma_y(x)}\right)^2\right] \times \left\{\exp\left[-\tfrac{1}{2}\left(\frac{Z-H}{\sigma_z(x)}\right)^2\right] + \alpha\,\exp\left[-\tfrac{1}{2}\left(\frac{Z+H}{\sigma_z(x)}\right)^2\right]\right\} \qquad (1)$$

where

u = the mean wind speed in the dispersal region,

Q = the effective average rate of pheromone emission in molecules sec.^{-1},

H = the effective height of emission in m with $\sigma_y(x)$ and $\sigma_z(x)$ being the lateral and vertical diffusivities of plume concentration in meters, respectively.

α = a reflection coefficient that varies from 0 to 1.

When $\alpha = 0$, this means complete absorption of pheromones at the ground level, and $\alpha = 1$ means total reflection. Also implicit in the analysis is the obvious condition that the windspeed u and associated turbulence is greater than the Fickian diffusion of pheromone in the x direction. C will have units of molecules m^{-3}.

For concentrations calculated at ground level ($z = 0$), equation (1) simplifies to:

$$C(x,y,0,\,H) = \frac{Q(1+\alpha)}{2\pi\sigma_y(x)\,\sigma_z(x)\,u}\,\exp\left[-\tfrac{1}{2}\left(\frac{y}{\sigma_y(x)}\right)^2\right] \cdot \exp\left[-\tfrac{1}{2}\left(\frac{H}{\sigma_z(x)}\right)^2\right] \qquad (2)$$

where the concentration is to be calculated along the centerline of the plume ($y=0$).

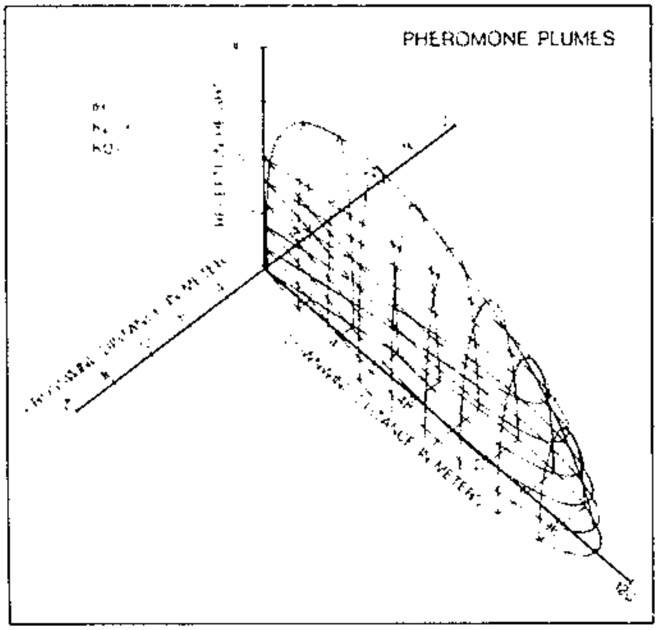


Figure 2.--Pheromone plume dimensions. The threshold pheromone concentration at the plume surface is 10 percent of ground-level centerline concentration.

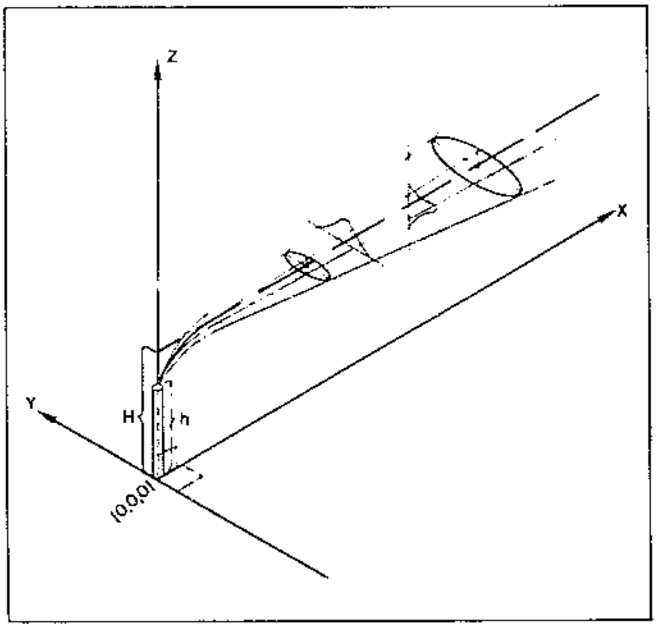


Figure 3.--Coordinate system showing Gaussian distribution in the horizonal and vertical. h = source height, H = effective plume centerline.

Further simplification yields

$$C(x,0,0;H) = \frac{Q(1+\alpha)}{2\pi\sigma_y(x)\,\sigma_z(x)\,u}\exp\left[-\tfrac{1}{2}\left(\frac{H}{\sigma_y(x)}\right)^2\right] \quad (3)$$

For a ground-level source, such as attempted in the analysis of Bossert and Wilson (1963) where $H = 0$, the plume can be described by the relationship

$$C(x,0,0;0) = \frac{Q(1+\alpha)}{2\pi\sigma_y(x)\,\sigma_z(x)\,u} \quad (4)$$

In many pollution studies, the emission source itself has a significant velocity in the vertical direction, causing a rise ΔH in the plume above the actual emission height H. This phenomenon can be ignored in the current analyses as emission from biological organisms is unlikely to have enough velocity to affect the location of the centerline of the plume. Throughout this paper, α in equation (1) is set equal to 1. That is, there is total reflection at ground level.

FOREST DISPERSAL COEFFICIENTS

Many of the economically important insect pests utilizing gaseous pheromone communication systems reside in crop or forest habitats. Some forest-dwelling pests that use pheromone communication for aggregation and host-tree attack include the southern pine beetle, mountain pine beetle, and western pine beetle (*D. brevicomis* Lec.).

Studies on plume dispersal in dense vegetation canopies are scarce and their results often classified or unpublished. The results presented in this paper depend to a large extent upon the conclusions of four major studies which were made available to us.[2]

From these studies, we have drawn the following conclusions.

(1) Vegetation density has a strong influence on the dispersal characteristics within a forest. Although the windspeed within a forest is not strongly coupled to that outside the forest, the presence of generators of turbulence (tree trunks, branches, leaves, etc.) substantially increases the lateral diffusivity of the forest environment. Thus, the dispersal coefficients within the forest (σ_y and σ_z) for any given windspeed profile are different than would be expected for similar conditions of open terrain.

(2) Air temperatures above and within the forest were found to be dominating factors. Common forest daytime conditions result in an inversion regime within the stem zone and lapse condition within the upper portion of the canopy.

For the biological reader, these latter terms need some clarification. The turbulent structure of the atmosphere was classified by Pasquill (1961) into stability classes. These classes are defined in terms of incoming solar radiation during the day, or equivalent cloud cover during the night, together with windspeed at a height of about 10 m (see table 1). Other schemes of stabilit classes based on lapse rates (i.e., vertical temperature gradient from the canopy floor and the equivalence to Pasquill's stability classes) are often made. For example, see tables 2, 3, and 4. A lapse condition describes an unstable micrometeorological regime with a negative upward air temperature gradient. An inversion condition is a stable micrometeorological regime where the air temperature gradient is negligible or reversed downward. Pasquill (1961) devised a method for estimating σ_y and σ_z *v.* downwind distance for the various stability classes. These schemes are unfortunately based on data collected over open terrain and are therefore not reliable for regions covered with vegetation.

Dispersal experiments conducted by Melpar, Inc. (1969), in rain forest canopies found that lateral dispersion was enhanced while transport was greatly reduced for equivalent stability conditions outside the canopy. On cloudy days the Melpar group found that rapid vertical mixing occurred in the stem zone with a small inversion normally occurring in the upper portion of the plume, thus giving rise to a situation similar to fumigation. This condition resulted in the greatest concentration observed in this study being at ground level.

With clear skies, sunlight is absorbed by the upper layers of the leaf canopy, which in turn heats the air and produces instability in the canopy zone and an inversion beneath the dense canopy. The aerosol below the dense vegetation tended to be trapped until it flowed, by a thermal chimney, rapidly out of the rain forest. A thermal chimney can occur where less dense vegetation or small canopy openings allow solar

---

[2] These studies were undertaken by the U.S. Army Dugway Proving Grounds (TRC-343) in a woodlot complex (1969); Litton Systems, Inc., in a deciduous forest for desert Test Center, report number 3004 (1969); the U.S. Army Electronic Command, ECOM-68-68-1 (1969); and Melpar (1969) in jungle canopy.

Table 1.--Relation of turbulence types to weather conditions (after Pasquill 1961).

A = Extremely unstable conditions	D = Neutral conditions[1]	F = Moderately stable conditions
B = Moderately unstable conditions	E = Slightly stable conditions	G = Extremely stable conditions
C = Slightly unstable conditions		

Surface windspeed (m/sec)	Daytime insolation			Nighttime conditions	
	Strong	Moderate	Slight	Thin overcast or ≥ 4/8 cloudiness[2]	≤ 3/8 cloudiness
< 2	A	A-B	B		
2	A-B	B	C	E	F
4	B	B-C	C	D	E
6	C	C-D	D	D	D
> 6	C	D	D	D	D

[1] Applicable to heavy overcast, day or night.

[2] The degree of cloudiness is defined as that fraction of the sky above the local apparent horizon which is covered by clouds.

Table 2.--Insolation as a function of solar altitude (after Turner 1964).

Solar altitude (a)	Insolation	Insolation class number
60° < a	strong	4
35° < a ≤ 60°	moderate	3
15° < a ≤ 35°	slight	2
a < 15°	weak	1

Table 3.--Stability class as a function of net radiation and windspeed (after Turner 1964).

Windspeed (knots)	Net radiation index						
	4	3	2	1	0	-1	-2
0,1	1	1	2	3	4	6	7
2,3	1	2	2	3	4	6	7
4,5	1	2	3	4	4	5	6
6	2	2	3	4	4	5	6
7	2	2	3	4	4	4	5
8,9	2	3	3	4	4	4	5
10	3	3	4	4	4	4	5
11	3	3	4	4	4	4	4
≥12	3	4	4	4	4	4	4

energy to penetrate to the forest floor and heat the ground and adjacent air, which becomes buoyant and rises through the canopy opening. Deposition, by contrast, was highly dependent on turbulence and was increased when an inversion trapped the released material below the crown, aiding the downwind transport process.

A rain forest represents the opposite extreme to that of open terrain. Most vegetation systems do not have the vegetation density of a rain forest; therefore, their dispersal characteristic will be somewhere between the above extremes.

Table 4.--Stability class as a function of vertical temperature profile.[1]

Stability classification	Pasquill category	Temperature change with height °C/100 m
Extremely unstable	A	-1.9
Moderately unstable	B	-1.9 to -1.8
Slightly unstable	C	-1.7 to -1.6
Neutral	D	-1.5 to -0.6
Slightly stable	E	-0.5 to 1.4
Moderately stable	F	1.5 to 4.0
Extremely stable	G	4.0

[1] From Blue Hills Station units 1 and 2, Environmental Report Vol. III, 1973.

It is obvious that σ_y and σ_z are the most important parameters of plume dispersal in a forest. Cramer, Record, and Vaughan (1958) have concluded that the diffusivity of wind in the horizontal direction, hence σ_y, contains implicit information on site roughness and other factors that determine diffusion. Similarly σ_z contains implicit information on wind profile and site roughness. The results of the deciduous forest dispersion experiments by Litton Systems, Inc. (1969), provide further evidence that σ_y and σ_z are universal diffusion indices. That is, diffusion data can be reported in terms of σ_y and σ_z (see Pasquill 1974).

The predicted dosage in these studies, based on the Gaussian model, show that 75 percent of the predicted concentrations are within a factor of 2 of the observed values, and 97 percent are within a factor of 4. The diffusivities σ_y and σ_z in these studies were calculated from a simple power formula as suggested by Cramer et al. (1964) and Smith and Singer (1966). This formula gives σ_y and/or σ_z as a function of downwind distance and stability class. The power law used to calcualte σ_y and σ_z in the TRC-343 studies was based on the data from which the numbers for the various coefficients were derived. The concentration predictions based on the data from which the various parameters were derived indicated average concentrations within a factor of 2 about 50 percent of the time and within a factor of 10 on 87 percent of the comparisons.

Table 5.--Forest stability categories.

Category	Temperature profile	Equivalent Pasquill classes
Inversion	ΔT 1.5	F and G (moderately stable to extremely stable)
Intermediate	$0 \leq \Delta T \leq 1.5$	D and E (neutral to slightly stable)
Buoyant	ΔT 0	A, B, and C (extremely unstable to slightly unstable)

Table 6.--Best fit parameters of σ_y and σ_z.

S.D.	Stability category (from table 5)	r	a	b
σ_y	All three	100	4.0	1.4
σ_z	Inversion	100	3.8	0.2
	Intermediate	100	6.86	0.42
	Buoyant			
	Upward σ_y	100	7.5	0.6
	Downward σ_z	100	3.8	0.2

It is important to realize that the wind profile in crop and forest canopies, particularly in neutral atmosphere, is a function of height (z) and that it indirectly affects the value of σ_z. This profile can be predicted by the log law based upon the studies of Singer and Raymor (1957). Bussinger (1975) shows the wind profiles for various types of canopies as a function of relative height. If one extrapolates his curves to a pine forest canopy (*Pinus taeda* and *P. ponderosa*), the profile will be almost vertical and will show little change of u with z. However, it has been suggested that for atmospheric motion near the ground under neutral buoyancy, the log law wind profile is valid only under carefully selected conditions. It is also apparent that no other existing theoretical profile affords a better description of the wind. Thus, no reasonable alternative to the above approach appears to exist at this time.

On comparing the structure of the forests used in the TRC-343, Litton Systems, Inc., ECOM, and Melpar studies, we found that the closest to the *P. taeda* and *P. ponderosa* forests is the one used in the TRC studies. Therefore, we will adopt in this analysis the parameters employed in the TRC study to calculate σ_y and σ_z. In addition the stability classes pertinent to the forest micrometeorology have been condensed into three categories--buoyant, intermediate, and inversion--based on the temperature change (ΔT) in °C between 0.5 m and 8 m from the floor of the canopy (table 5).

For each of these categories, there is an appropriate standard deviation for the plume. This is calculated from the power law of Cramer et al. (1958). The power law equation for σ_y, the lateral deviation has the form

$$\sigma_y = a\left(\frac{x}{r}\right)^b \qquad (5)$$

where *a* and b are fitting parameters. The parameter *a* reflects the effect of the understory of the forest, *b* relates to the micrometeorology of the forest in terms of the stability class, and *r* is a common scaling factor equal to 100. The parameters used in the following analyses are outlined in table 6.

In the vertical direction, the power law equation for σ_z, the vertical diffusivity, includes an additional term *h*, the height of the inversion layer:

$$\sigma_z = a\left(\frac{x}{r}\right)^b + \frac{h}{4} \qquad (6)$$

Where no inversion layer exists, such as in the buoyant and intermediate categories, *h* has a value equal to zero.

RESPONSES OF THE MODEL

One of the most important quantities of pheromone dispersion is the concentration of released pheromones as a function of downwind distance from the source, because it will eventually determine the upwind flight behavior of the beetle. A convenient procedure to calculate pheromone dispersion downwind is to determine the ground-level (i.e., the beetles are at z = 0) centerline (i.e., y = 0) concentration for a number of downwind distances (x) and plot these values on log-log paper for various effective heights of emission (H) and for a given stability class. Another interesting quantity is to plot plume centerline concentration (i.e., z = H) as a function of downwind distance and make comparisons to ground-level centerline concentration. For general computations the above two types of plots are expressed as $(\frac{Cu}{Q})\ m^{-2}$ v. (x)m, which with the knowledge of Q and u make it easy to determine C as a function of x. Figures 4 and 5 give ex-

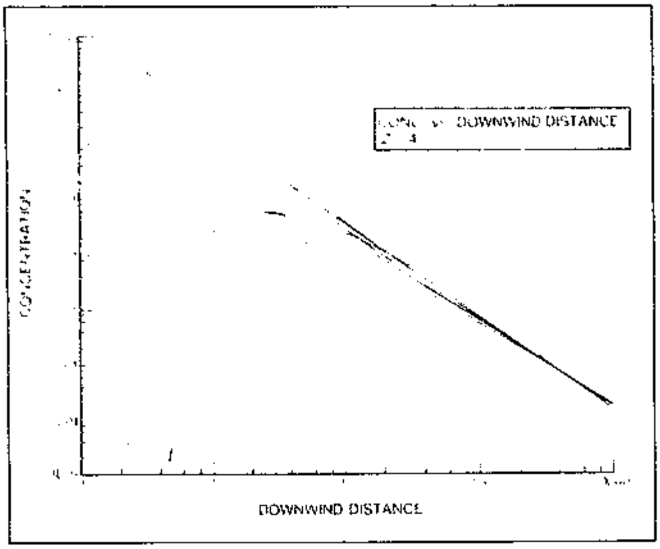


Figure 4.--Pheromone centerline concentration $(cu/Q)m^{-2}$ v. downwind distance. The beetles are at 4 m above the ground. Neutral class. H = 1 to 8 m.

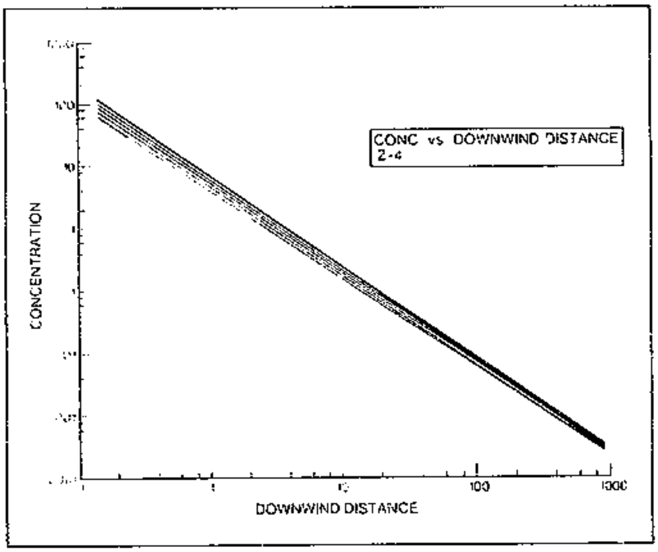


Figure 5.--Pheromone centerline concentration $(cu/Q)m^{-2}$ v. downwind distance. The beetles are at 4 m above the ground. Stable class. H = 1 to 8 m.

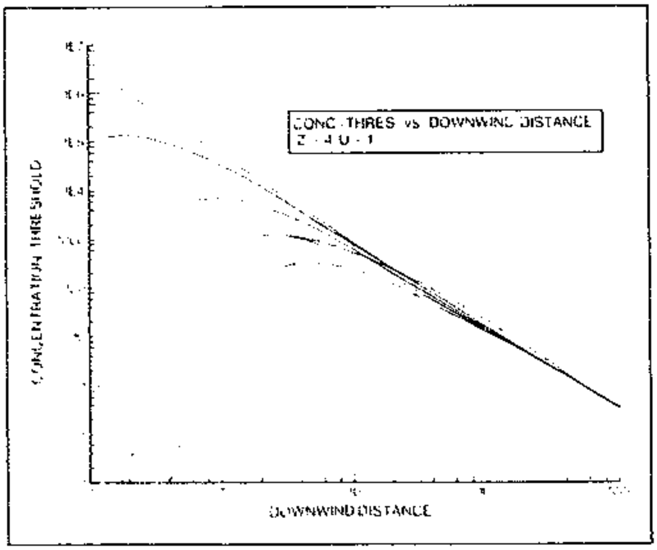


Figure 6.--The ratio of plume centerline pheromone exposure ϕ to beetle exposure threshold Q_T v. downwind distance at wind velocity u = 1 msec^{-1}. Neutral class. The beetles are at 4 m above the ground. H = 1 to 8 m.

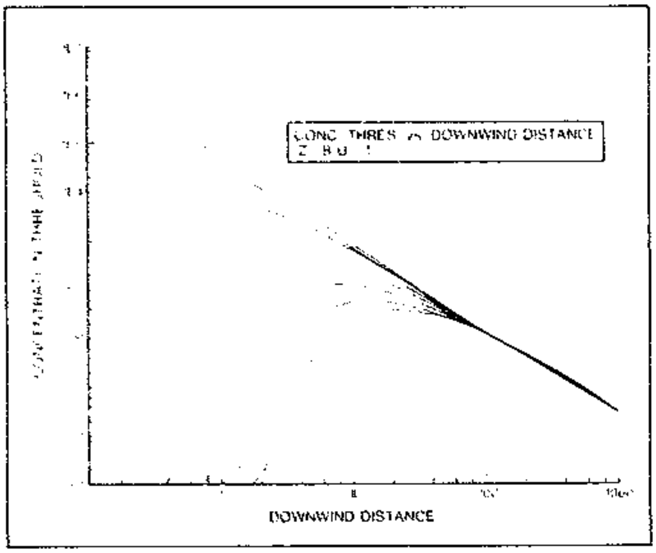


Figure 7.--The ratio of plume centerline pheromone exposure ϕ to beetle exposure threshold Q_T v. downwind distance at wind velocity u = 1 msec^{-1}. Neutral class. The beetles are at 8 m above the ground. H = 1 to 8 m.

amples of these plots for the most important stability classes of the forest.

An interesting quantity to calculate is the ratio of C in molecules/m^3 to the threshold concentration (T) that can elicit flight response from the beetle, as a function of downwind distance x, for given emission heights H, wind velocity u, and emission rate Q--or better still, the ratio of exposure, ϕ', as a function of downwind distance x as shown in figures 6 and 7. The distance at which the ratio is equal to 1.0 should be the threshold distance of the effective area. Also, the distance at which C/T or $\frac{\phi}{\phi'}$ reaches a maximum is the distance at which beetle activity is expected to reach a peak. Such information could provide guidelines for optimizing the utility of pheromones for control measures.

Maximum concentration v. downwind distance data for any reception height and various stability classes could be obtained from figures 4 and 5 or by differentiating equation (1) with respect to x and equating it to zero. For simplicity we assume

$$\sigma_y = a\sigma_z \quad \text{and} \quad \frac{d\sigma_y}{dx} = a\,\frac{d\sigma_z}{dx}$$

and for centerline ground level concentration

$$C_{max} = \frac{2Q}{\pi H^2 eu}\,\frac{\sigma_z}{\sigma_y} \qquad (7)$$

Because the maximum concentration occurs when $H^2 = 2\sigma_z^2$, the formula may be written in the following form:

$$C_{max} = \frac{2^{\frac{1}{2}}Q}{\pi Heu(\sigma_y)_{max}} \qquad (8)$$

where the notation indicates that the value of σ_y to be used is the one applying at the maximum concentration distance, as shown in figure 8.

For plume axis concentration (i.e., at the level of the plume centerline where Z $\neq$ 0), one obtains the relation

$$\frac{C(x,0,z;H)}{C(x,0,0;H)} = \frac{\frac{1}{2}\,[1.0+\exp-\frac{1}{2}\,(\frac{2H}{\sigma_z})^2]}{\exp-\frac{1}{2}(\frac{H}{\sigma_z})^2} \qquad (9)$$

where the plume centerline is at z = H. However, since the maximum ground level concentration occurs approximately at the distance where $\sigma_z = \frac{1}{\sqrt{2}}$ H (this approximation is much better for unstable conditions than for stable conditions), equation (9) becomes equal to 1.38. This

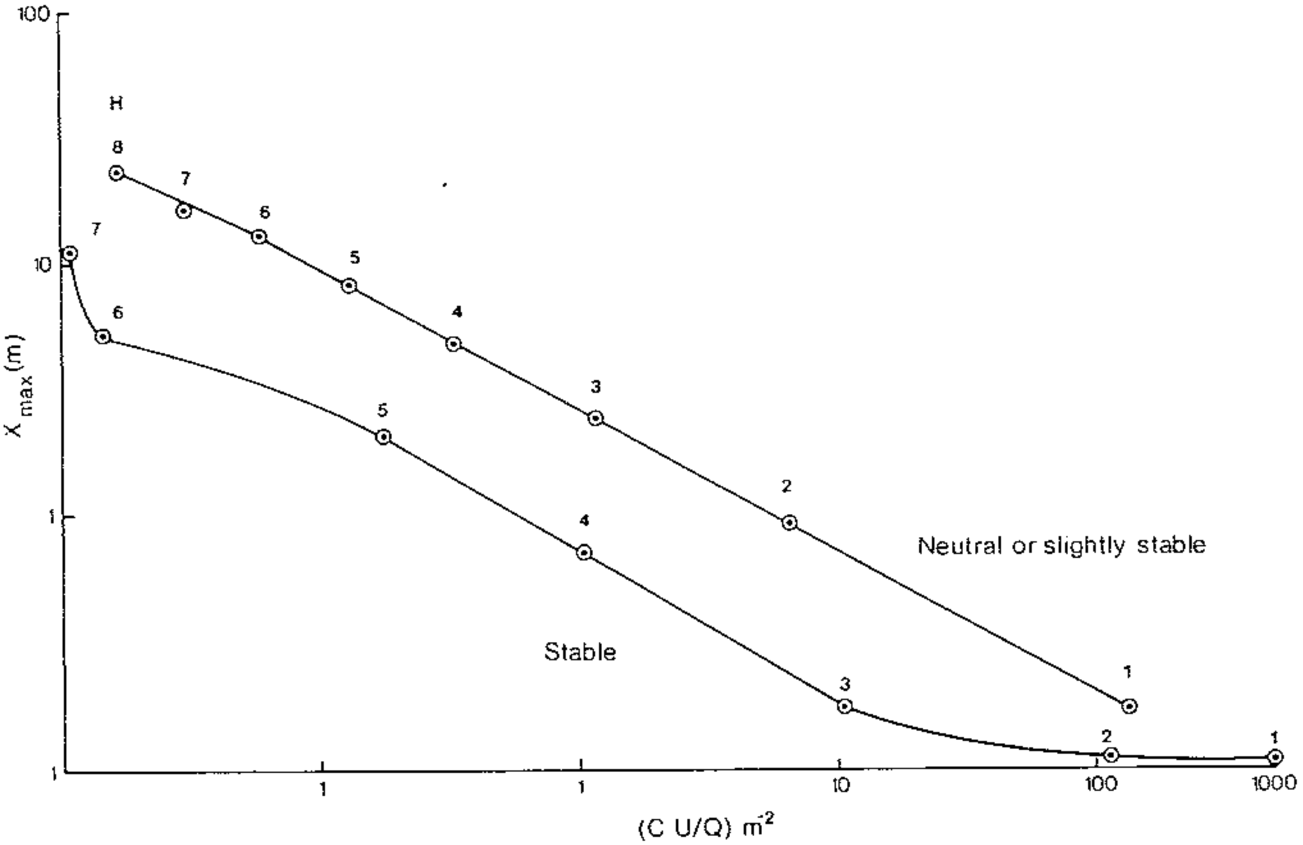


Figure 8.--Distance of maximum ground-level pheromone concentrations as a function of stability class and emission height.

calculation indicates that at the distance of maximum ground-level concentration, the concentration at plume centerline is greater by about one-third.

The independent variable in equations (5) and (6) is downwind distance *x*. Therefore, the plume spreads both sideways and vertically with downwind distance. To show this effect, equal concentration isopleths will be calculated for the Y direction. The following method is used to estimate these isopleths. The first step involves determining the axial position of the plume, which is established from the mean wind direction. The relationship between ground-level centerline concentration and ground-level off-axis concentration at a distance *y* is used; that is,

$$\frac{C(x,y,0;\ H)}{C(x,0,0;\ H)} = \exp\left[-\tfrac{1}{2}\left(\frac{y}{\sigma_y}\right)^2\right] \tag{10}$$

The y coordinate of a particular isopleth from the x axis can then be determined at each downwind distance, *x*. The lateral distance y_F where the concentration has dropped to F, a given percentage, of its value on the plume axis could be obtained from equation (1) as

$$y_F = \left[2\sigma_y^2 \ln \frac{100}{F}\right]^{\frac{1}{2}} \tag{11}$$

Similarly, the z coordinates of a particular isopleth from the x axis could be determined at each downwind distance *x* from the relation

$$z_F = \left[2\sigma_z^2 \ln \frac{100}{F}\right]^{\frac{1}{2}} \tag{12}$$

These isopleths will be a function of emission heights H and stability class. Similar contour lines are also generated for various receptor or assay heights, i.e., $z \neq 0$. Figure 9 shows ground-level concentration isopleths for intermediate (neutral stability class) conditions for a 1-meter emission height. Similar graphical output for 2-, 4-, and 8-m emission heights show that when the

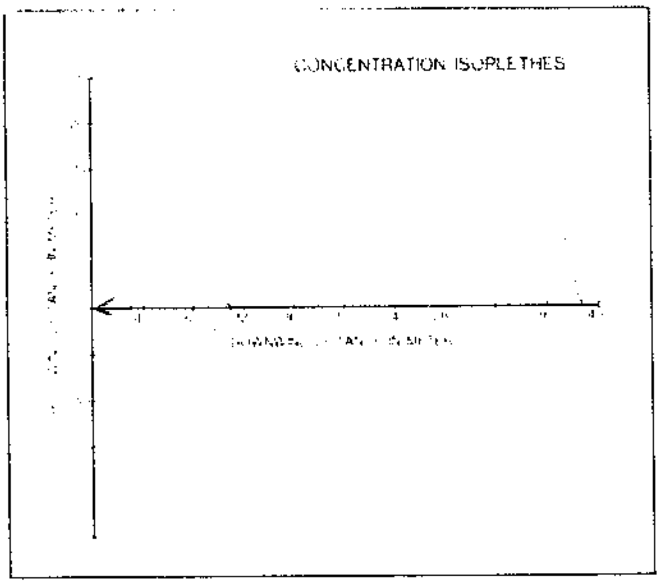


Figure 9.--Ground-level concentration isopleths for intermediate (neutral) stability class and emission height of 1 m. The innermost, the intermediate, and the outermost isopleths represent 10, 1, and 0.1 percent of the centerline concentration. Concentration is expressed in $(cu/Q)m^{-2}$.

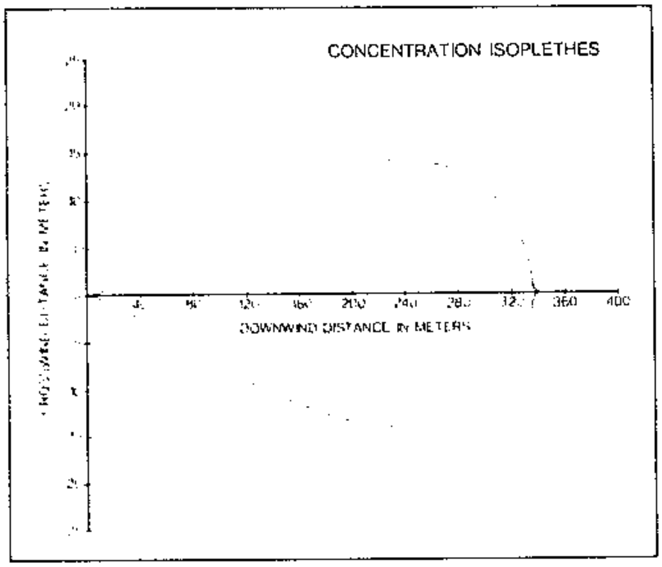


Figure 10.--Ground-level concentration isopleth for intermediate stability class and emission height of 8 m. Note that only the 0.1 percent isopleth remains. The concentration of each isopleth is equal to the concentration downwind along the *x* axis at the point of intersection.

emission height is raised, the ground-level concentration decreases. When the source height is raised to 8 m, the 10 percent and 1 percent isopleths do not intersect the ground-level plane (fig. 10). Figure 11 is a three-dimensional concentration isopleth for 4-m receptor height. This 3-d plot outlines the plume envelope within which the concentration is above the plume surface level. If the surface concentration represents the beetle response threshold, then the beetle population beyond this envelope is not induced to fly toward the source. The volume enclosed within the envelope represents an effective sphere of influence with respect to insect attraction toward the source.

The effect of emission height is shown even more clearly in a plot of surface concentration patterns from a continuously emitting source. The ground surface concentration pattern is shown in figure 12 for an emission height of 1 m and is therefore comparable to figure 9. The pheromone concentration for a beetle emission 1 m in height would be essentially zero at the base of the tree, rising rapidly to a peak value at some downwind distance, x max, and decreasing regularly thereafter. The concentration is always higher along the projection of the plume axis on the ground than on either side. Figures 13 and 14 show the ground surface concentration patterns for 4- and 8-m emission heights under the same intermediate (neutral stability) micrometeorological category. Similar surface concentration patterns for planes located at various heights could also be generated representing assay beetles flying at various heights above the ground.

While the surface concentration patterns are a useful means of visualizing the plume, insects operate in a vertical plane as well as a horizontal plane. Plots of height v. concentration for various distances downwind give a convenient method for comparing different types of meteorological conditions. Figures 15 and 16 compare vertical plume profiles for inversion and intermediate micrometeorological conditions for an emission height of 2 m. Note the radical difference between these profiles. In the inversion profile the concentration at 32 m downwind is very similar to the intermediate profile at the same downwind distance. For shorter downwind distances, the profile's shapes become radically different, with the inversion condition maintaining a broad front. Unlike the intermediate condition, it produces a sharp, localized concentration near the source. The buoyant condition is distinct in that concentration drops off radically in the downwind as well as downward vertical direction. The plume tends to

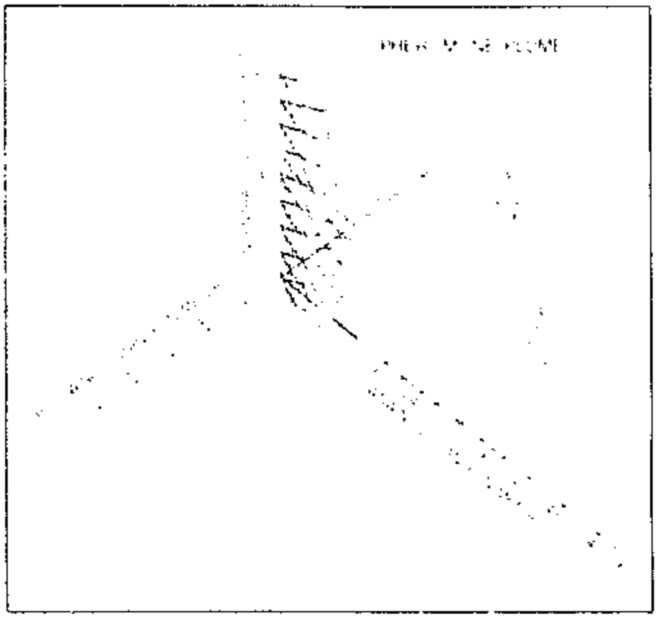


Figure 11.--Pheromone plume made of three-dimensional isopleths at 0 to 8 m above the ground. The inner isopleths represent 10 percent and the outer, 1 percent of their corresponding centerline concentrations, respectively, for the neutral class and emission height of 4 m.

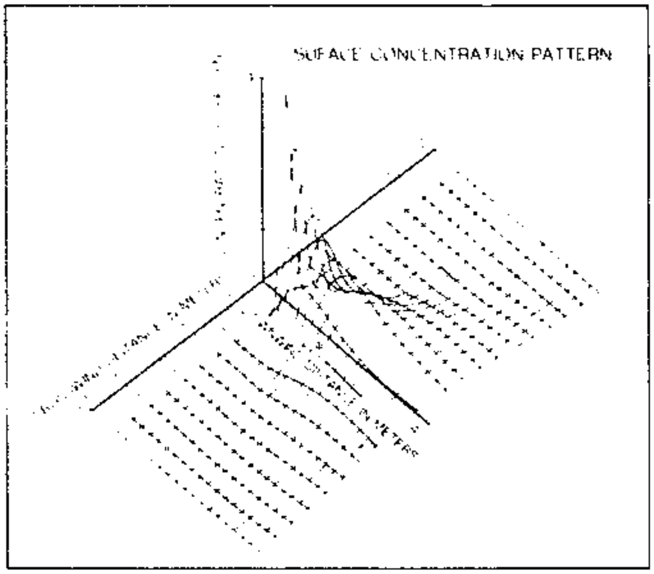


Figure 12.--Pheromone ground surface concentration $(cu/Q)m^{-2}$ as a function of downwind distance (x) and crosswind distance (y) for the intermediate class and emission height of 1 m.

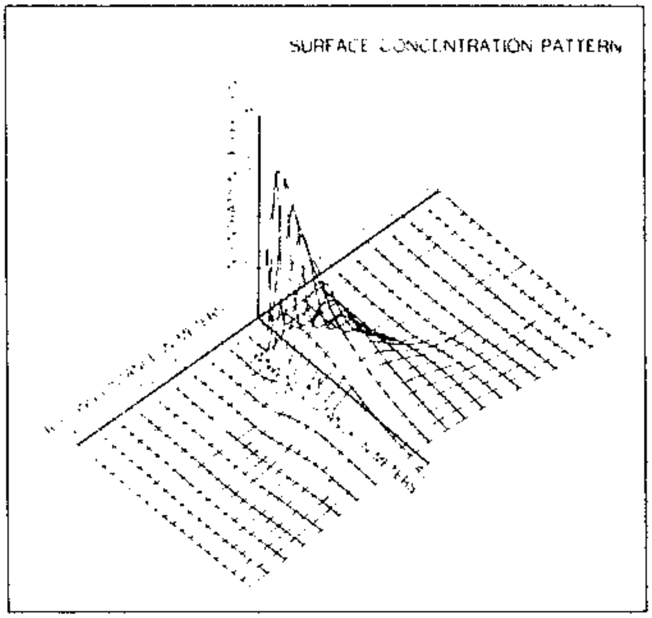


Figure 13.--Pheromone ground surface concentration $(cu/Q)m^{-2}$ as a function of downwind distance (x) and crosswind distance (y) for the intermediate class and emission height of 4 m.

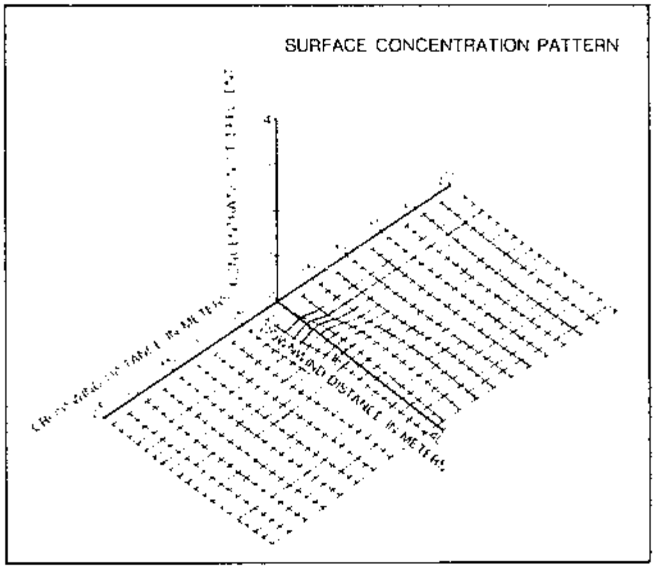


Figure 14.--Pheromone ground surface concentration $(cu/Q)m^{-2}$ as a function of downwind distance (x) and crosswind distance (y) for the intermediate class and emission height of 8 m.

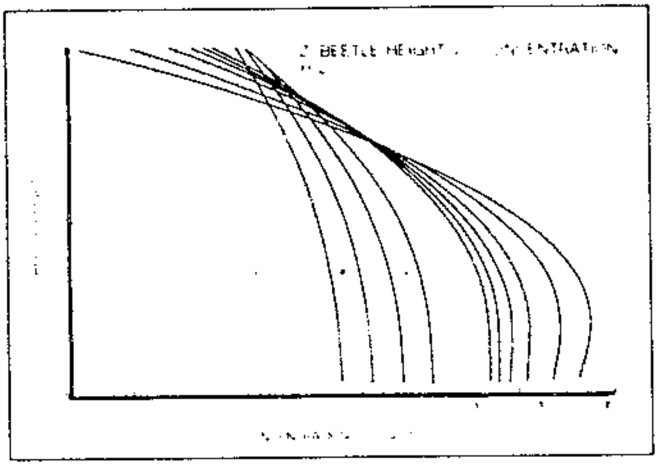


Figure 15.--Concentration profile of pheromone plume parallel to the tree length as a function of downwind distance (x) and for the inversion class. The emission height is 2 m.

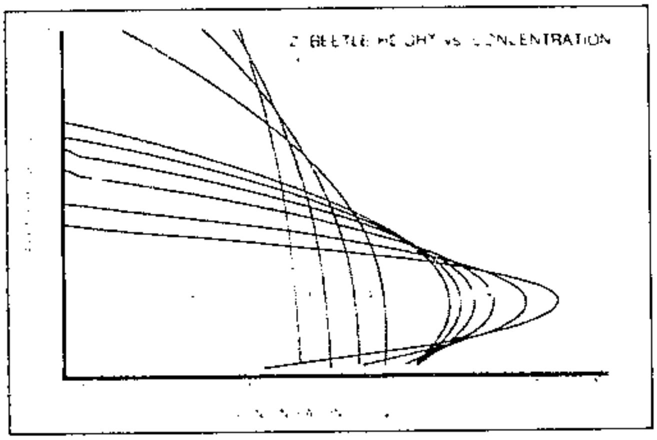


Figure 16.--Concentration profile of pheromone plume parallel to the tree length as a function of downwind distance (x) and for the intermediate class. The emission height is 2 m.

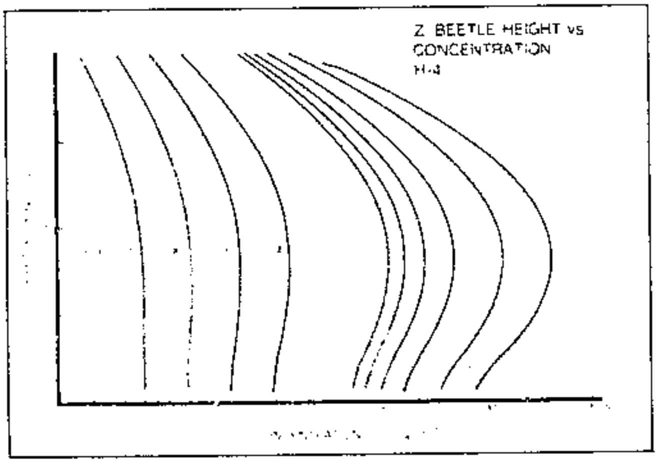


Figure 17.--Concentration profile of pheromone plume parallel to the tree length as a function of downwind distance (x) and for the inversion class. The emission height is 4 m.

rise upward out of the forest. Only beetles at high levels within the canopy would receive the signal, but they would be unlikely to fly down to the source due to their typical behavioral response. (*See also* figs. 17 and 18.)

MULTIPLE SOURCES

In a real ecosystem pheromone is emitted from multiple sources, i.e., many beetle-infested trees. The principle of superposition makes it possible to calculate and sum the concentrations (and/or doses) at a given point in space due to all the sources using the Gaussian distribution formulation developed above. Concentration profiles due to any number of trees located at any point (x,y) in space, for various emission heights and emission rates under different meteorological conditions, are calculated. Figure 19 illustrates some of these profiles. The important observation is that the concentration of pheromone in between trees increases drastically, which in effect traps the beetles in an atmosphere of pheromone and induces them to land on the nearest tree. When the distances between trees are reduced, the pheromone concentration, as expected, increases even more, as shown in figures 19 and 20.

Equal concentration isopleths due to multiple sources can be calculated. Numerically, it comes to exactly the same thing if one calculates the concentration at a point (x,y) from a number of arbitrarily distributed sources A,B,C at height H, or if one calculates (after reversing the mean wind direction) for a single source located at point (x,y;h) and of strength equal to combined strength of the actual sources, the summation of concentrations that would result at the various actual source locations as illustrated in figure 21A and B.

The outlined Gaussian model is based upon four studies of dispersion within forests but has not been related to pheromone dispersion. At first sight, this appears an impossible task. An experiment to measure concentration gradients of pheromone within a forest under different wind and stability classes would be an extremely difficult, arduous, and costly undertaking. One much simpler approach is to use pheromone-sensitive insects as the assay technique. Insects have considerably greater ability to sense small quantities of pheromone than do chemical sensors designed by man. In addition, the usefulness of pheromone dispersion model relates to its ability to explain and/or to predict insect behavior. Therefore, support for the model is dependent upon observations at the biological level.

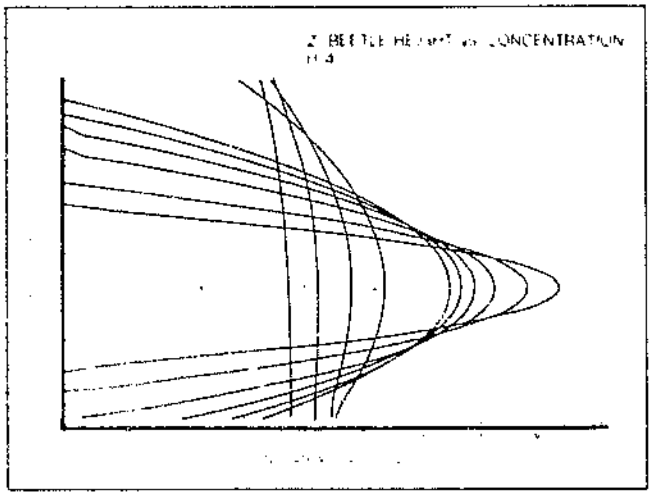


Figure 18.--Concentration profile of pheromone parallel to the tree length as a function of downwind distance (x) and for the intermediate class. The emission height is 4 m.

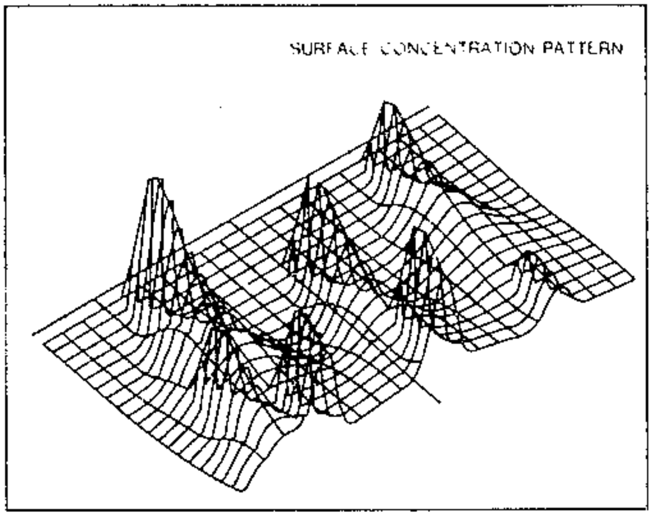


Figure 19.--The resultant pheromone ground surface concentration as a function of downwind distance (x) and crosswind distance (y) for eight trees at random (x,y). Emission height is 4 m for the intermediate class and various emission rates.

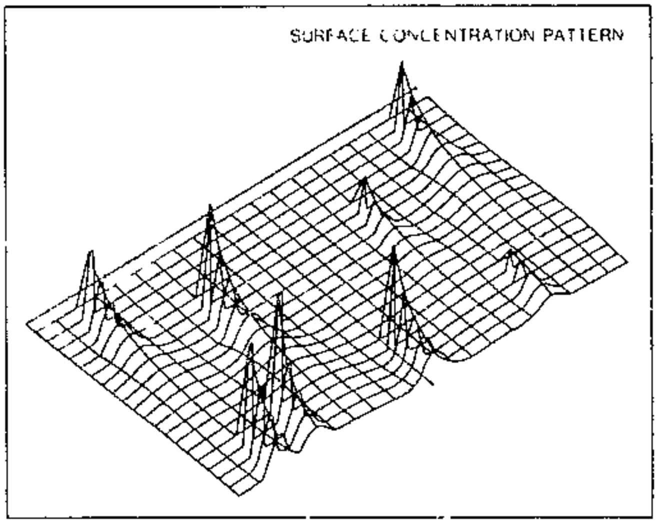


Figure 20.--The resultant pheromone ground surface concentration as a function of downwind distance (x) and crosswind distance (y) for eight trees at random (x,y). Emission height is 4 m for the inversion class and various emission rates.

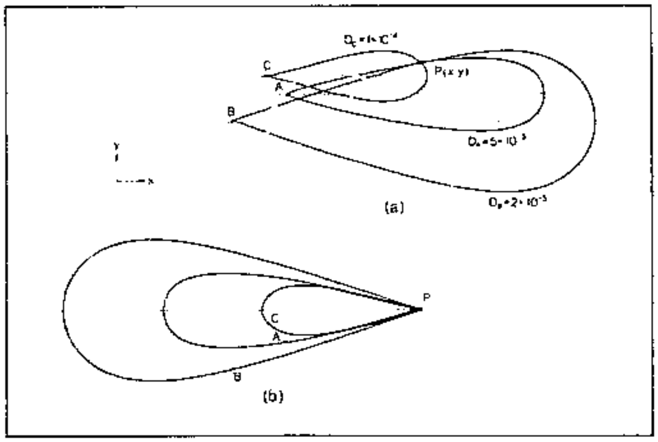
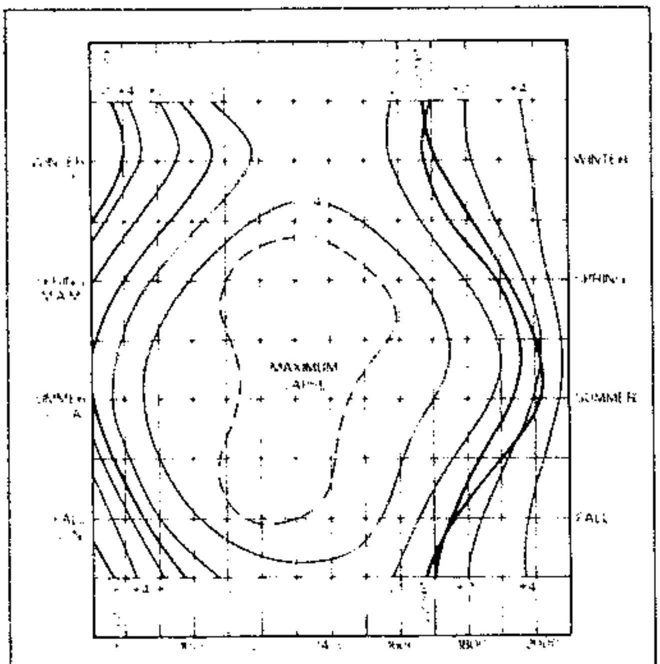


Figure 21.--*A*: Dose ispleths due to sources A, B, and C. *B*: Dose isopleths due to source P(x,y) of strength equal to combined strength of sources A, B, and C. (After Gifford 1959.)

BIOLOGICAL SUPPORT FOR MODEL

The studies of Payne (1974, 1979) and others have clearly established the importance of pheromones in regulating flight, population aggregation, and attack behavior of the southern pine beetle. Similar studies (e.g., Wood and Bedard 1977) have established a similar response for the western pine beetle. Given these physiological responses, it would be expected that these insects would show marked responses to micrometeorological conditions. Inversion phenomena such as fumigation, trapping, and looping should result in enhanced flight, aggregation, and attack. By contrast, buoyant, clear days with high lapse rates should reduce flight activity and attack behavior during the midday period. On days when thunderstorms threaten or overcast conditions occur, the associated inversion conditions prior to rainfall would be expected to produce pronounced beetle activity. To ascertain whether these qualitative predictions of the model are reasonable and realistic, we now discuss two studies of beetle activity with meteorological conditions.



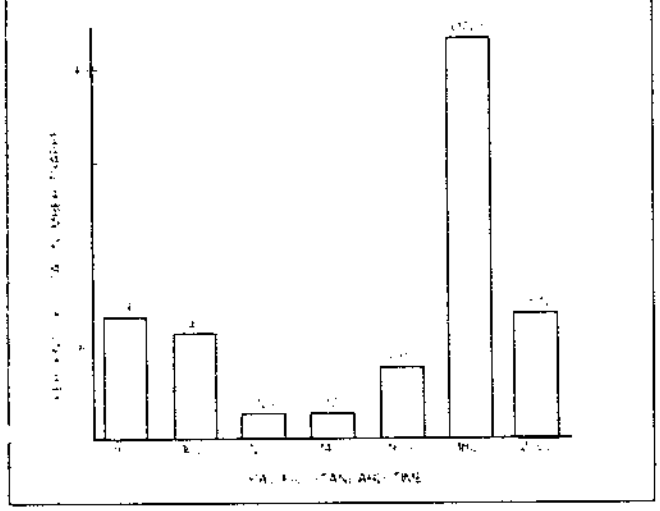


Figure 22.--*Upper*: Seasonal variation in the vertical temperature difference (°F) between 1.5 and 120 m for each daylight hour of the day. Data collected over 2-year period at the National Reactor Testing Station in Idaho (DeMarrais and Islitzer 1960).

Figure 22.--*Lower:* Diurnal arrival pattern of mountain pine beetle on a sugar pine under natural attack, as measured by sticky traps (two each at 3, 6, and 9 m) on the tree bole. Fish Camp, Calif., June 20, 1970). The number trapped during each time interval is in parentheses. (After Edson 1978.)

The first study was undertaken by Edson (1978) in the Sierra Nevada Mountains of central California. Edson studied the influence of weather on the arrival and attack sequence of the mountain pine beetle at attractive tree bolts. In this environment, two distinct periods of the day could be distinguished. On a typical summer day, the sky was clear with local surface heating until some point in the late afternoon, when the influence of the ocean became dominant, causing fog to move into the area and up the valley as a front. The micrometeorology of this area is not available to the authors. There is information for conditions at the National Reactor Testing Station in Idaho, which is too far from the ocean to experience "late afternoon fumigation." Temperature profiles were collected with an open fetch over a height of 120 m. Figure 22 Upper shows the temperature profiles at this site for the different seasons of the year for the daylight period. Only daylight conditions need to be considered because pine beetle flight activity ceases between sunset and sunrise.

The California site would have a similar profile except that the onset of inversion would occur approximately 2 hours earlier in the evening. Figure 22 Lower shows the pattern of mountain beetle flight and attack (as measured by sticky-trap catches) for a typical clear summer day. The morning period with lower temperatures just after sunrise has activity which is less than that observed in the late afternoon. The influence of meteorological conditions is most clearly shown in figure 23. Edson found the optimal conditions for the flight of bark and ambrosia beetles during the midday period to be related to prestorm weather conditions that favor the persistence of pheromone plumes. Under these conditions, pheromone concentration in the beetles' flight zone can increase due to stable air masses within the forest canopy (fig. 23C). Edson also observed that during overcast conditions, mountain pine beetles were trapped throughout the day, and in highest numbers just prior to and during light rain mists (fig. 23B). Conversely, on hot, cloudless days, the chimney effects characteristic of unstable conditions adversely affect the formation of pheromone plumes during the midday period. It is only with the advent of the cooling, more stable afternoon breeze, with or without fog, that plume formation is enhanced, leading to pronounced beetle activity in the late afternoon (fig. 23A).

The Southern States have a somewhat similar meteorological pattern without the pronounced late afternoon fumigation. The pattern is somewhat similar to that

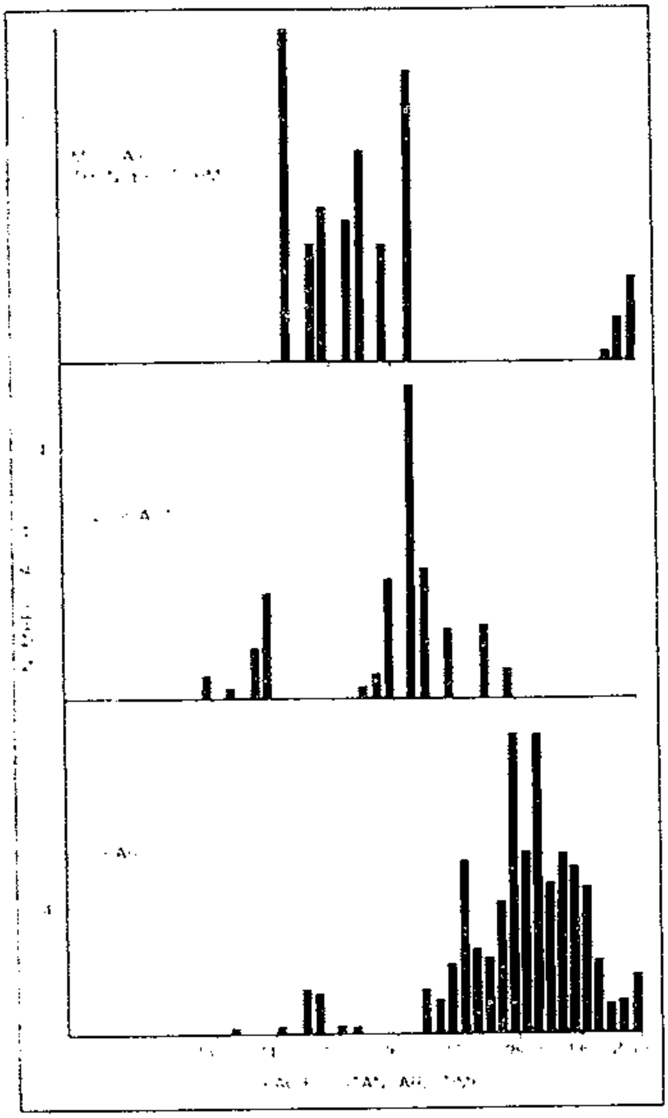
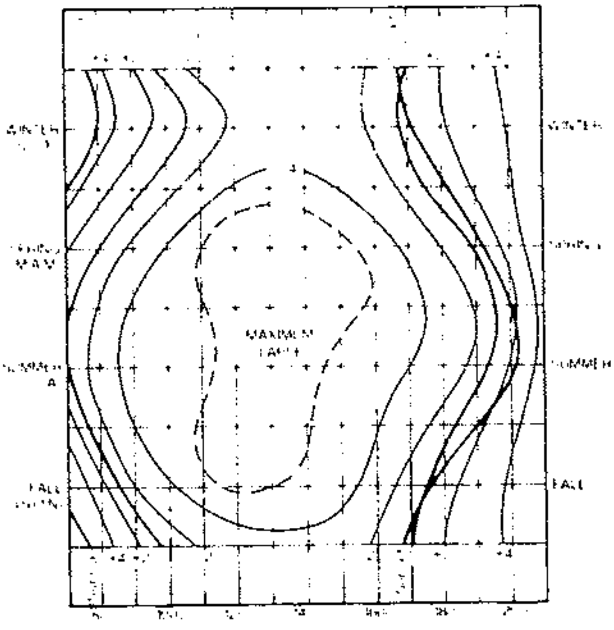


Figure 23.--Diurnal response of the mountain pine beetle to attractive lodgepole pine bolts infested with combinations of male and female beetles during (a) clear weather (August 1972), (b) overcast weather (July 1972), and (c) midday thunderstorm weather (July 1973). Lake Tahoe, Calif. (After Edson 1978.)



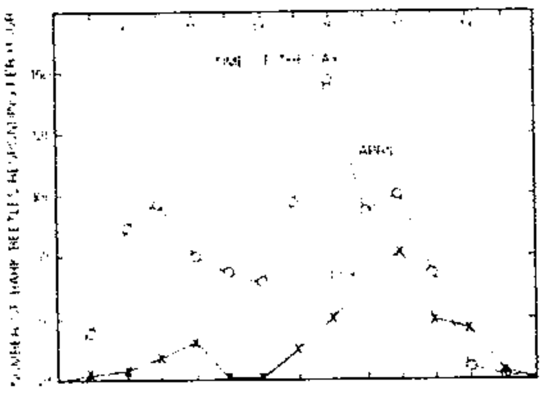


Figure 24.--*Upper*: Same as figure 12. From National Reactor Testing Station in Idaho. (DeMarrais and Islitzer 1960.)

Figure 24.--*Lower*: Seasonal changes of diurnal flight pattern of *Dendroctonus frontalis*. (Vité et al. 1964.)

measured in Idaho. Vité et al. (1964) measured the diurnal pattern of response to attractants of the SPB. They demonstrated that flight activity typically was depressed during noon and early afternoon periods. From this analysis, the observed pattern can be explained in terms of the seasonal variations in lapse rate. A comparison of their results [shown in figure 24 for April (spring) and July (summer)] with the lapse profiles shown in figure 24 (upper) reveals that relatively stable conditions occur in the morning and afternoon periods. As the season progresses from spring to summer, the lapse period appears to increase in duration within the forest canopy. Thus it is likely that the diurnal vertical temperature profile within southern forests may show somewhat different form from that observed for Idaho, although the general pattern will probably remain similar.

Vité et al. (1964) also indicated that on cloudy days and with the onset of rainstorms, unusually high beetle flight activities were repeatedly observed. Under such conditions, the lapse rate below the cloud level is much less than on clear days and more stable conditions are created, thus trapping the pheromones under the canopy (Singer and Raymor 1957).

TECHNOLOGY TRANSFER

Many researchers in the fields of behavioral chemicals, forest management, and pine beetle control have realized the basic and applied utilities of pheromone dispersal in a forested ecosystem such as the pine forest. From the applied point of view, the model provides an essential tool for proposed forest management strategies such as artifical pheromone release, confusion strategies, bioattractant releases, and controls on insecticide spraying programs. It is also extremely important to design the proper release source for behavioral chemicals and bioattractants, with the right emission rate. To give the user numerical answers to his questions for the purposes of implementation of control tactics we developed an interactive computer code, stored on a cassette tape for a minicomputer. The code is structured so that the user needs to answer only a few questions concerning weather conditions, tree spacings, and beetle density.

According to the weather conditions, the *state* of the environment is determined using the classification given in table 7 for any given *wind velocity.* The effective attractive areas, pheromone concentration profiles, and emission rates are then computed based on the state of the environment and the wind velocity and for any given source elevation. On the basis of the above computations, three important pieces of information will be returned to the user:

(1) a decision of whether it is suitable to conduct the experiment or not,

(2) the amount of pheromone needed to conduct the experiment successfully (or any other behavioral chemical, insecticide, ... etc.), and

(3) the rate of emission from a source of a given design.

It should be emphasized here that we still need to include in the model the influence of the wind rose, i.e., wind direction and its frequency in that direction, which will determine the dominant direction of dispersion.

Table 7.--Classification of weather conditions.

Temperature	Sun	Rain	State
> 30°C	Sunny	No	1
> 30°C	Cloudy	No	2
< 30°C	Sunny	No	3
< 30°C	Cloudy	No	4
< 30°C	Cloudy	Mist	5
< 30°C	Cloudy	Rain	6

DISCUSSION

Condensing stability classes into three micrometeorological categories is an attempt to simplify the model for use in forest pest management as well as fundamental research in olfactory communication within vegetated regions. It is also likely that the spatial variability of the forest will tend to obscure a finer stability classification. Because this is a pioneer study, the concepts and classification of meteorological conditions have been kept as simple as possible. Further complexity can be introduced at a later date if warranted by future experimental studies.

Biological data from two locations provide strong support for the qualitative predictions of the model. Pheromone communication appears to be ineffective under buoyant atmospheric conditions. This fact has generally not been appreciated. The implications of this model are far reaching. It suggests that olfactory communication is limited to times of the day in which meteorological conditions allow pheromone concentrations to build up. In general it will favor early morning and late afternoon periods except when thunderstorms are imminent or overcast conditions occur.

Pheromone communication may tend to be more effective during winter than summer, due to the increased buoyancy of summer periods. However, the increase in effectiveness of olfactory communication in winter will be offset by the lower temperatures, which affect beetle flight (White and Franklin 1976) plus the decreased hours of daylight. Summer is interesting in that it has the most pronounced inversion conditions (fig. 22 Upper). Therefore, it is difficult to generalize about the influence of season on pheromone communications. The level of activity during the winter may in fact be lower than that during summer.

It is expected that the spring and fall periods with mild temperatures, medium day lengths, and lack of pronounced lapse conditions will favor pheromone communication at least in areas that have extreme temperatures in summer and winter. This is borne out in the case of the SPB. Population increase is most pronounced in spring and fall, with population decreasing in winter and summer (Thatcher and Pickard 1964). Though there are probably many causes of this pattern, the impact of meteorological conditions upon pheromone communication should be considered as a contributory factor. Weather should also be considered as a factor in any planned use of pheromones as a behavioral control agent. Inadvertent application of these chemicals under lapse conditions would be ineffective and a costly waste of expensive chemicals. Future studies must clearly establish the appropriate application condition for pheromones. An added support to our hypothesis of the role of the micrometeorology on the dispersion of beetle pheromones and hence beetle mass aggregation is found in the work of Coster et al. (1978).

LITERATURE CITED

Barad, M. L., and D. A. Haugen. 1959. A preliminary evaluation of Sutton's hypothesis for diffusion from a continuous point source. J. Meteorol. 16(1):12-20.

Batchelor, G. K. 1949. Diffusion in a field of homogeneous turbulence to atmospheric diffusion. Aust. J. Sci. Res. 2:437-450.

Batchelor, G. K. 1950. Application of the similarity theory to atmospheric diffusion. Quart. J. Roy. Meteorol. Soc. 76(328):133-146.

Blue Hills Stations, 142, Units 1 and 2, BHS--1 and 2 ER, Chapter 6.1, p. 14, 1973. Environmental report, construction permit stage, Vol. III, Newton County, Texas. Bechtel Power Corporation, Norwalk, California. (Contract 9559-14-N-019 Gulf States Utilities Co.).

Bossert, H. W., and E. O. Wilson. 1963. The analysis of olfactory communication among animals. J. Theoret. Biol. 5:443-469.

Bussinger, J. H. 1975. Aerodynamics of vegetated surfaces. *In* Heat and mass transfer in the biosphere. D. A. de Vries and N. H. Afgan, eds. John Wiley and Sons, New York.

Coster, J. E., T. L. Payne, L. J. Edson, and E. R. Hart. 1978. Influence of weather on mass aggregation of southern pine beetles at attractive host trees. South. Entomol. 3(1): 14-20.

Cramer, H. E., G. M. DeSanto, R. K. Dumbauld, P. Morggenstein, and R. N. Swanson. 1964. Meteorological prediction techniques and data system. Report GDA-64-3-G, Geophysical Corporation of America, Bedford, Mass.

Cramer, H. E., F. A. Record, and H. C. Vaughan. 1958. The study of the diffusion of gases or aerosols in the lower atmosphere. Report AFCRC-TR-58-239, Dept. of Meteorology, MIT, Cambridge, Mass.

DeMarrais, G., and N. F. Islitzer. 1960. Diffusion climatology of the national reactor testing station, USAEC Report IDO-12015, Weather Bureau, Idaho Falls, Idaho.

ECOM-3. 1970. Dispersion of air tracers into and within a forested area: 3. Tr. ECOM-68-GS-3, October 1970. U.S. Army Electronic Command, Atmospheric Sciences Laboratory, Fort Huachuca, Arizona.

Edson, L. J. 1978. Host colonization and the arrival sequence of the mountain pine beetle and its insect associates. Ph.D. dissertation. Univ. of California, Berkeley. 196 p.

Gifford, F. 1959. Computation of pollution from several sources. Int. J. Sci. Poll. 2:109-110.

Hewson, E. W., G. C. Gill, and G. J. Walke. 1963. Smoke plume photography study, Big Rock Point Nuclear Plant, Charlevoix, Michigan. Progress Report No. 3, Publication 04015-3-P, Dept. of Meteorology and Oceanography, Univ. of Michigan, Ann Arbor, Mich.

Kaissling, K. E. 1971. Insect olfaction. *In* Handbook of sensory physiology, vol. 4. p. 351-431. I. Beidler, ed. Springer-Verlag, New York.

Lin, C. C., and W. H. Reid. 1963. Turbulent flow, theoretical aspects. *In* Handbuch der Physik, Vol. 8, Part 2, p. 438-523. Springer-Verlag, Berlin.

Litton Systems, Inc. 1969. Deciduous forest diffusion study. Rept. 3004, Vol 1. Minneapolis, Minn.

Melpar, Inc. 1968. Diffusion under a jungle canopy. U.S. Army Dugway Proving Ground. Dugway, Utah. Vol. 1, 1969.

Pasquill, F. 1961. The estimation of the dispersion of windborne material. Meteorol. Mag. 90(1063):33-49.

Pasquill, F. 1974. Atmospheric diffusion. John Wiley and Sons, New York.

Payne, T. L. 1974. Pheromone perception. *In* Pheromones. p. 35-61. M. C. Birch, ed. Elsevier, New York.

Payne, T. L. 1979. Pheromone and host odor perception in bark beetles. *In* Neurotoxicology of insecticides and pheromones. p. 27-58. T. Narahashi, ed. Plenum, New York.

Richardson, L. F. 1926. Atmospheric diffusion shown on a distance neighbour graph. Proc. Roy. Soc. (London), Ser. A, 110:709-737.

Roberts, O.F.T. 1923. The theoretical scattering of smoke in turbulent atmosphere. Proc. Roy. Soc. (London), Ser. A, 104:640-654.

Schmidt, W. 1925. Der Messenaustausch in Freier Luft und Verwandte Erscheinungen. *In* Probleme der kosmischen Physik, Vol 7. Verlag Von Henri Grand, Hamburg.

Singer, I. A., and G. S. Raymor. 1957. Analysis of meteorological tower data, April 1950-March 1952. USAEC Rep. BNL-461. Brookhaven National Laboratory, Brookhaven, Mass.

Smith, M. E., and I. A. Singer. 1966. An improved method of estimating concentrations and related phenomena from a point source emission. J. Appl. Meterol. 5:631-639.

Sutton, O. G. 1953. Micrometeorology. McGraw-Hill Book Company, Inc., New York.

Taylor, G. I. 1921. Diffusion by continuous movements. Proc. London Math. Soc. (2)20:-196-202.

Thatcher, R. C., and L. S. Pickard. 1964. Seasonal variations in activity of the southern pine beetle in east Texas. J. Econ. Entomol. 57:810-812.

TRC-343. 1969. Aerosol diffusion over woodlot complexes. Vol. 1. U.S. Army Dugway Proving Ground, Dugway, Utah.

Turner, D. B. 1964. A diffusion model of an urban area. J. Appl. Meteorol. 3:83-91.

Vité, J. P., R. I. Gara, and H. D. von Scheller. 1964. Field observations on the response to attractants of bark beetles infesting southern pines. Contrib. Boyce Thompson Inst. 22(8):461-470.

White, R. A., Jr., and R. T. Franklin. 1976. Activity of the southern pine beetle in response to temperature. J. Ga. Entomol. Soc. 11(4): 370-372.

Wood, D. L., and W. D. Bedard. 1977. The role of pheromones in the population dynamics of the western pine beetle. *In* Proceedings XV International Congress of Entomology. p. 643-652. D. White, ed. Entomol. Soc. Am., College Park, Md. [Washington, D.C., Aug. 1976.]

ACKNOWLEDGMENTS

It is a pleasure to acknowledge the following for their interesting observations and clarifying discussions: Mr. George Blair, Mr. Robert Cox, Dr. Gene Pulley, Dr. Thomas L. Payne, Dr. Jim Richerson, Dr. Don W. DeMichele, and Dr. Robert N. Coulson.

APPENDIX

Plume: A volume or part of space in which the average pheromone concentration of all points is equal to or greater than some value. A vertical cross section through the centerline of this space looks like a plume or a feather. The centerline of the plume is parallel to the mean wind direction.

Plume centerline: The plume centerline is the axis of the plume parallel to the meanwind direction, i.e., the x axis. H is the height of the plume centerline and as explained in the text, H = Z. (*See* figure 3.)

Fickian diffusion and diffusivity: The flow of a substance in a given direction under the action of a concentration gradient. Fick stated in his first law of diffusion that S_i--the flux of a species i--is given by

$$S_i = -D_i \frac{\partial C_i}{\partial x}$$

where S_i is the rate of transfer of species i per unit area across a fixed surface, C_i is the concentration of i, and D_i is the diffusivity or the diffusion coefficient of species i in the x direction. The negative sign is consistent with downgradient flux.

Wind profile: The change of the mean windspeed with elevation, i.e., the mean windspeed vertical gradient.

Looping: Except for a thin layer of air close to the surface, the atmosphere is essentially always turbulent--characterized by random fluctuations in windspeed and direction caused by swirling or eddy motion of the air. These eddies are generated in two ways. As wind moves over natural surfaces, the friction with the surface generates turbulence, called mechanical turbulence. Turbulence is also generated when air is heated at a surface and moves upwards due to buoyancy. A plume is said to be "looping" when, in addition to the small-scale mechanical turbulence that tears the plume apart and spreads it with distance, the thermal updrafts and downdrafts cause the entire plume to be transported upward or downward. The plume from a smokestack on a hot day makes a striking demonstration of a looping plume.

Fumigation: The rapid settling downward to the ground of material that has accumulated aloft during a period of atmospheric stability, an occurrence that is common after dawn, when the nocturnal temperature inversion is rapidly dissipated by warming due to solar heating of the ground.

Trapping: A condition during which the effluent diffuses rapidly below the base of an elevated inversion but is prevented by the stable layer from diffusing to greater heights. (For illustration, see Hewson, Gill, and Walke 1963.)

MODELS OF THE ATTACK PROCESS OF THE SOUTHERN PINE BEETLE ON INDIVIDUAL LOBLOLLY PINES

Barry G. Hynum[1]

Abstract.--Two simple mathematical models are presented which characterize the attack process of the southern pine beetle, *Dendroctonus frontalis* Zimm., on loblolly pine, *Pinus taeda* L. The first model relates new attacks to cumulative old attacks. The second model relates attraction to cumulative old attacks. Attraction is defined as the number of landing beetles per gallery start, and attacks are considered "old" after 24 hours. The models have three parameters: peak number of landing beetles per gallery start, peak gallery initiation rate, and the final attack density. The significance of the variance of parameters between trees is discussed. Variations in aerial density of beetles, beetle pheromone production potential, beetle thresholds for gallery initiation, and host factors are suggested as factors determining parameter values.

INTRODUCTION

Two critical areas of southern pine beetle (SPB) research are host selection and aggregation. The processes seen during these two beetle activities are important for two reasons: (1) site and stand susceptibility rating is dependent on a healthy concept of these two research foci, and (2) much of the within-tree brood development is dependent on what takes place during aggregation.

In order to define susceptibility we need to ask questions like "Why do beetles attack the initial tree?" This is akin to asking why beetles attack a loblolly pine instead of a sweet gum tree. Are some hosts really preferable to others? Here we are discussing the first trees to be attacked, lightning-struck trees excluded. These questions should be answered before extensive research into suscepbility associations.

Aggregation on a tree determines a number of subsequent developmental and spot growth parameters. The speed of aggregation determines how fast a host is saturated and how fast beetles will reemerge and be available to attack new hosts. The variation in beetle attacks per 100 cm^2 strongly affects brood production through drying if not through variation in gallery elongation and egg deposition.

ASSUMPTIONS

To formulate the model I will make the following assumptions. An orderly, repeatable, mechanistic relationship between attacking beetles and beetles in galleries is assumed, based on pheromone research by Renwick and Vité (1969) and Payne et al. (1978). That is, an attacking beetle produces pheromone, which signals flying beetles. Three other assumptions will be made:

(1) The aerial density of beetles is relatively constant and homogenous over the observation area.

(2) Pheromones released by beetles in galleries are distributed similarly on a spatial and temporal basis.

(3) Beetles attracted to a tree under attack are proportional in number to the pheromones emitted by beetles on that tree.

METHODS

In 1978, observers checked 31 loblolly pine trees near Cut-and-Shoot, 12 mi east of Conroe, Montgomery County, Texas. On each tree field crews marked off a section of bole 0.66 m long with flagging at 3 and 3.66 m. They counted gallery starts in the quadrat and marked them with a color-coded staple every 24 hours on each tree. The area examined for gallery starts was reduced to a one-third m section of bole from 3.33 to 3.66 m on a tree after the attack density reached 1 gallery/100 cm^2 and to a one-sixth m section of bole from 3.50 to 3.66 m on a tree after the attack density reached 2 galleries/100 cm^2. This procedure was instituted to facilitate timely counting and to keep human error (counting fatigue) constant.

---

[1] The author is Entomologist III, Texas Forest Service, Lufkin.

TB 1630 (1980) USDA TECHNICAL BULLETINS UPDATA
MODELING SOUTHERN PINE BEETLE POPULATIONS SYMPOSIUM PROCEEDINGS ASHEVILLE
2 OF 2

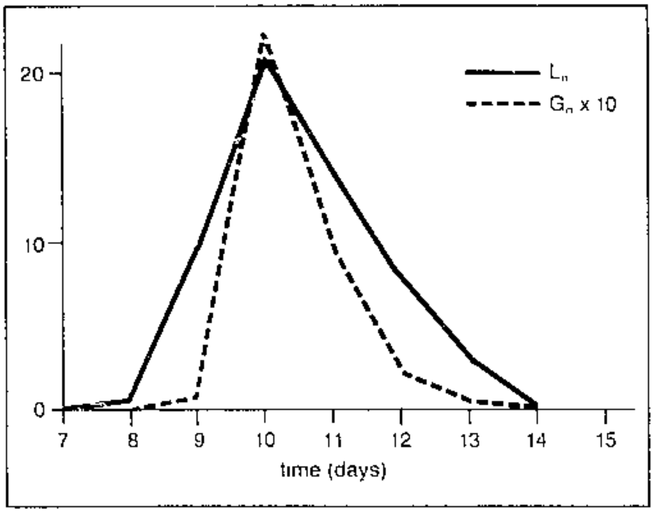


Figure 1.--Temporal progression of landing beetles per 100 cm² (L_n) and gallery starts per 100 cm² (G_n) where n = the time in days.

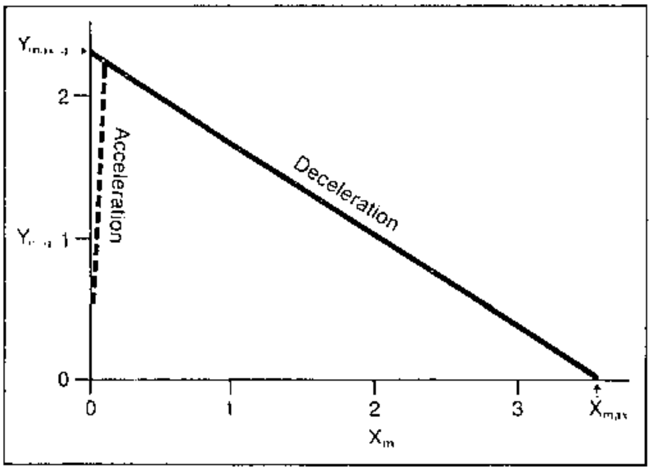


Figure 2.--Graphical representation of the model for the SPB gallery initiation rate. $Y_{n,g}$ is gallery starts on day n, X_m is cumulative day-old gallery starts, $Y_{max,g}$ is a parameter that represents the maximum potential gallery initiation rate, and X_{max} is a parameter that represents the final attack density.

On these trees, landing beetles were caught in two 336-cm² plastic window traps attached to each tree at a height of 4 m. The barrier dimensions are 21 cm long by 16 cm wide excluding the water trap. Collections were made every 24 hours, in the morning. Beetles were stored in 70 percent ethanol. Of the 31 trees observed, 29 were killed by SPB.

Gallery starts and landing beetles were all converted to beetles per 100 cm².

The relationships between the gallery initiation rate and cumulative day-old gallery starts, and between the attraction rate and cumulative day-old gallery starts were examined graphically and statistically (with correlation analysis). Landing beetles are attracted by beetles already in galleries or those initiating galleries. Landing beetles/cumulative gallery start will be used as an index of attraction and is defined for use in this paper as the attraction rate. Data were examined on an individual tree basis and with all trees combined. The general shape of the relationship was determined from examinations of the data for all individual trees. Then parameters were estimated using least squares.

MODELS AND DISCUSSION

The typical time course of SPB colonization on a tree looks like figure 1. This perspective does not show the relationship between new attacks and old attacks like figure 2. The data show that there is a brief, initial phase I will define as accleration of the gallery initiation rate: the rate of daily attacks increases up either to $Y_{max,g}$ or until it intersects the deceleration line, both of which will be defined later. This paper does not treat acceleration of the gallery initiation rate because the experimental design was inadequate for this phase. Following the acceleration phase is a linear phase I will define as deceleration of the gallery initiation rate: the rate of daily attacks decreases linearly from $Y_{max,g}$ to zero. The deceleration line is defined as a line drawn between $Y_{max,g}$ and X_{max} (fig. 2):

$$Y_{n,g} = Y_{max,g} (1-d X_m) \qquad (1)$$

where

$d = 1/X_{max}$

$Y_{n,g}$ = the daily gallery initiation rate on day n

$Y_{max,g}$ = maximum potential gallery initiation rate

$X_m = \sum_{m=o}^{n-1} G_m$ = cumulative day-old gallery starts

$X_{max} = \sum_{m=o}^{N} G_m$ = final attack density

N = the last day of the attack process

n = current day number

G_m = gallery starts per 100 cm² on the _m_th day.

As gallery starts increase, X_m approaches X_{max}. This causes the equation

$$1-d\ X_m \qquad (2)$$

to approach zero; the bounds of equation (2) are 1 and 0 so that Y_n ranges linearly between $Y_{max,g}$ and zero. Biologically this means that each attacking female beetle or beetle pair in a gallery for 24 or more hours produces a fixed amount of inhibitory effect so that the gallery initiation rate decreases linearly with cumulative day-old gallery starts.

The foregoing simple model is very similar in concept to the tree-attack models used in TAMBEETLE (Feldman, Curry, and Coulson 1980) and in algorithm to the mountain pine beetle model developed by Crookson et al. 1978. In a number of ways it oversimplifies the problem of describing the attack process of *Dendroctonus* bark beetles. For this reason, I have developed a second model for the landing process.

The typical time course of SPB landing on a tree is depicted in figure 1. This perspective does not show the relationship between attraction (beetles induced to land per gallery start) and day-old attacks like figure 3. Again, data show that there is a brief, initial phase which I will define as the acceleration of attraction: the rate of attraction increases rapidly up either to $Y_{max,a}$ or until it intersects the deceleration line for attraction, both of which will be defined subsequently. This paper does not treat acceleration of attraction because the experimental design was inadequate for treatment of this phase. Following the acceleration of attraction is a linear phase here defined as the deceleration of attraction: the rate of daily attraction decreases linearly from $Y_{max,a}$ to zero. The deceleration line for attraction is defined as a line drawn between $Y_{max,a}$ and X_{max} (fig. 3):

$$Y_{n,a} = Y_{max,a}\ (1-d\ X_m) \qquad (3)$$

where

$Y_{n,a}$ = daily rate of attraction on the *n*th day, and

$Y_{max,a}$ = a maximum possible daily rate of attraction

and the terms in the parenthetical expression are the same as in equation (2).

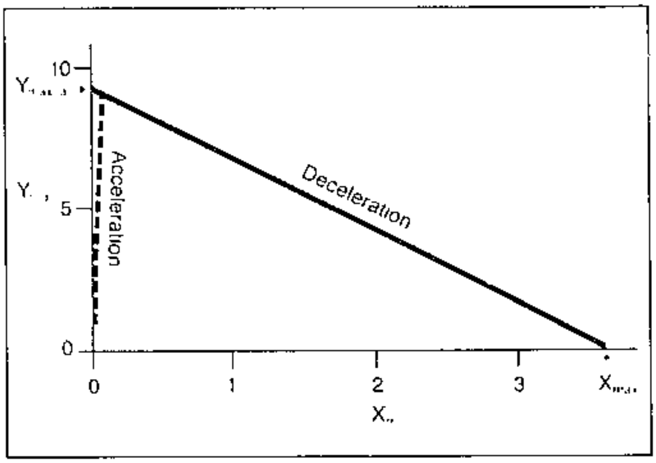


Figure 3.--Graphical representation of the model for the SPB attraction rate. $Y_{n,a}$ is the attraction generated per beetle, X_m is cumulative day-old gallery starts, $Y_{max,a}$ is a parameter that represents the maximum potential attraction generated per beetle, and X_{max} is a parameter that represents the final attack density.

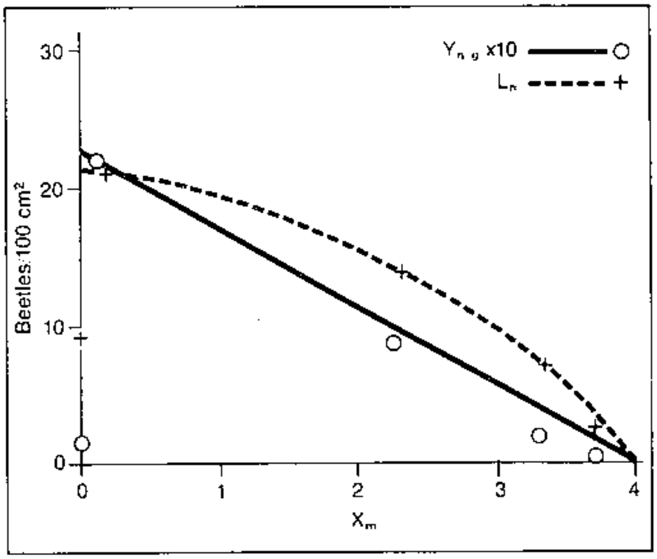


Figure 4.--Observed and predicted values of the gallery initiation rate ($Y_{n,g}$) and the rate of landing beetles (L_n) for a typical loblolly pine attacked by SPB. Only the deceleration phase is depicted; the predicted landing rate is given by the dashed line and the predicted gallery initiation rate is given by the solid line. Observed landing rates are designated with (o) and observed gallery initiation rates are designated with (+). X_m is cumulative day-old gallery starts. The starting gallery initiation rate used to initiate the model was from observed data (0.08 gallery starts), the parameter used are 2.2 for $Y_{max,g}$, 9.7 for $Y_{max,a}$, and 4.1 for X_{max}.

Again, equation (2) ranges linearly between 1 and 0 so that $Y_{n,a}$ varies between $Y_{max,a}$ and 0. Biologically this means that attacking female beetles or beetle pairs have a fixed negative or inhibitory effect on attraction which accumulates with cumulative day-old gallery starts.

To predict the actual beetle landing rate, equation (3) must be rearranged.

Since

$$Y_{n,a} = L_n/(Y_{n,g} + X_m) \qquad (4)$$

where

L_n = landing beetles per 100 cm² per day,

by substituting equation (2) for $Y_{n,g}$ we have

$$\frac{L_n}{Y_{max,g}(1-d\ X_m) + X_m} = Y_{max,a}(1-d\ X_m) \qquad (5)$$

or

$$L_n = c_o + c_1\ X_m + c_2\ X_m^2 \qquad (6)$$

where

$$c_o = (Y_{max,a})\ (Y_{max,g}) \qquad (7)$$

$$c_1 = Y_{max,a}\ [1-2d\ (Y_{max,g})] \qquad (8)$$

$$c_2 = d\ (Y_{max,a})\ \ (d\ Y_{max,g}-1) \qquad (9)$$

The constant c_o is effectively a maximum landing rate possible, c_1 and c_2 are factors that act negatively on the speed of landing as day-old gallery starts accumulate.

To simulate the attack process on a tree where the parameters $Y_{max,g}$, $Y_{max,a}$, and X_{max} are known, all that is needed is a starting gallery initiation rate. An initial value for the gallery initiation rate can be selected at random from the range of values between zero and $Y_{max,g}$. Figure 4 shows an example of observed and predicted landing and gallery initiation rates.

Since d is the reciprocal of X_{max}, $Y_{max,g}$, $Y_{max,a}$, and X_{max} are the parameters of the attack process model. The variation in these parameters may be significant (table 1). For example, hosts that are attacked and killed by low numbers of beetles may also produce less brood or take longer to kill, thus bringing about smaller spots. Alternatively, hosts that are attacked by greater numbers of beetles may be more resistant and thus inhibit an infestation altogether; however, once an infestation is begun, the number of trees killed might be very high due to the high rate of attack which will permit quick reemergence and perhaps participation by one beetle in the killing of several trees. The causal factors for these parametric variations are foci for future research. Factors that may determine the parameters of the model are the aerial density of beetles, beetle pheromone production potential, beetle thresholds for gallery initiation, and/or host factors. Research relating these parameters to potential driving variables would be of great value in defining host and stand susceptibility.

Table 1.--Means, standard deviations, maximum and minimum values, and ranges for model parameters.

	Mean	S.D.	Max.	Min.	Range	N
$Y_{max,g}$	2.6	1.0	4.8	0.7	4.1	29
$Y_{max,a}$	6.9	1.6	17.1	2.9	14.2	29
X_{max}	4.7	1.3	8.0	2.0	6.0	29

LITERATURE CITED

Crookson, N. L., R. C. Roelke, D. G. Burnell, and A. R. Stage. 1978. Evaluation of management alternatives for lodgepole pine stands using a stand prognosis model. *In* Theory and practice of mountain pine beetle management in lodgepole pine forests. p. 114-122. D. L. Kibbe, ed. Forest, Wildlife and Range Exp. Stn., Univ. of Idaho, Moscow.

Feldman, R. M., G. L. Curry, and R. N. Coulson. 1980. The use and structure of the TAMBEETLE spot dynamics model. *In* Modeling southern pine beetle populations. [Asheville, N.C., Feb. 1980.] F. M. Stephen, J. L. Searcy, and G. D. Hertel, eds. U.S. Dep. Agric. For. Serv., Tech. Bull. 1630. Comb. For. Pest Res. Develop. Prog., Pineville, La.

Payne, T. L., J. E. Coster, J. V. Richerson, L. J. Edson, and E. R. Hart. 1978. Field response of the southern pine beetle to behavioral chemicals. Environ. Entomol. 7:578-582.

Renwick, J.A.A., and J. P. Vité. 1969. Bark beetle attractants: mechanism of colonization by *D. frontalis*. Nature (London) 224:1222-1223.

BEHAVIORAL CONSIDERATIONS IN QUANTIFYING THE IMPACT OF *THANASIMUS DUBIUS* (F.) ADULTS ON BARK BEETLE POPULATIONS[1]

T. Evan Nebeker and Russell F. Mizell III[2]

Abstract.--We discuss behavioral factors affecting the role of *Thanasimus dubius* in relation to prey populations, giving consideration to factors that influence host-habitat and host selection. Hunger is assumed to be a major factor in determining predator response and impact. Data concerning these various factors are presented and discussed as to their role in quantifying the impact of *T. dubius* on bark beetle populations.

INTRODUCTION

The southern pine beetle (SPB), *Dendroctonus frontalis* Zimmermann, has a number of predators and parasites associated with it throughout its life cycle. One of these is a checkered clerid beetle, *Thanasimus dubius* (F.), which exhibits a high degree of temporal and spatial synchrony with the SPB (Coster et al. 1977, Dixon and Payne 1979, and Reeve 1975). Vité and Williamson (1970) have shown that this predator is attracted to frontalin, the aggregation pheromone of SPB, and to host-tree oleoresins in the field. *T. dubius* also responds to ipsdienol, the aggregation pheromone of *Ips* spp., in the laboratory (Mizell 1980) and in the field (R. L. Billings, personal communication). This predator is clearly able to locate the host habitat and sites of aggregating prey. These are important considerations when assessing the potential importance of a given predator in relation to a prey population. However, the ability to locate aggregating SPB does not give any indication as to the degree of prey specificity, another important component, this predator might exhibit given a multiple-host environment. Nor does this ability indicate whether this predator is important in regulating a prey population such as the SPB.

Moore (1972) measured the abundance of *T. dubius* in five geographic locations in North Carolina. Using the consumption rate (2.2 SPB adults/day/predator for 5 to 10 weeks) of Thatcher and Pickard (1966), Moore suggested that *T. dubius* was a major SPB predator. His work does not provide any indication as to the potential of beetle regulation, however.

Turnbow (1976) measured consumption rates of *T. dubius* adults in the laboratory and concluded that prey species, predator body size, sex, and oviposition cycles are important factors regulating intake of prey. In addition to the predation of SPB adults by *T. dubius* adults, the clerid larvae are predaceous on immature SPB and other subcortical insects. Nebeker and Purser (1980) have described the relationship of temperature and prey type to developmental time of *T. dubius* larvae.

The status of this predator as a key mortality factor for the southern pine beetle is still questionable. But, based on the above information, this apparently tightly coupled system may well serve as a model for investigating a highly evolved predator-prey system.

We believe that information from detailed behavioral studies, combined with measurements of direct mortality at different population densities and predator conditions is essential for a precise understanding of the system. This paper presents our concept of factors that influence *T. dubius* adult predation, such as host selection, hunger, and prey density. In addition, we will discuss information available, information lacking, and implications of this information in a management system.

---

[1] This study was supported by the Mississippi Agricultural and Forestry Experiment Station and in part by the Expanded Southern Pine Beetle Research and Applications Program. The findings and opinions are the sole responsibility of the authors.

[2] The authors are, respectively, Associate Professor and Graduate Research Assistant, Dept. of Entomology, Mississippi State University, Mississippi State, Miss.

BEHAVIORAL COMPONENTS

Determining the impact of *T. dubius* on a prey population can be approached in many different ways. Our initial efforts have utilized a behavioral approach that follows somewhat the logic presented by Holling (1959 and 1966) and Hassell (1976). Conceptually, the flow of information is presented in figure 1. This frame will allow us to look at (1) rates of predation primarily considering time spent in a given activity, under specific conditions, and (2) eventual development of a predictive model.

Hunger is assumed to be the major motivation determining the behavioral activity of *T. dubius*. Fluctuations in the degree of hunger determine the host-habitat and/or host selection. Behavioral thresholds modulated by hunger may change response specificity at two levels: (1) the response to behavioral compounds or concentrations of compounds, thus determining host selection and alternately prey species; and (2) the range of prey acceptance (size and species), thus determining host selection, suitability, and

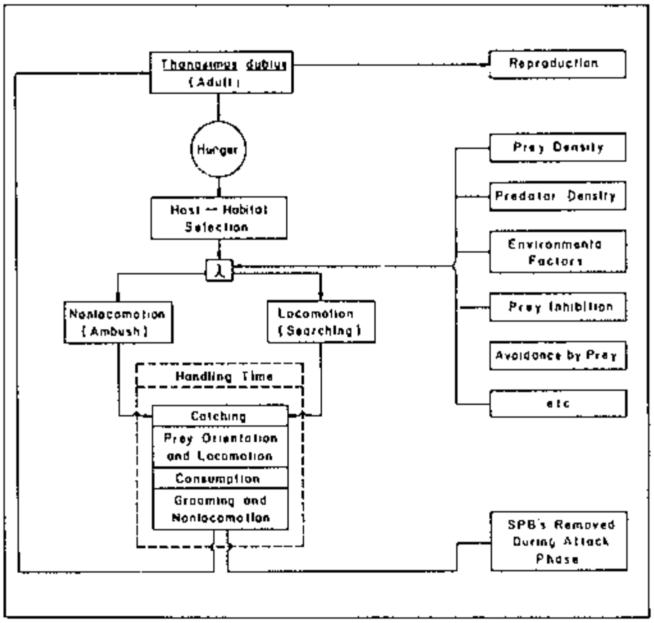


Figure 1.--Factors influencing the predatory behavior and impact of *Thanasimus dubius* adults on a prey population such as the SPB.

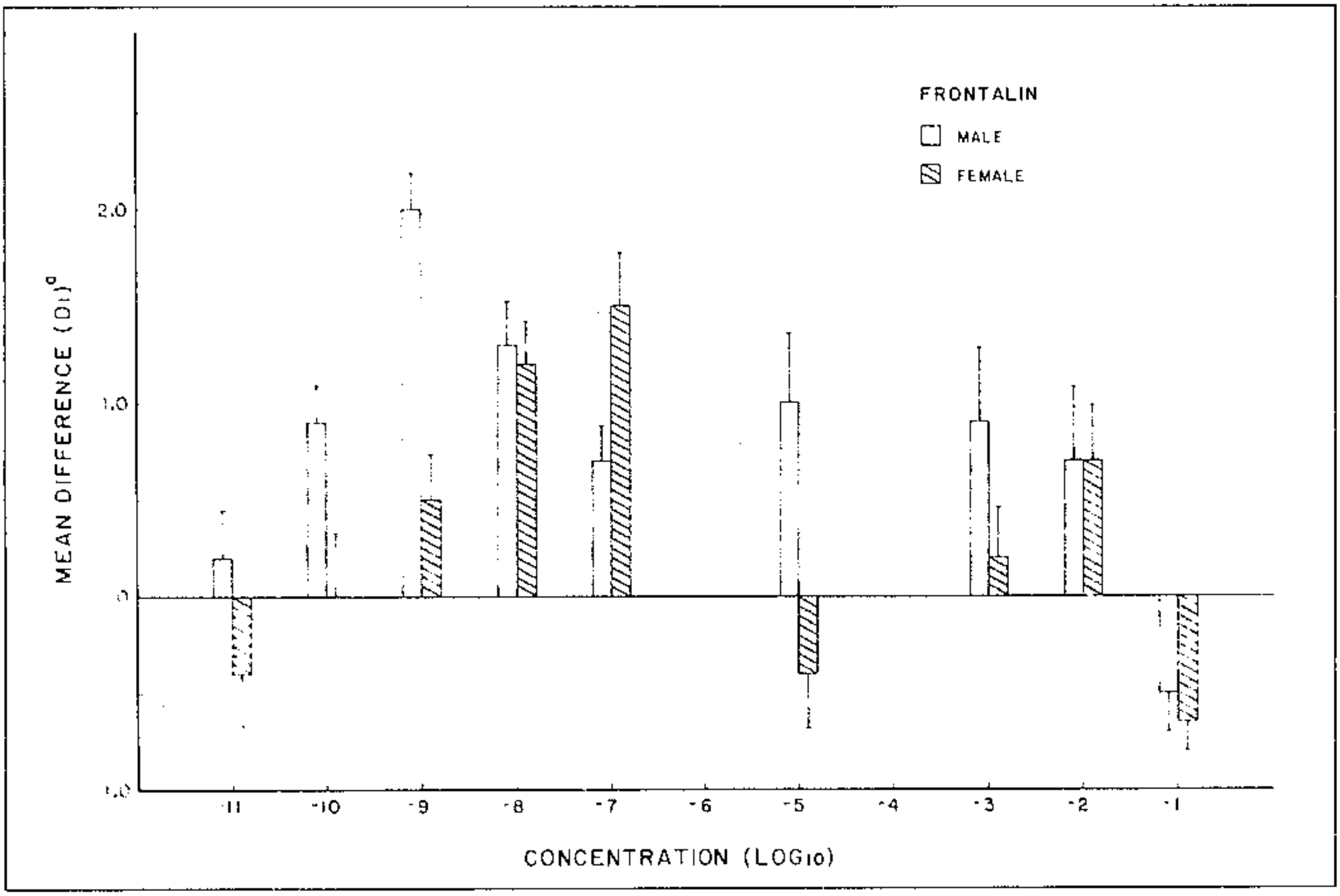


Figure 2.--Response of *Thansimus dubius* to frontalin. $\bar{D}_i$ = treatment - control, each treatment and control replicated 10 times with 10 *T. dubius* per replicate.

acceptability. Host-habitat selection and host utilization may then affect oviposition rate (see Mizell 1980). A list of acceptable *T. dubius* prey in the laboratory is available (Turnbow 1976).

Based on the above observations, we believe that host-habitat selection is determined primarily by the response of *T. dubius* to bark beetle behavioral chemicals and tree volatiles released during the attack phase. In order to determine what compounds *T. dubius* might respond to in the field, individually or in combination, a series of experiments was conducted in the laboratory using a wind tunnel similar to the one described by Visser (1975). The major difference was in increase in dimensions. Methodologies for these experiments are described by Mizell (1980). Responses to various bark beetle pheromones and host volatiles are presented in figures 2-6. In general, it appears that *T. dubius* responds to both *Dendroctonus* and *Ips* attractants. But this does not rule out the possibility of preference at this level. Additional experimentation is required to address this question.

Once *T. dubius* has responded and arrived at a host-habitat, the next step is host selection. From a series of experiments in the laboratory utilizing three prey species (SPB, *I. avulsus*, and *Callosobruchus maculatus* [a laboratory rearing alternate host], Mizell (1980) reached the following conclusions: (1) If the predator was starved prior to exposure to the three hosts, there were no differences in encounters and no demonstrable preference. (2) When the predator was not in a state of hunger, there was demonstrated a preference for *I. avulsus* over SPB, and SPB was preferred over *C. maculatus*. Size of prey (ease of handling) was the most important variable determining host acceptance. Prey of a smaller size were preferred. Hence, preference can be demonstrated at this level in relation to hunger.

After prey acceptance, *T. dubius* exhibits a set of behavioral sequences. Frazier et al. (1980) have provided a functional description of this predatory behavior on SPB. Both sexes of the clerid perform a sequence of five stereotyped acts (see fig. 1): either searching (locomotion) or ambush (nonlocomotion), followed by catching, prey orientation and locomotion, consumption, and finally grooming and nonlocomotion. "Handling time" of the predator is defined as the behavioral acts of catching through grooming and nonlocomotion. Handling time was found to be significantly longer for male prey than for female prey (table 1). Data concerning the time spent in each of these behavioral acts are presented in table 2. Nebeker et al. (1980) described methods of collection and maintenance of *T. dubius* for these biological and behavioral studies.

Table 1.--Handling time (in minutes) of southern pine beetle prey by adult Thanasimus dubius predators (Frazier et al. 1980)

Predator sex	Prey sex Male	Female	Mean
Male	15.07	10.92	12.99
Female	12.55	10.06	11.31
Mean	13.81	10.49*	

*Significant difference by Mann-Whitney test at P = .05.

Table 2.--Components of predation for the clerid beetle, Thanasimus dubius (Frazier et al. 1980)

Predator sex	Prey sex	Searching $\bar{X}_T$	Locomotion/prey orientation $\bar{X}_T$	Consumption $\bar{X}_T$	Grooming/non-locomotion $\bar{X}_T$	Percent efficiency
Male	Male	5.5 (±2.4)	1.1 (±0.4)	9.2 (±0.8)	3.9 (±0.9)	77
Male	Female	5.0 (±1.8)	0.6 (±0.2)	7.9 (±0.3)	5.0 (±0.5)	77
Female	Male	6.3 (±2.3)	0.7 (±0.2)	8.9 (±0.8)	7.1 (±2.0)	71
Female	Female	6.3 (±3.4)	1.4 (±0.7)	8.9 (±0.7)	4.0 (±0.4)	100

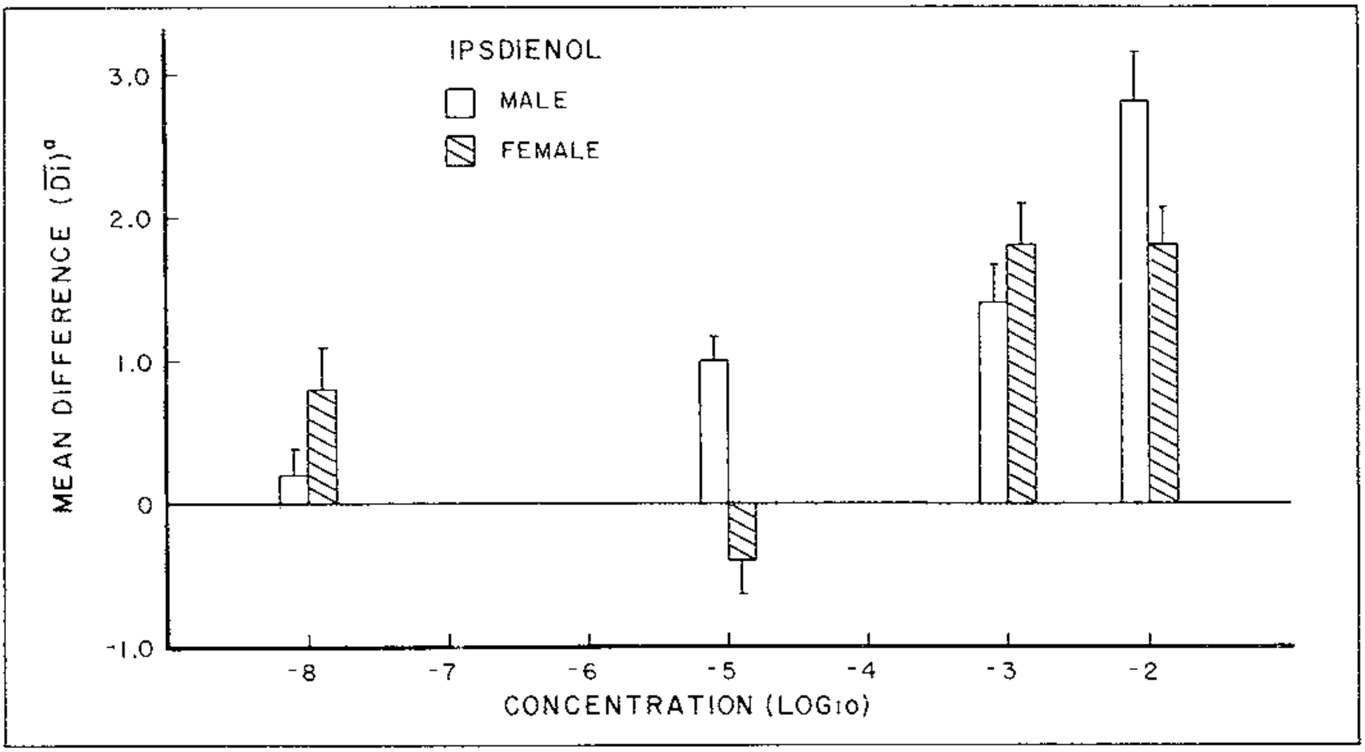


Figure 3.--Response of *Thansimus dubius* adults to ipsdienol. $\bar{D}_i$ = treatment - control, each treatment and control replicated 10 times with 10 *T. dubius* per replicate.

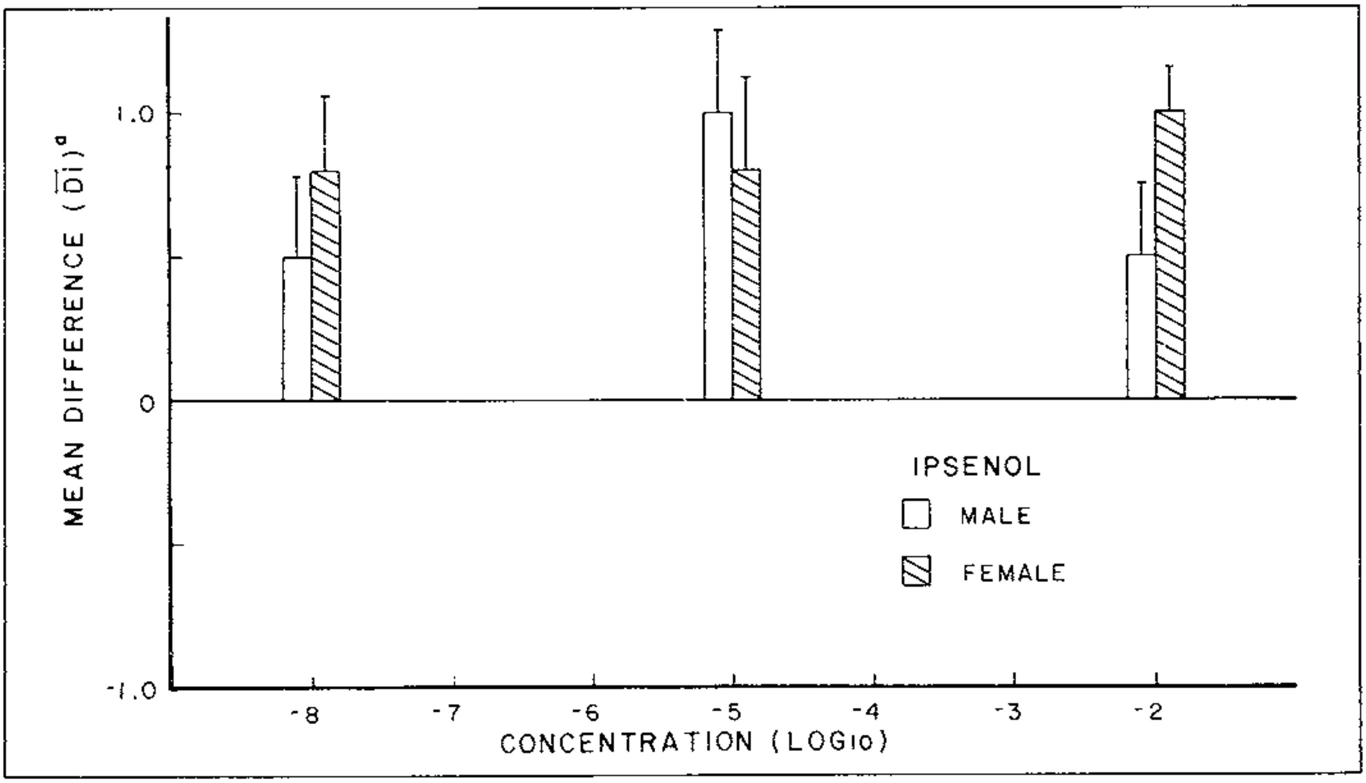


Figure 4.--Response of *Thanasimus dubius* adults to ipsenol. $\bar{D}_i$ = treatment - control, each treatment and control replicated 10 times with 10 *T. dubius* per replicate.

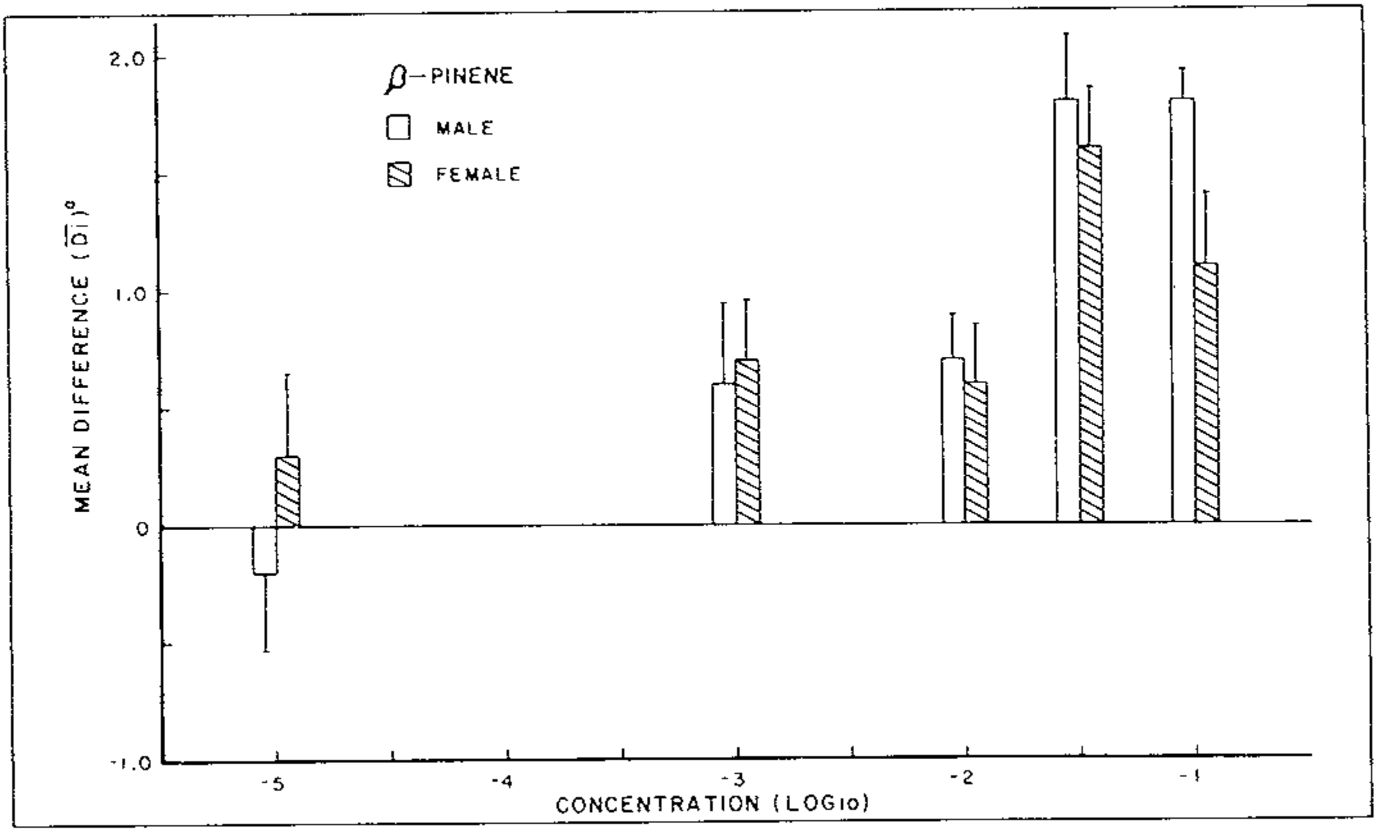


Figure 5.--Response of *Thanasimus dubius* adults to β-pinene. $\bar{D}_i$ = treatment - control, each treatment and control replicated 10 times with 10 *T. dubius* per replicate.

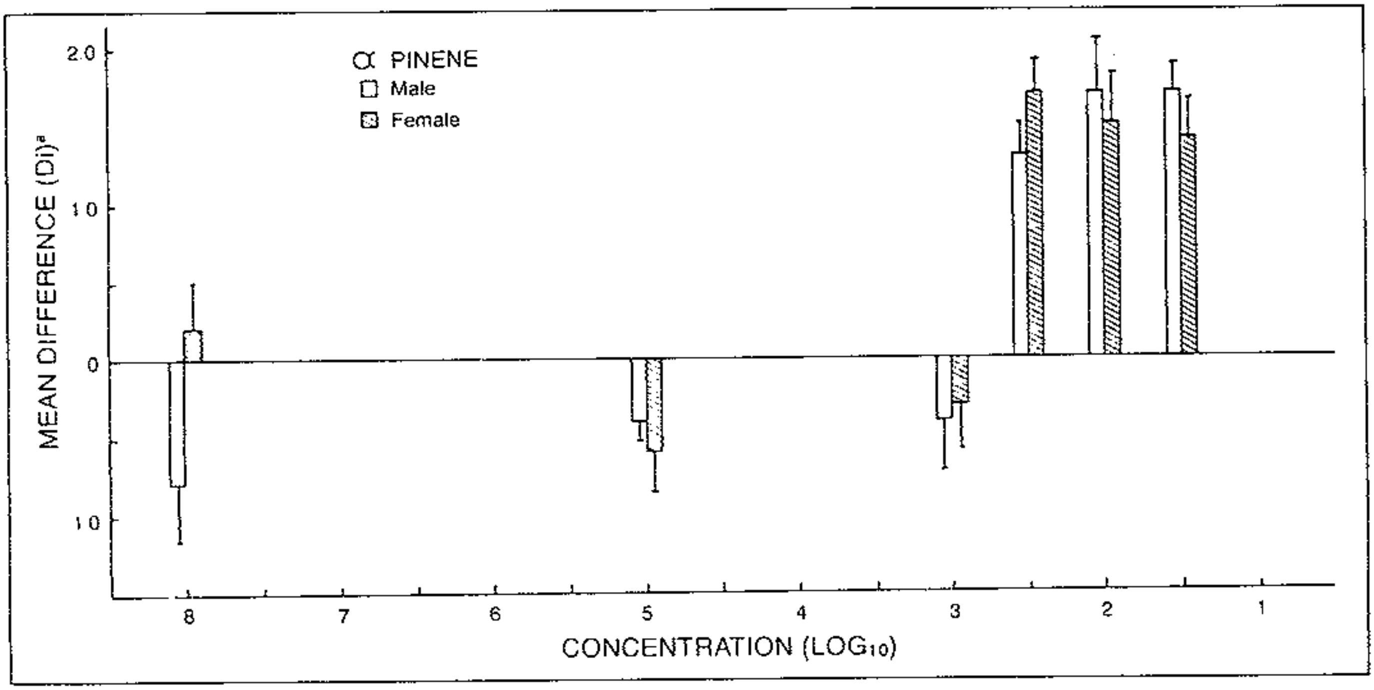


Figure 6.--Response of *Thanasimus dubius* adults to α-pinene. $\bar{D}_i$ = treatment - control, each treatment and control replicated 10 times with 10 *T. dubius* per replicate.

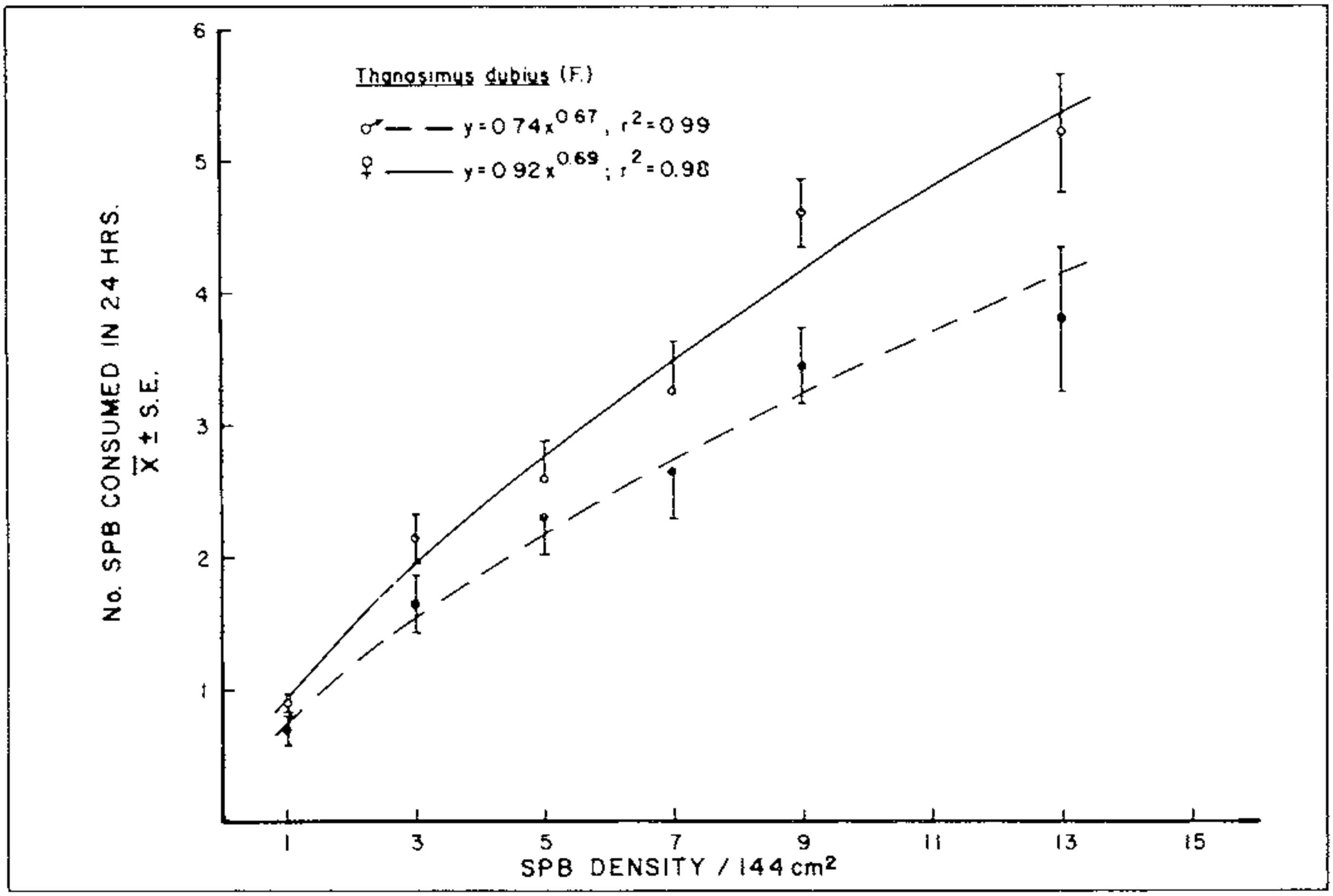


Figure 7.--Functional response of *Thanasimus dubius* adults to various densities of SPB. In all cases the predator density was 1 and all predators were starved for 24 hours before experimentation.

FUNCTIONAL RESPONSE

After locating the host-habitat and host, the predator is then exposed to varying densities of prey. We have found that the basic response of *T. dubius* to changes in prey density follow in general a type II functional response (fig. 7). Turnbow (1976) and Mizell (1980) reached a similar conclusion using different methodologies. The methodologies followed here are described by Nebeker and Frazier[3].

The time frame in which the functional response study is conducted is of critical importance. For example, the increase in number consumed between densities 7 and 9 (fig. 7) is most likely a function of experimental design, in particular the 24-hour time period. This time period is long enough to cover more than one activity cycle (feeding cycle).

It is important to note that the period of starvation (hunger level) prior to exposure to the various prey densities will influence these results. Figure 8 illustrates this in general. These results were obtained from studies concerning the effects different periods of starvation (12, 24, 48, and 72 hours) have on predator feeding. Details of the methods are described by Mizell (1980). The results (fig. 8) indicate that *T. dubius* can feed to satiation in < 1 hour. Meal weight (mg consumed/mg predator body weight) or number of prey consumed increased with increasing periods of starvation. The duration of

---

[3] Nebeker, T. E., and J. L. Frazier. 1976. A detailed investigation of chemical communication and predatory efficiency in the *Thanasimus dubius-Dendroctonus frontalis* system. Final Progress Report to the Expanded Southern Pine Beetle Research and Application Program.

the feeding time necessary to reach satiation (T_s in fig. 8) ranged from 18 to 33 minutes in relation to the length of prior starvation. The length of satiation (digestive pause) after feeding was not significantly different for the four starvation periods, averaging 3 hours in duration.

In the period following this first feeding cycle and digestive pause, a second feeding cycle begins and consumption changes according to the initial starvation. This phenomenon has particular significance when examined in light of the mass attack phase of the SPB prey population, and warrants further study.

PREDATOR-PREY EXPOSURE TIME

Another important component in assessing the impact of a predator on a prey population is the time the two are exposed to each other. In this case *T. dubius* arrives simultaneously with the SPB (Dixon and Payne 1979; Nebeker and Frazier, unpublished data). The number of prey the predator is exposed to depends on the arrival rate of the prey population and the time of day and duration of prey population arrival, along with time that the prey remain an available resource. For example, the SPB is not an acceptable prey item once it has entered the tree and becomes covered with resin. In field experiments we conducted with starved *T. dubius*, the predator never accepted SPB adults covered in resin but readily accepted resin-free SPB adults and other prey. The SPB adults were obtained from trees just coming under attack and working the pitch tube. Hence, estimates for this component will have to be generated from studies describing the colonization process.

Two additional components--prey inhibition and avoidance by the prey--influence the rate of predation and are associated with exposure time. While determining the behavioral sequence and handling time, we observed at least two mechanisms for avoiding predation. First, when the clerids find their prey, the SPB sometimes drop from the surface. We observed this in the laboratory and field. Bunt (1979) also observed this behavior in the field and estimated that 14 percent of the time this avoidance occurs, interfering, of course, with the colonization process. The second mechanism for avoiding predation was prey inhibition. The adult predator was observed encountering an adult SPB and even attempted to capture the prey but released the prey immediately as if it had encountered some offensive substance. The explanation of this behavior is still under investigation.

MODEL DEVELOPMENT

Research efforts are just beginning on the development of a predictive model. The generalized model presented below takes the form that includes the behavioral sequences and considerations discussed above. The initial form of the SPB-DESTROYER model is as follows:

$$\frac{SPB_A}{TD} = \frac{\alpha\ SPB_D\ T_E}{1+\alpha T_H SPB_D}$$

where

SPB_A = southern pine beetle adults removed during the attack phase

TD = *T. dubius* adult density

α = attack rate or rate of successful search

SPB_D = southern pine beetle density the predator is exposed to

T_E = total time prey is exposed to predator and acceptable
$= T_S + T_A + T_H\ SPB_D + \beta$

T_S = total time spent searching

T_A = total time spent in ambush

T_H = total handling time--catching, orientation, locomotion, consumption, and grooming

β = time doing other things (e.g., mating, etc.)

This model follows basically the same form as presented by Hassell (1976) for predator type II functional responses. The assumptions implicit in the equation are discussed by Royama (1971) and Rodgers (1972). One of their most important points is that no allowance is made in the equation for the decrease in available prey as they are eaten or removed (Hassell 1976). However, we suggest it is a minor point in this situation because the prey are continually replenished and the exposure ratio (prey/predator) during the initial attack phase in the field actually increases. Availability of prey needs to be considered in future model development.

Several parameters associated with the form of the model need to be considered from a behavioral point of view. The attack rate or rate of successful search can be influenced by a number of factors, including the condition of the

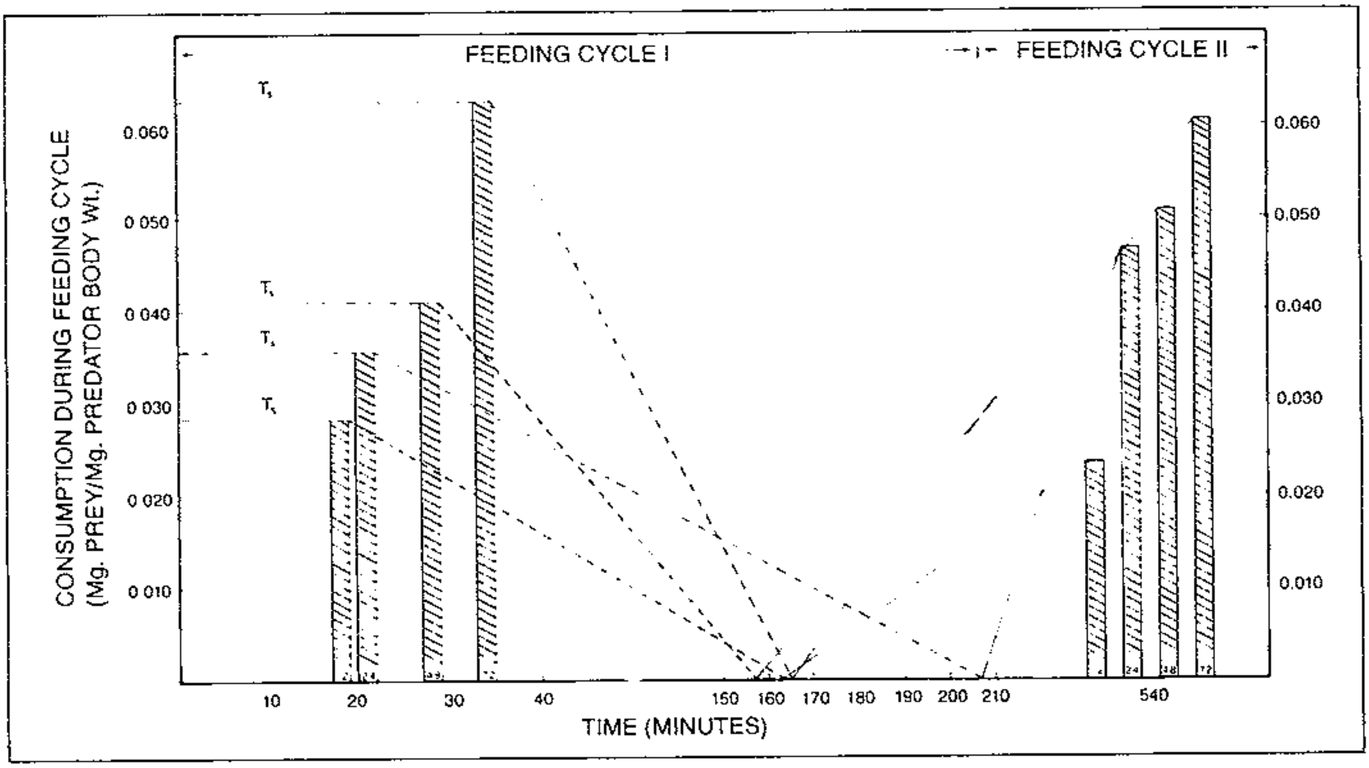


Figure 8.--Time to satiation (T_s), amount consumed, and length of the first two feeding cycles for *Thanasimus dubius* adults as a function of hunger.

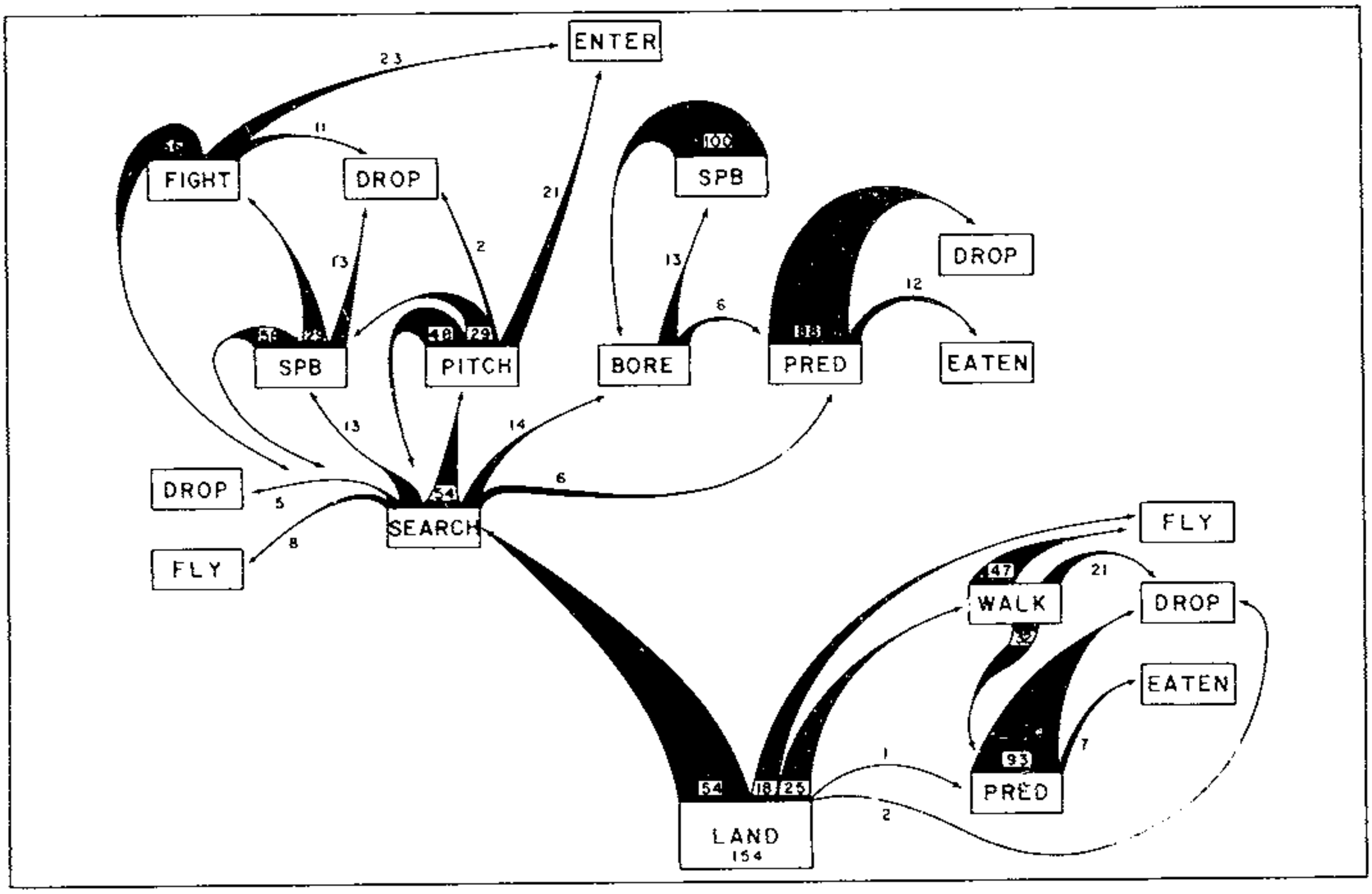


Figure 9.--Behavioral sequence flow diagram of SPB behavior on the bark of host trees. Percentages of SPB within a behavior category which proceed to another are included, based on a total of 154 SPB. (After Bunt 1979).

Table 3.--Effect of sensory interference on predation by the clerid beetle Thanasimus dubius on Dendroctonus frontalis (Frazier et al. 1980)

Treatment	Number of encounters	Number of captures	Percent efficiency	Number consumed	Percent consumed	Mean searching time (min)	Mean consumption time (min)
Normal	13	10	77	10	100	5.5 (±2.4)	9.2 (±0.8)
Blinding	14	10	71	8	80	1.2 (±0.4)	8.7 (±0.9)
Antennectomy	29	7	24	6	86	5.5 (±2.2)	9.8 (±0.6)
Labial palpectomy	43	5	12	4	80	10.9 (±1.7)	10.1 (±1.4)
Maxillary palpectomy	36	10	28	5	50	10.3 (±1.7)	7.7 (±1.2)
Antennectomy + Labial palpectomy	35	7	20	7	100	9.3 (±1.8)	12.2 (±1.0)
Anntennectomy + Labial and maxillary palpectomy	89	2	2	2	100	13.6 (±1.0)	8.7 (±0.5)

predator arriving at the site of the aggregating prey. Table 3 illustrates the fact that predator efficiency (ability to recognize and capture suitable prey) decreases as various sensory structures are removed. This is not to say that predators arriving at aggregating sites are in these particular conditions, but that variation between predators may be due to some kind of sensory interference, resulting in a lower rate of successful search or rate of removal. As table 2 showed, the rate of successful search (percent efficiency) is rather high. According to observations by Bunt (1979), however, this rate may be overestimated (*see* fig. 9). Here, 22 SPB encountered predators (21 SPB encountered *T. dubius* and one encountered *Temnochila virescens*). Ten of these encounters resulted in the predator making an unsuccessful effort to capture the SPB; 10 encounters resulted in no contact, as the predator showed no interest in the SPB; and 2 encounters resulted in the SPB being consumed (Bunt 1979).

SUMMARY

Thanasimus dubius has been demonstrated to respond to the pheromones of *D. frontalis* and *Ips*. Specificity has not been demonstrated at this level, however. In the laboratory, satiated *T. dubius* adults prefer *Ips*. Also established is the fact that no preference is evident for this predator when starved. Hence the physiological condition of the predator determines its role in association with the acceptable prey. Observations are lacking as to other acceptable prey in the field. Once this predator has located the host tree, the number of prey attacked is dependent on the time since the last meal. Satiation is reached within the first hour of feeding and lasts for approximately 3 hours. Hence, one can calculate the number of prey that *T. dubius* can potentially attack. This number will be influenced by (1) the number and rate of arrival of the aggregating prey population that the predator is exposed to, and (2) the predator population itself. Currently, we are lacking methodology for estimating the predator population in a given area.

we do have information on the numbers landing on a tree, but the time spent on the tree and in the area is of importance in quantifying the impact of a predator on a prey population.

The predator behavior is fairly consistent and stereotypic. Hence, reliable estimates of time involved in various behavioral events are available and quantifiable. This fact suggests that the behavioral approach is acceptable.

Speculation

We have been discussing the predatory behavior of *T. dubius* adults. But we need to consider the predator behavior of *T. dubius* larvae in order to quantify fully the impact of the predator population on SPB and other bark beetle populations. It is evident that the adult predators influence the dynamics of the colonization process. This influence is dependent on the condition of the predators (time since last predation) arriving at the prey aggregation sites. In addition, the density of the arriving predator population will greatly influence the colonization process. We suggest the result of this influence might be one or both of the following. Given the simultaneous arrival of the predator-prey population, the predator population may cause a delay in the colonization process, creating a condition where the exposure time (predator-prey) is increased. Additional predation thus occurs. This we observed, on a limited scale, in an exclusion experiment we conducted. Using gallery length constructed as the statistic for comparison, we found that during the first 6 days of attack, SPB constructed more gallery in the areas where the predator was excluded. The resulting delay in the colonization process may also result in increased mortality to the attacking SPB adults because of interference. Also, the beetles do not enter the tree quickly, so they do not become covered with resin, which inhibits predators. Further this delay or increase in colonization time will influence the overall generation time, thus decreasing by a fraction the number of generations per calendar year. The second result might influence the size of the initial spot and spot growth. Given that *N* SPB adults are required to colonize a particular tree and successfully utilize the resource, more of the arriving population would be required to successfully attack fewer trees when the predator population is present.

We realize these statements are highly speculative and these hypotheses difficult to test. However, as we gain a greater understanding of the dynamics of this predator and other predator and parasite populations, we should be able to demonstrate their role and impact clearly. Ultimately we can consider management implications, augmentation, and predator-parasite improvement. At this point, it is clear that an effort should be made to conserve both predator and parasite populations during SPB salvage operations.

LITERATURE CITED

Bunt, W. D. 1979. Southern pine beetle behavior on the bark of host trees during mass attack. M.S. thesis. Stephen F. Austin State University, Nacogdoches, Tex. 52 p.

Coster, J. E., T. L. Payne, E. R. Hart, and L. J. Edson. 1977. Aggregation of the southern pine beetle in response to attractive host trees. Environ. Entomol. 6:725-731.

Dixon, W. N., and T. L. Payne. 1979. Aggregation of *Thanasimus dubius* (F.) on trees under mass attack by the southern pine beetle. Environ. Entomol. 8:178-181.

Frazier, J. L., T. E. Nebeker, R. F. Mizell III, and W. E. Calvert. 1980. Predatory behavior of the clerid beetle *Thanasimus dubius* (F.) on the southern pine beetle. Canad. Entomol. [In review.]

Hassell, M. P., J. H. Lawton, and J. R. Beddington. 1976. The components of arthropod predation. I. The prey death rate. J. Anim. Ecol. 45:135-164.

Holling, C. S. 1959. Some characteristics of simple types of predation and parasitism. Canad. Entomol. 91:385-398.

Holling, C. S. 1966. The functional response of invertebrate predators to prey density. Mem. Entomol. Soc. Can. 48:1-86.

Mizell, R. F. III. 1980. *Thanasimus dubius* (F.): some behavioral factors regulating its predatory role. Ph.D. dissertation. Mississippi State University, Mississippi State.

Moore, G. E. 1972. Southern pine beetle mortality in North Carolina caused by predators and parasites. Environ. Entomol. 1:58-65.

Nebeker, T. E., and G. C. Purser. 1980. Relationship of temperature and prey type to developmental time of the bark beetle predator *Thanasimus dubius* (F.) (Coleoptera:Cleridae). Canad. Entomol. [In press.]

Nebeker, T. E., G. C. Purser, and R. F. Mizell III. 1980. Collection and maintenance of *Thanasimus dubius* (F.) for biological and behavioral studies. J. Ga. Entomol. Soc. [In press.]

Reeve, R. J. 1975. Temporal and spatial distribution of flying *Dendroctonus frontalis* Zimmerman (Coleoptera: Scolytidae) and the predator *Thanasimus dubius* (F.) (Coleoptera: Cleridae) in and near small infestations. M.S. thesis. Stephen F. Austin State University, Nacogdoches, Tex. 69 p.

Rogers, D. J. 1972. Random search and insect population models. J. Anim. Ecol. 41:369-383.

Royama, T. 1971. A comparative study of models for predation and parasitism. Res. Pop. Ecol. Kyoto Univ. Suppl. 1:1-91.

Thatcher, R. C., and L. S. Pickard. 1966. The clerid beetle, *Thanasimus dubius*, as a predator of the southern pine beetle. J. Econ. Entomol. 59:955-957.

Turnbow, R. W., Jr. 1976. Prey consumption, survivorship and oviposition by adults of the bark beetle predator *Thanasimus dubius* (F.) (Coleoptera: Cleridae). M.S. thesis. Oregon State University, Corvallis. 91 p.

Visser, J. H. 1975. The design of a low-speed wind tunnel as an instrument for the study of olfactory orientation in the Colorado potato beetle (*Leptinotarsa decemlineata*). Entomol. Exp. and Appl. 20:275-288.

Vité, J. P., and D. L. Williamson. 1970. *Thanasimus dubius*: prey perception. J. Insect Physiol. 16:233-239.

EVALUATING THE CONTRIBUTION OF COMPONENT PROCESSES IN THE DYNAMICS OF SOUTHERN PINE BEETLE INFESTATIONS[1]

John L. Foltz, Paul E. Pulley, and Don N. Pope[2]

Abstract.--A model is described for simulating southern pine beetle populations through time. The attacking population during a given time period is calculated by summing the numbers of newly emerged brood and reemerged parental females from within the infestation, plus immigrant females from other infestations The numbers of new and reemerged females are calculated using previous attacks, brood increase ratios, within- and between-tree survival rates, and the distributions of brood emergence and parent reemergence through time.

Simulations and analysis show those combinations of parameter values which lead to increasing, stable, and decreasing populations. Also included are the FORTRAN program for operating the model and methods for using the output and model parameters to calculate the finite and intrinsic rates of increase, the net reproductive rate, and the mean generation time of simulated populations.

INTRODUCTION

Until a few years ago most investigations of bark beetle population dynamics concentrated on the within-tree processes of colonization, reproduction, and brood mortality. Data were commonly summarized as within-tree life tables or as brood increase ratios, the number of emerging brood relative to the parental population. The analyses of these data in relation to the dynamics of bark beetle infestations often assumed that there was no between-tree mortality of adults, no overlapping of generations except during a brief reproductive period, and that each adult colonized only one tree and produced just one brood. These assumptions are obviously untrue for the southern pine beetle, *Dendroctonus frontalis* Zimmermann. An alternative concept to the traditional life-table analysis is required for understanding the dynamics of infestations by this bark beetle.

In this paper we present a simple model for simulating infestations of the southern pine beetle. The model provides a conceptual framework for drawing together the within-tree processes of colonization, reproduction, parental reemergence, brood mortality, and brood emergence, along with the between-tree mortality and migration of new and old adults. Simulations will show the relative effects of the above processes on the growth of SPB infestations. Also we present the model structure and computer code which can be used in teaching basic principles of population dynamics.

THE MODEL

Construction

The objective of the model is to simulate the number of new attacks that occur during successive time periods within a defined geographic area. Obviously many biotic and abiotic factors affect the number of attacks, but for the moment we ignore such factors and construct a model using the basic life-cycle processes of the insect.

A southern pine beetle infestation begins when immigrant beetles colonize a susceptible tree in a previously uninfested area (fig. 1). Later, some of the parent beetles reemerge to reproduce again in the same or another infestation (= spot). The emerging brood adults will also be a source of attacking beetles as time progresses. The rates of immigration, oviposition, development, within- and between-tree mortality, and emigration determine how quickly a spot expands or collapses.

---

[1] Texas Agricultural Experiment Station paper no. TA 14589.

[2] The authors are, respectively, Assistant Professor, Dept. of Entomology and Nematology, University of Florida, Gainesville; Associate Research Engineer, Data Processing Center, Texas A. & M. University; and Graduate Assistant, Dept. of Industrial Engineering, Texas A. & M. University, College Station.

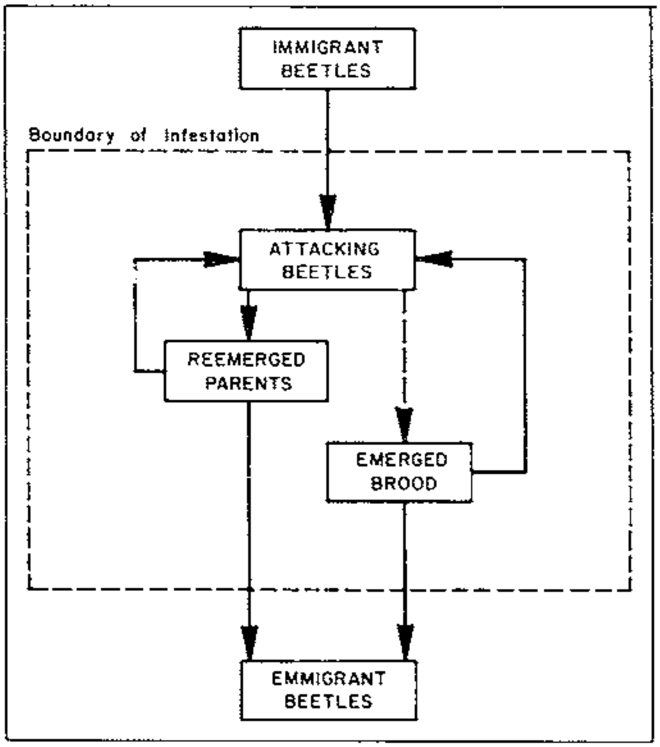


Figure 1.--Sources of attacking beetles in a *D. frontalis* infestation.

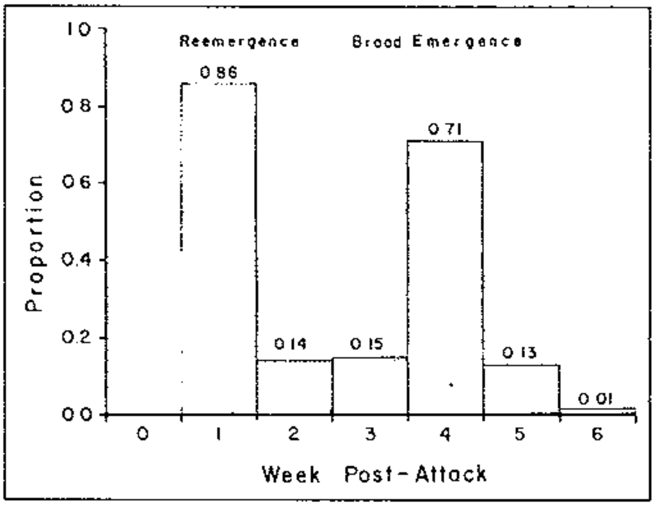


Figure 2.--Hypothetical proportions of total reemergence and emergence in the *j*th week subsequent to attack.

Figure 2 shows typical distributions for *D. frontalis* reemergence and brood emergence on trees during summer outbreaks in Texas. We know from previous studies (Coulson et al. 1978, 1979; Fargo et al. 1978) that most of the attack and colonization of a tree occurs in ca. 1 week, most of the reemergence occurs the following week, and the greatest proportion of the brood emerge the fourth week following initial attack. The proportions indicated for each week in figure 2 are used in the simulations throughout the paper.

The simulation model is derived by considering the number of attacking females (A_i) of the *i*th week to be composed of reemerged (R_i) and new brood females (B_i) from earlier attacks in the same infestation plus immigrant (IM_i) females from adjacent spots.[3]

Algebraically the model is

$$A_i = R_i + B_i + IM_i \qquad (1)$$

The number of reemerged females in equation (1) is calculated as

$$\begin{aligned} R_i &= MR \cdot SR \cdot FR_1 \cdot A_{i-1} + MR \cdot SR \cdot FR_2 \cdot A_{i-2} + \ldots \\ &= MR \cdot SR \cdot \sum_{j=1}^{M} (FR_j \cdot A_{i-j}) \\ &= CR \cdot \sum_{j=1}^{M} (FR_j \cdot A_{i-j}) \qquad (2) \end{aligned}$$

where

MR = the multiplier for the proportion of the attacking population which reemerges ($0 \leq MR \leq 1.0$)

SR = the between-tree survival rate, i.e., the probability that a reemerged female will successfully attack again ($0 \leq SR \leq 1.0$)

CR = $MR \cdot SR$, the proportion of an A_i cohort which eventually reemerges *and* successfully attacks again ($0 \leq CR \leq 1.0$)

FR_j = the fraction of total reemergence of each A_i cohort which occurs in the *j*th time period subsequent to attack ($\sum_{j=1}^{M} FR_j = 1.0$; $j = 1,2,\ldots,M$).

---

[3] Note that all variables in this model are defined and calculated for the females only.

Combining the MR and SR parameters simplifies the simulations that follow, because a single CR value serves for all the MR and SR combinations which produce that value.

The calculation of the B_i term in equation 1 is

$$B_i = MB \cdot SB \cdot FB_1 \cdot A_{i-1} + MB \cdot SB \cdot FB_2 \cdot A_{i-2} + \ldots$$

$$= MB \cdot SB \cdot \sum_{j=1}^{M} (FB_j \cdot A_{i-j})$$

$$= CB \cdot \sum_{j=1}^{M} (FB_j \cdot A_{i-j}) \qquad (3)$$

where

MB = the multiplier indicating the number of progeny females emerging per parent female in the attacking cohort (the brood increases ratio, $MB \geq 0$)

SB = the between-tree survival rate of emerged females ($0 \leq SB \leq 1.0$)

CB = MB·SB, the coefficient for number of brood per parent female which emerge *and* successfully reproduce in the same infestation ($CB \geq 0$)

FB_j = the fraction of the emergence occurring in the *j*th time period subsequent to attack ($\sum_{j=1}^{M} FB_j = 1.0$; $j = 1,2,\ldots,M$).

As before, combining MB and SB into the parameter CB simplifies the simulations.

The third term for calculating the attacking population is the number of immigrant females, IM_i. We recognize that these beetles must be either emerged or reemerged insects. But because they are immigrants and their number is not a function of previous A_i, they are separated from R_i and B_i.

Substituting equations 2 and 3 into equation 1 yields the model for calculating *D. frontalis* attacks through time:

$$A_i = CR \cdot \sum_{j=1}^{M} (A_{i-j} \cdot FR_j) + CB \cdot \sum_{j=1}^{M} (A_{i-j} \cdot FB_j) + IM_i \qquad (4)$$

Every mathematical model of a biological system is based upon a series of assumptions about that system. It is important that these assumptions be identified and stated so that the simulations can be judged for validity and applicability. The simulations reported in this paper have the following assumptions.

(1) MR incorporates all factors affecting the proportion of females that reemerge.

(2) SR incorporates all factors affecting between-tree survival of reemerged females.

(3) MB incorporates all factors affecting the brood increase ratio.

(4) SB incorporates all factors affecting between-tree survival of brood females.

(5) The FR_j and FB_j distributions in figure 2 are constant through time.

(6) MR, SR, MR, and SB are independent, and all are time invariant.

(7) Immigration is limited to the initial attacking cohort.

(8) Emigration is equivalent to between-tree mortality and is thus included in SR and SB.

Comparing Simulations

Graphical Analysis

The objectives of our simulations were to study the relative effects of within-tree reproduction, brood mortality, parental reemergence, brood emergence, between-tree mortality, and migration on spot growth. The model is a valid framework for these objectives, although it does not mimic real-world infestations. Study of the behavior of the simulations can provide us with insights into possible real-life occurrences in beetle spots.

Table 1 contains the initial output from one simulation and shows how R_i, B_i, and IM_i are calculated and summed to produce A_i. The spot begins with 1,000 immigrant females and a suitable number of males to assure 100 percent mating and fertilization. New attacks in weeks 2 and 3 are reduced because there is no immigration and only reemerged females are present to expand the infestation. The number of attacks increases in weeks 4 and 5 as most of the brood from the A_1 parents emerge. Attacks decrease slightly in the next 2 weeks, but then rise sharply as there is another large input of new brood females.

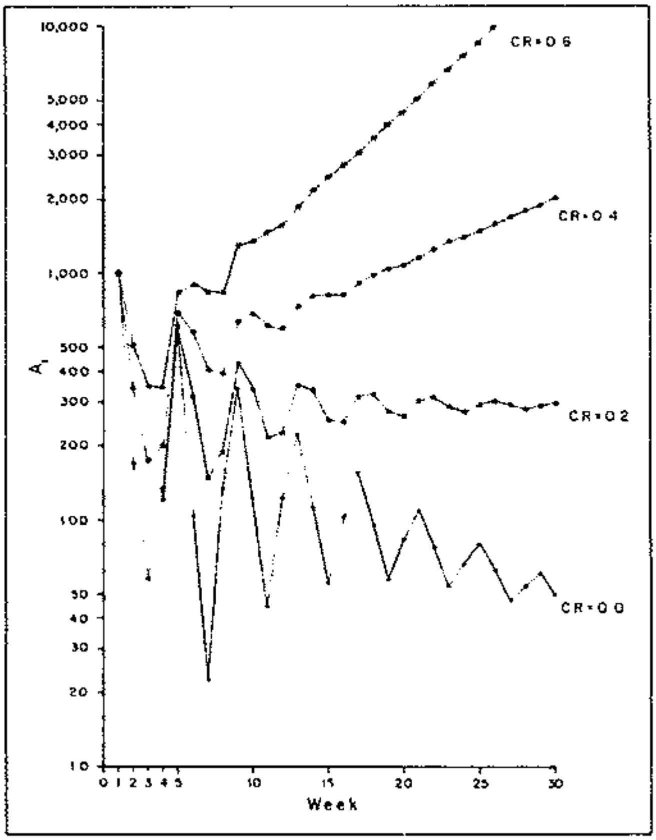


Figure 3.--Plot of A_i from equation 4 for various CR values. CB = 0.80 and the other parameters are as listed in table 1.

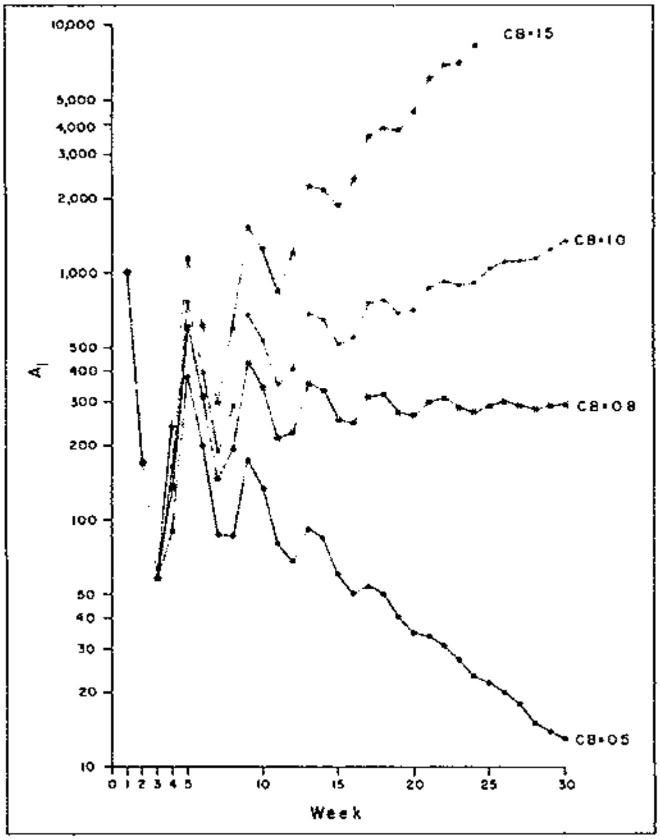


Figure 4.--Plot of A_i from equation 4 for various CB values. CR = 0.20 and the other parameters are listed in table 1.

Figures 3 and 4 are plots of A_i through time and show how different values of CR and CB affect spot growth. Infestation dynamics are affected in two ways when the CR parameter varies from 0.0 to 0.6 and the other parameters are constant (fig. 3). First, the greater the CR value, the more rapidly the spot increases. Second, as CR increases, there are fewer ups and downs in new attacks before the spot begins increasing. The initial oscillations in new attacks result from the uneven age distribution of early populations. These oscillations diminish as the ratio $R_i:B_i$ stablilizes with increasing i.

Figure 4 illustrates how different CB values affect infestation dynamics when CR = 0.20. When there are 0.8 successful progeny per attack (CB = 0.80), the number of attacking females (A_i) decreases from the original 1,000 immigrants to stabilize at approximately 292 attacks per week. The spot ultimately becomes extinct whenever CB is less than 0.80. As CB values increase above 0.80, the infestation increases at a greater rate. Simulations for other combinations of CR and CB show that constant A_i values develop whenever CR + CB = 1.0. That is, new attacks become constant when MR·SR + MB·SB = 1.0. Thus, in the absence of immigration, summations of the parameters < 1.0 are indicative of declining populations, while summations > 1.0 indicate increasing populations.

FR_j and FB_j are important elements in the rates of increase or decrease of infestations. The earlier the occurrence of reemergence or emergence, the faster the population changes. The population changes less rapidly when these processes are delayed by a factor such as cooler temperatures.

IM_i was set at zero for all i > 1 in the simulations reported in table 1 and figures 3 and 4. Continued immigration can sustain a spot that otherwise would decline and can obviously make an expanding spot grow larger at an even faster rate.

Table 1.--Simulation of *D. frontalis* population dynamics.[1]

Week i	Reemerged Beetles R_i	New Brood Beetles B_i	Immigrant Beetles IM_i	Total Attacking A_i
1	0	0	1000	1000
2	430	0	0	430
3	255	0	0	255
4	140	225	0	365
5	175	1162	0	1337
6	600	710	0	1310
7	657	453	0	1110
8	569	746	0	1315
9	643	1794	0	2437
10	1140	1911	0	3051

$\lambda = 1.2535 \quad r_m = 0.2259 \quad R_0 = 3.0000 \quad T = 4.8633$

[1] See text for population model. Constants used: CR = 0.50; CB = 1.50; FR_j = 0.86, 0.14, 0, 0, 0, 0; FB_j = 0, 0, 0.15, 0.71, 0.13, 0.01.

These simulations illustrate the behavior of the model when one coefficient is varied while the others remain constant. The simulations were not intended to imitate real infestations, but only to show how spots might increase or decrease due to a change in one coefficient.

Numerous possibilities exist for improving the reality and sensitivity of the simulation model. For example, changing the basic time unit to days and allowing immigration to occur over an extended period would afford more realism. Another possible way to improve the realism of the model is to have the parameters change through time rather than being held constant. This alteration can be accomplished by using submodels in which the parameters are calculated as functions of various biotic and abiotic inputs. Such realism and sensitivity can be obtained only by increasing the complexity of computation and assumptions, however.

The oscillations noted in figures 3 and 4 illustrate the dangers inherent in predicting the course of *D. frontalis* infestations based on the ratio of new attacks to earlier attacks. Sometimes such a ratio may indeed indicate that weather, predators, host resistance, etc., are affecting the spot. But it may be that we are merely observing a temporary fluctuation in new attacks resulting from the uneven age structure of the beetle population.

The observation that infestations will increase whenever the sum of the CR and CB values is > 1.0 raises several interesting questions with regard to the control of spots. First, can these two parameters be estimated with a reasonable degree of confidence so that the future development of a newly discovered infestation might be predicted? Also, what factors might be directly or indirectly manipulated to reduce CR and CB so that an outbreak might be prevented or an existing spot will decline more rapidly? At the present time these questions cannot be answered satisfactorily.

Demographic Parameters

An alternative to the graphical methods of figures 3 and 4 for assessing the effects of changing the parameter values in equation 4 is to calculate and compare the four population parameters often calculated from life and fertility tables (Southwood 1965). Implicit assumptions for the calculations are a stable age distribution, constant environmental conditions, and unlimited resources. *The finite rate of increase*, λ, is the number of times the population increases per unit of time. In the absence of immigration it is calculated as

$$\lambda = \frac{A_{i+1}}{A_i} \qquad (5)$$

An additional assumption is that A_i, the number of successful attacks in the *i*th time period, changes at the same rate as the SPB population. Computationally, the parameter value is obtained by including λ as part of the computer output when simulating equation 4 and running the simulation through the initial oscillations until λ is constant. The λ values for the four curves in figure 4 are contained in table 2. Obviously, λ = 1.00 indicates a stable population, whereas smaller values indicate declining populations and the larger values, increasing populations.

Table 2.--Demographic parameters for the four simulations shown in figure 4. (CR = 0.2 in all simulations.)

Simulation	λ	r_m	R_o	T
CB = 0.5	0.8971	-0.1086	0.6250	4.33
C3 = 0.8	1.0000	0.0000	1.0000	----[1]
CB = 1.0	1.0537	0.0523	1.2500	4.27
CB = 1.5	1.1601	0.1485	1.8750	4.23

[1] Cannot be calculated when $r_m = 0$.

Another useful parameter for comparing the rates of change of different populations is the *intrinsic rate of increase*, r_m, which is calculated as

$$r_m = \ln \lambda \qquad (6)$$

Negative values of this parameter indicate declining populations and positive values, expanding populations.

The number of reproductively successful offspring per parent female is the *net reproductive rate*, R_o, of a population. R_o is equivalent to the number of successful female offspring per attack (CB) times the average number of attacks per female. Because CR is the probability that an attacking female will attack and reproduce again, the average attacks per female is the sum of the series 1 + CR + CR² + ... With $0 \leq CR \leq 1$ and increasing k, $\sum_{k=0} CR^k$ approaches the limit $\frac{1}{1-CR}$.

Thus

$$R_o = CB\ (\frac{1}{1-CR}) \qquad (7)$$

Note that when $R_o = 1.0$, CR + CB = 1.0, which proves the earlier empirical observation that populations are stable when CR + CB = 1.0.

Generation time T is a fourth population parameter and indicates the time required for the population to expand or diminish by the amount equivalent to R_o. It is calculated as

$$T = \frac{\ln R_o}{r_m} = \frac{\ln R_o}{\ln \lambda} \qquad (8)$$

provided $R_o \neq 1.0$ and $r_m \neq 0$.

The most informative of the demographic parameters for evaluating the effects of the equation 4 coefficients are λ and r_m. Not only do these parameters indicate whether the population is increasing or decreasing, but they also indicate the rate at which it is changing. Equation 7 for calculating R_o is particularly useful because it quickly shows whether a specific combination of MR, SR, MB, and SB values produces an increasing or decreasing population.

APPLICATIONS AND DISCUSSION

Simulation models are useful tools for investigating the dynamics and management of insect populations (Berryman and Pienaar 1974). The modeling effort itself is useful because it forces us to consider all aspects of a problem and points out gaps in our knowledge (Ruesink 1975). Also, a valid model can be manipulated in ways that would be cost prohibitive or impossible in nature, so models can be used to estimate nonmeasurable quantities or evaluate the impacts of several management strategies applied simultaneously. Furthermore, the completed model is an excellent tool for teaching others since it contains much pertinent information on the population.

Knowledge Gaps

Most of the *D. frontalis* research to date has concentrated on reproduction and the subsequent within-tree mortality of the developing brood, i.e., MB, the brood increase ratio. However, the simulations emphasize the necessity of also understanding what affects the other life-cycle components in order to understand or predict the dynamics of spot. For example, future research should include efforts to describe the effects of such factors as temperature, predation, attack density, nutritional value of the phloem, and age of the female on MR, the reemergence probability of attacking beetles.

The between-tree survival of reemerged and newly emerged adults (SR and SB) are certainly important in spot dynamics, but are the most difficult of the components to study. Predation by *Thanasimus dubius* (F.) is one obvious mortality agent of between-tree adults (Turnbow, Franklin, and Nagel 1978); mites, nematodes, and disease are less obvious. Knowledge of insect flight capacity and response to pheromones, weather conditions, host stimuli, and host resistance will be needed in developing predictive models for SR and SB. We would not expect SR and SB to be identical, nor should they be independent.

The general patterns for the reemergence and emergence distributions, FR_i and FB_i, may bear the same relationship for a variety of conditions. During certain times of the year, however, the temporal relationship of reemergence (Cooper and Stephen 1978) and emergence may change, causing increased intraspecific competition at pheromone sources or complete absence of sources.

Estimating Unmeasured Components

The between-tree survivorhip of reemerged and newly emerged beetles has never been measured, but we can use equation 7 and some information from the literature to determine some likely values. Moore (1978) reports that infestations are stable ($R_o = 1.0$) when the emergence:attack ratio is 5.0 (MB = 2.5), while Cooper and Stephen (1978) and Coulson et al. (1978) report reemergence rates (MR) ranging from ca. 0.5 to 1.0. When MR = 0.5 and SR increases from 0.0 to 1.0, SB decreases from 0.4 to 0.2. On the other hand, if we use MR = 1.0, SB ranges from 0.4 down to 0.0. Using an SR estimate at 0.5, SB would be 0.3 and 0.2 for MR values of 0.5 and 1.0, respectively. Thus, it appears that at least 60 percent of the new brood may die or disperse in stable infestations.

Assessing Treatments

Equation 7 can be used to assess the possible effects of a treatment applied to control an infestation. For example, Richerson and Payne (1979) report that brevicomin isomers reduce beetle landings and egg numbers on treated trees. How does this treatment affect the overall population? In other words, what are the effects on MR, SR, MB, SB, and A_i? Average number of attacks per tree is apparently reduced, but we have no information on total attacks in the spot. Presumably SR and SB are reduced because this treatment causes the flying beetles to disperse. If MR and MB remain the same, then the lower SR and SB result in a reduced R_o. On the other hand, the lower attack density could result in more eggs per female (Coulson et al. 1976), and MB could increase sufficiently to compensate for the reduced SB. In this latter case the net effect is no change in R_o. This example illustrates the need to study and understand how treatments affect all population processes.

CONCLUSION

The analysis of this simple model of *D. frontalis* infestations indicates that reemerged females can have a marked effect on the increase or decline of a spot and must not be ignored or discounted as has often happened in the past. Also, techniques need to be developed for studying the between-tree dispersal and mortality of adults so that these important components of spot dynamics can be adequately understood. As we increase our understanding of SPB infestations, such factors as tree and stand conditions, weather, and insect population levels can be included in the model, and we will be better able to consider alternative strategies for controlling this pest. Finally, although the preceding discussion has concentrated on the applicability of the model for understanding SPB infestation dynamics, equation 4 can be readily adapted for simulating the dynamics of many other insects that sequentially colonize portions of their habitat.

LITERATURE CITED

Berryman, A. A., and L. V. Pienaar. 1974. Simulation: a powerful method of investigating the dynamics and management of insect populations. Environ. Entomol. 3:199-207.

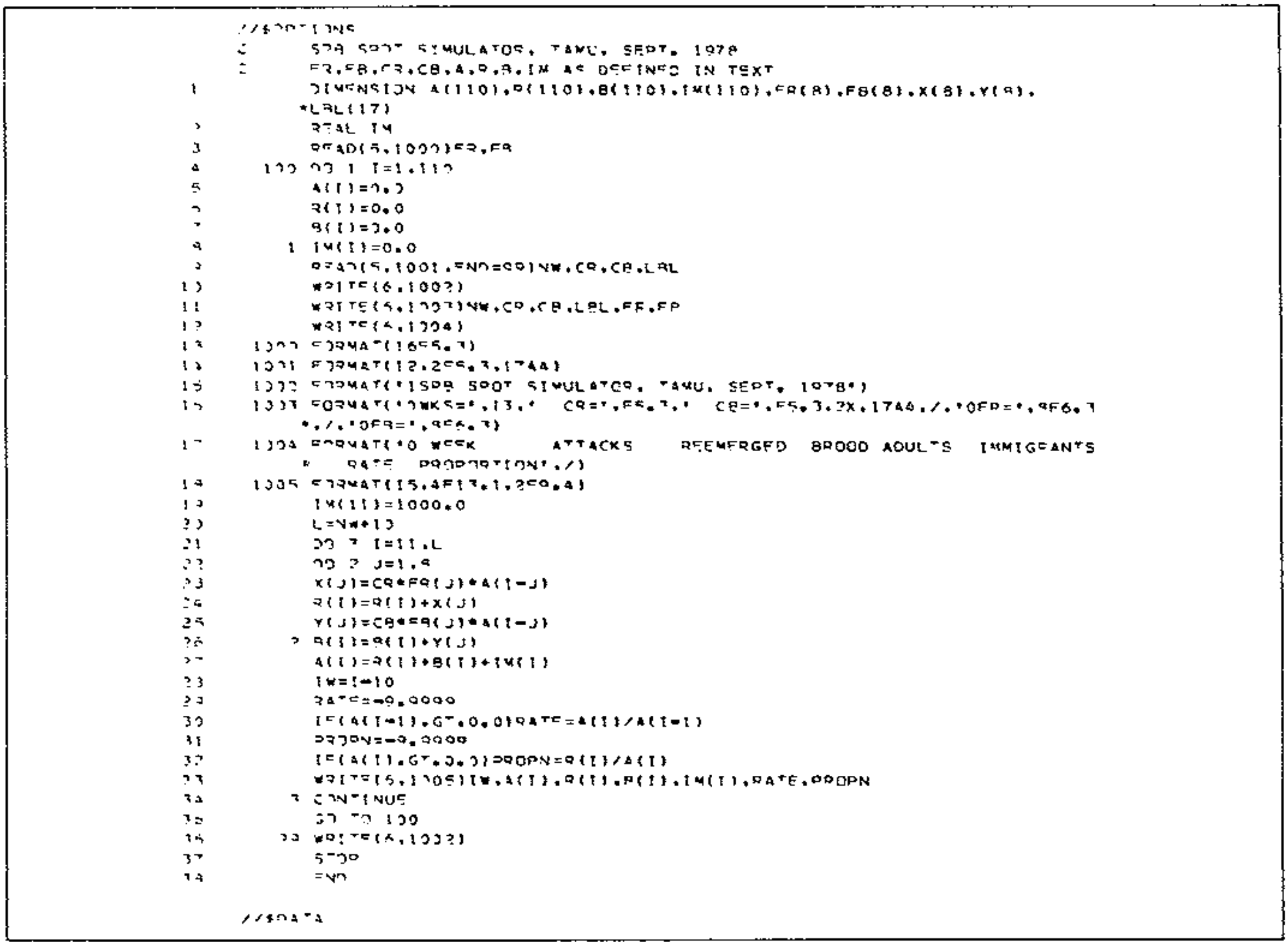
Cooper, M. E., and F. M. Stephen. 1978. Parent adult reemergence in southern pine beetle populations. Environ. Entomol. 7:574-577.

Coulson, R. N., A. M. Mayyasi, J. L. Foltz, F. P. Hain, and W. C. Martin. 1976. Resource utilization by the southern pine beetle, *Dendroctonus frontalis* (Coleoptera:Scolytidae). Can. Entomol. 108:353-362.

Coulson, R. N., W. S. Fargo, P. E. Pulley, J. L. Foltz, D. N. Pope, J. V. Richerson, and T. L. Payne. 1978. Evaluation of the reemergence process of parent adult *Dendroctonus frontalis* (Coleoptera:Scolytidae). Can. Entomol. 110:475-486.

Coulson, R. N., W. S. Fargo, P. E. Pulley, D. N. Pope, J. L. Foltz, and A. M. Bunting. 1979. Spatial and temporal patterns of emergence for within-tree populations of *Dendroctonus frontalis* (Coleoptera:Scolytidae). Can. Entomol. 111:273-287.

Fargo, W. S., R. N. Coulson, P. E. Pulley, D. N. Pope, C. L. Kelley, and J. L. Foltz. 1978. Spatial and temporal patterns of within-tree colonization by *Dendroctonus frontalis* (Coleoptera:Scolytidae). Can. Entomol. 110:1213-1232, 1376.



```
        //$OPTIONS
        C       SPB SPOT SIMULATOR, TAMU, SEPT. 1978
        C       FR,FB,CR,CB,A,R,B,IM AS DEFINED IN TEXT
  1             DIMENSION A(110),R(110),B(110),IM(110),FR(8),FB(8),X(8),Y(8),
               *LBL(17)
  2             REAL IM
  3             READ(5,1000)FR,FB
  4         100 DO 1 I=1,110
  5             A(I)=0.0
  6             R(I)=0.0
  7             B(I)=0.0
  8           1 IM(I)=0.0
  9             READ(5,1001,END=99)NW,CR,CB,LBL
 10             WRITE(6,1002)
 11             WRITE(6,1003)NW,CR,CB,LBL,FR,FB
 12             WRITE(6,1004)
 13        1000 FORMAT(16F5.3)
 14        1001 FORMAT(I2,2F5.3,17A4)
 15        1002 FORMAT('1SPB SPOT SIMULATOR, TAMU, SEPT. 1978')
 16        1003 FORMAT('0WKS=',I3,'  CR=',F5.3,'  CB=',F5.3,2X,17A4,/,'0FR=',8F6.3
               *,/,'0FB=',8F6.3)
 17        1004 FORMAT('0 WEEK       ATTACKS    REEMERGED  BROOD ADULTS  IMMIGRANTS
               *   RATE  PROPORTION',/)
 18        1005 FORMAT(I5,4F13.1,2F9.4)
 19             IM(11)=1000.0
 20             L=NW+10
 21             DO 3 I=11,L
 22             DO 2 J=1,8
 23             X(J)=CR*FR(J)*A(I-J)
 24             R(I)=R(I)+X(J)
 25             Y(J)=CB*FB(J)*A(I-J)
 26           2 B(I)=B(I)+Y(J)
 27             A(I)=R(I)+B(I)+IM(I)
 28             IW=I-10
 29             RATE=-9.9999
 30             IF(A(I-1).GT.0.0)RATE=A(I)/A(I-1)
 31             PROPN=-9.9999
 32             IF(A(I).GT.0.0)PROPN=R(I)/A(I)
 33             WRITE(6,1005)IW,A(I),R(I),B(I),IM(I),RATE,PROPN
 34           3 CONTINUE
 35             GO TO 100
 36          99 WRITE(6,1002)
 37             STOP
 38             END

        //$DATA
```

Figure 5.--FORTRAN program for simulating attacks per week in southern pine beetle infestations.

Moore, G. E. 1978. Factors for determining population trends in southern pine beetle spots. Environ. Entomol. 7:335-342.

Richerson, J. V., and T. L. Payne. 1979. Effects of bark beetle inhibitors on landing and attack behavior of the southern pine beetle and beetle associates. Environ. Entomol. 8:360-364.

Ruesink, W. G. 1975. Analysis and modeling in pest management. *In* Introduction to insect pest management. p. 352-376. R. L. Metcalf and W. H. Luckman, eds. John Wiley and Sons, New York.

Southwood, T.R.E. 1966. Ecological methods. p. 286-291. Methuen, London.

Turnbow, R. J., Jr., R. T. Franklin, and W. P. Nagel. 1978. Prey consumption and longevity of adult *Thanasimus dubius*. Environ. Entomol. 7:695-697.

APPENDIX

The FORTRAN program for operating the simulation model reported in the text is shown in figure 5 and an example of the output is contained in figure 6. The following comments will help the user to understand and implement the program.

Line 3. The distributions for reemergence and emergence for the 8 weeks following each attack period are read in once and remain fixed for all subsequent runs. The vectors FR and FB are in the first data card and have format as in line 13.

Line 4. This is the reentry point for successive runs.

Line 9. This statement causes new run parameters to be read in where NW = number of weekly cycles to be computed, CR and CB are as defined in the text, and LBL is a comment of 68 characters or

```
SPB SPOT SIMULATOR, TAMU, SEPT, 1979

WKS= 40  CR=0.451  CB=0.507   EXAMPLE (FR AND FB FROM TEXT)

FR= 0.250 0.140 0.000 0.000 0.000 0.000 0.000 0.000

FB= 0.000 0.000 0.150 0.710 0.130 0.010 0.000 0.000

 WEEK       ATTACKS     REEMERGED  BROOD ADULTS  IMMIGRANTS   RATE  PROPORTION

   1        1000.0          0.0          0.0        1000.0  -9.9999   0.0000
   2         387.9        387.9          0.0           0.0   0.3879   1.0000
   3         213.6        213.6          0.0           0.0   0.5507   1.0000
   4         198.4        107.3         91.1           0.0   0.9289   0.5410
   5         556.8         90.4        466.4           0.0   2.8063   0.1624
   6         494.0        228.5        265.5           0.0   0.8873   0.4625
   7         373.6        226.7        146.9           0.0   0.7562   0.6070
   8         331.5        176.1        155.4           0.0   0.8874   0.5312
   9         454.0        152.1        301.9           0.0   1.3697   0.3351
  10         489.0        197.0        292.0           0.0   1.0772   0.4029
  11         451.8        218.3        233.5           0.0   0.9240   0.4832
  12         422.8        206.1        216.7           0.0   0.9357   0.4876
  13         461.1        192.5        268.6           0.0   1.0907   0.4175
  14         495.3        205.5        289.7           0.0   1.0741   0.4150
  15         495.8        221.2        274.6           0.0   1.0010   0.4462
  16         486.4        223.6        262.8           0.0   0.9810   0.4597
  17         499.9        220.0        279.9           0.0   1.0277   0.4401
  18         522.1        224.6        297.5           0.0   1.0445   0.4301
  19         533.9        234.1        299.8           0.0   1.0226   0.4384
  20         537.3        240.1        297.2           0.0   1.0064   0.4468
  21         546.5        242.1        304.4           0.0   1.0171   0.4430
  22         561.9        245.9        316.0           0.0   1.0283   0.4376
  23         575.7        252.5        323.2           0.0   1.0245   0.4386
  24         585.4        258.8        326.6           0.0   1.0168   0.4420
  25         595.7        263.4        332.3           0.0   1.0176   0.4422
  26         609.0        268.0        341.0           0.0   1.0223   0.4401
  27         622.9        273.8        349.1           0.0   1.0228   0.4396
  28         635.4        280.0        355.4           0.0   1.0231   0.4407
  29         647.7        285.8        361.9           0.0   1.0193   0.4413
  30         661.1        291.3        369.7           0.0   1.0207   0.4407
  31         675.3        297.3        378.0           0.0   1.0215   0.4402
  32         689.3        303.6        385.7           0.0   1.0208   0.4405
  33         703.2        310.0        393.2           0.0   1.0202   0.4408
  34         717.6        316.3        401.3           0.0   1.0205   0.4407
  35         732.6        322.7        409.9           0.0   1.0209   0.4405
  36         747.9        329.5        418.4           0.0   1.0208   0.4405
  37         763.2        336.3        426.9           0.0   1.0205   0.4407
  38         778.9        343.2        435.7           0.0   1.0205   0.4407
  39         795.0        350.3        444.7           0.0   1.0207   0.4406
  40         811.5        357.5        454.0           0.0   1.0207   0.4406
```

Figure 6.--Output from the FORTRAN program for simulating southern pine beetle infestations.

less for run identification. The format is given in line 14. One input card of this type is required for each run and any number of these cards can follow the first (FR, FB) data card.

Line 19. This statement sets the initial immigration at 1,000 beetles. Location 11 in the IM vector corresponds to the first week of attack. If subsequent immigrant attacks by week are to be introduced into the model, it will be necessary to insert additional values into subsequent locations of IM.

Line 34. This CONTINUE statement was inserted to allow for future modifications to the spot simulator. This is the last statement of the main process loop and if variations in CR, CB, FR, or FB are desired as a function of time (week = IW), such modifications should be made just prior to this statement. The user is cautioned that the vectors FR and FB may need to be restored before returning to the reentry point (line 4).

The seven output values of this program are defined as follows:

WEEK--week number IW.

ATTACKS--total beetle attacks during week IW.

REEMERGED--reemerged beetles involved in the attack during week IW.

BROOD ADULTS--newly emerged brood adults involved in the attack during week IW.

IMMIGRANTS--immigrant beetles arriving and attacking during week IW.

RATE--the rate of increase for attacks during week IW relative to attacks in the preceding week.

PROPORTION--proportion of reemerged beetles in the attacking population during week IW.

The 40-week simulation illustrated in figure 6 had a compilation time of 0.03 seconds and an execution time of 0.05 seconds on the Amdahl computer at the Data Processing Center, Texas A. & M. University. The core usage consisted of 2,000 bytes for the object code and an array area of 1,956 bytes.

ACKNOWLEDGMENTS

We are especially indebted to R. N. Coulson, W. S. Fargo, R. M. Feldman, and J. A. Gagne for the considerable time they spent with us discussing many ideas developed in this paper. We thank Drs. C. J. DeMars, F. B. Hain, T. E. Nebeker, F. M. Stephen, and J. L. Stimac for their comments and suggestions on earlier drafts. Audrey Bunting, Linda Frieda, and Glenda Benson provided important technical assistance.

The work reported here was supported by the USDA Expanded Southern Pine Beetle Research and Applications Program (CSRS grants 3265-6163 and 3014-1525). The findings and opinions expressed are those of the authors and not necessarily those of reviewers or the sponsoring agency.

A MODELING HIERARCHY FOR SOUTHERN PINE BEETLE

Harvey J. Gold, William D. Mawby, and Fred P. Hain[1]

INTRODUCTION

Most of the reports presented at this symposium are based on work that has been in progress under the sponsorship of the ESPBRAP. The modeling work relating to this project at North Carolina State University is of more recent duration. Our presentation is, therefore, a description of the framework in which we have approached the problem and a report on our progress in filling in that framework. Some aspects of the framework have been presented at a workshop on population dynamics of forest insects at low levels, held in Raleigh this past August.

Our starting point is the premise that low levels of southern pine beetle (SPB) are endemic to the forest system being considered. With this premise, the problem becomes that of studying the transition between the endemic and epidemic regimes. A preliminary problem is the definition of the concept of "epidemic" for the system.

We adopt the point of view that the endemic to epidemic transition is dependent upon the relatively rare (low probability) passing of a threshold, whose value is itself a random variable. This idea can most conveniently be discussed using a diagram patterned after that used by Ricker (1954) and by Takahashi (1964). In figure 1, Δt is any conveniently chosen time interval. It may, for example, coincide with intergeneration time. The 45° line is the *exact replacement line*. If the population dynamics is such that the $N(t)$ to $N(t+\Delta t)$ relation lies on this line, there will be no change in population size. Points at which the population dynamics relation crosses this line will be stationary points sometimes called equilibrium points of the population. If the population dynamics relation crosses with slope of < 45°, the stationary point will be *stable* in the following sense: a small displacement of the population from the stationary value will cause a response that will tend to bring it back toward the stationary value. If the population dynamics relation crosses with slope > 45°, the stationary point will be *unstable*: a slight displacement will tend to cause the population to head further away in the direction of the original displacement.

Figure 1 shows a curve with two stable stationary points at *a* and *c*. If the value at $N(t+\Delta t)$ can be treated as depending continuously on $N(t)$, any stable points at *a* and *c* must be separated by some unstable point, such as at *b*.

Diagrams of this type have been used to describe the dynamics of populations with multiple stationary points (e.g., *see* Holling 1973; Southwood 1975; May 1977; Thomson, Vertinsky, and Wellington 1979). In such cases, the lowest stationary point (corresponding to *a*) is often taken to represent a stable prey-predator balance. Once the prey population exceeds the value at point *b*, the predator or natural enemy population is no longer able to keep the prey population in check. It therefore "explodes" toward a new, possibly resource-limited stable stationary point, such as that shown at *c*.

For the southern pine beetle, however, it appears that the low level is imposed by limitation of resource to SPB functioning as an opportunistic colonizer. The resource available to it is the population of pines newly killed or weakened by some other primary factor. The threshold at point *b* represents the population density at which SPB is able to mass-attack a healthy tree. The resource now available to it becomes the entire pine forest.

Our general approach is to treat both the threshold value and the size of the southern pine beetle population as random variables so as to explicitly treat the probability of exceeding the threshold.

---

[1] The authors are, respectively, Professor and Director, Biomathematics Program, Dept. of Statistics; Graduate Research Assistant, Dept. of Statistics; and Associate Professor of Entomology, Forest Entomology Laboratory, North Carolina State University, Raleigh.

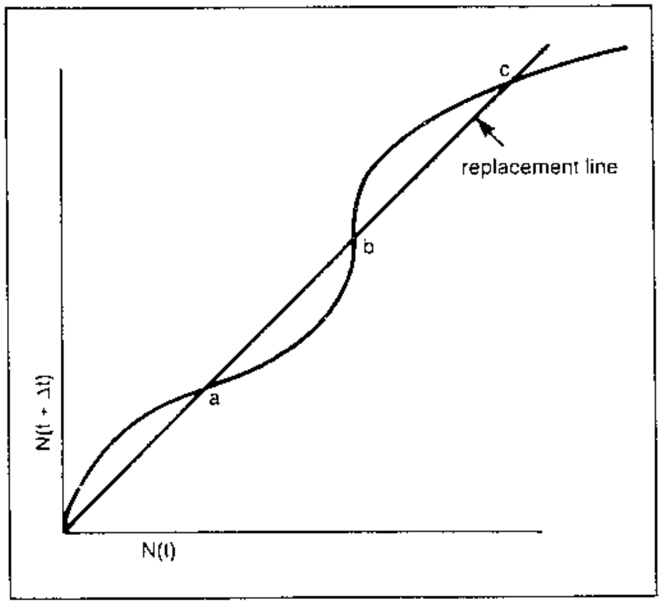


Figure 1.--Population dynamics curve with multiple stationary points. Further discussion may be found in Ricker (1954) and Takahashi (1964).

We look at the system in a *hierarchy of levels*: the individual tree level, neighborhood level, the quasi-uniform stand level, the locality of connected or contiguous stands, the level of a large geographical region. All levels must be considered in a full behavioral description of the system. The concepts of threshold and of the endemic/epidemic transition have a specific interpretation at each level.

BIOLOGICAL ASSUMPTIONS

We begin by proposing a set of biological assumptions on which the modeling framework is built.

(1) The insect is observed to have two modes of interaction with the host, which we class as endemic and epidemic. These are manifest on several scales as to both space and time.

(2) The endemic mode involves an especially intricate dependence upon forest environment and other organisms. It is at low population levels that beetle strategy changes from overcoming host resistance to selecting hosts--the process that insures beetle survival. Thus the selection of host material becomes more crucial than in epidemic condition. An understanding of how beetles survive at these low levels is necessary for an understanding of how epidemics arise.

(3) In endemic mode, generations overlap and more nearly approach change on a continuous time scale; in epidemic mode, generations are more clearly synchronized, especially in a climate with a hard-freeze winter.

(4) In epidemic mode, SPB is a primary invader of the host tree, requiring mass attack of, for example, 100 to 300 beetles. In endemic mode, SPB appears to be a secondary opportunistic invader; tree resistance has effectively been overcome by a primary agent (Younan 1979, Hain and McClelland 1980).

(5) A variety of factors can affect the resistance of trees to SPB attack: lightning, *Ips* infestation, water stress, nutrient stress, age, site-stand factors, etc. These can be divided into two groups, which may be termed stable and unstable. For the *stable* effectors, usually a small stress produces a small effect that may be reversed when the stress is relieved. The *unstable* effectors, such as blue-stain fungus infection, generally cause the tree to go into irreversible decline and induce its death.

(6) Resistance of a tree to attack and its suitability as a habitat once invaded may be positively correlated with each other (*see* Berryman 1976, with respect to the mountain pine beetle). The specific relation must be separately determined for each effector, possibly including competitive effects with *Ips* or cerambycids.

(7) The southern pine beetle is chiefly attracted by SPB pheromone. If the pheromone is scarce, beetles may be attracted to dying tree volatiles (Heikkenen 1977), possibly strengthened by *Ips* pheromone. (The results of Birch and Svihra[2] would seem to indicate the *Ips* pheromone adds no attractant for SPB. However, these results were under epidemic conditions, and the olfactometer results of Gara and Vité (1962) lead one to expect that this conclusion cannot be applied without verification to the endemic condition.)

(8) The southern pine beetle, in common with many other insects (Kennedy 1973), has at least two modes of travel: migratory long-range and local. (*See also* results of Gara and Vité 1962, on the mountain pine beetle.) Conditions

---

[2] Birch, M. C., and P. Svihra. 1978. Relationship between *Dendroctonus frontalis* and other bark beetle species in the Southern States. Unpublished final project report, ESPBRAP, Pineville, La.

leading to one or the other mode certainly involve local pheromone concentration and may involve site-stand conditions, weather, and conditions of brood development, as well as genotypic characteristics of the local SPB subpopulation (Namkoong et al. 1979). Gara and Vité have noted that under epidemic conditions, emergent beetles do not go into the migration mode, but they do so under endemic conditions. For many insects, it has been observed that once migration mode has been entered, it is unlikely to be immediately interrupted.

(9) Endemic infestations often seem to exhibit a significant edge effect; that is, a tree on the edge of a forest stand seems to have a higher probability of initial attack.

(10) Space-time trends seem to indicate persistant modes of infectious activity. Examination of North Carolina records indicates that statewide epidemics seem to last about 3 years, with variable periods between them (C. Doggett, personal communication).

In our conception of the endemic population, the unstable effectors of assumption (5) play a central role in maintaining the endemic population. The observations of Younan (1979) and of Bain (1980) suggest that attack by *Ips* beetles is of primary importance. The following propositions concerning *Ips* may be relevant:

(11) In endemic condition in North Carolina, SPB infestations have been observed to follow *Ips* infestations up to 2 to 3 weeks later. During this time, blue-stain fungus will have invaded the xylem, inducing onset of drying and tree death.

(12) A prior *Ips* infestation affects development of SPB, through the sensitivity of instars 2 and 3 to extremes (both high and low) of phloem moisture content (Wagner et al. 1979). Sensitivity of earlier stages has not been explicitly studied).

(13) *Ips* emergent brood tends to migrate after emergence (Anderson 1977), so that the distribution of *Ips*-infested trees would tend to be locally Poisson.

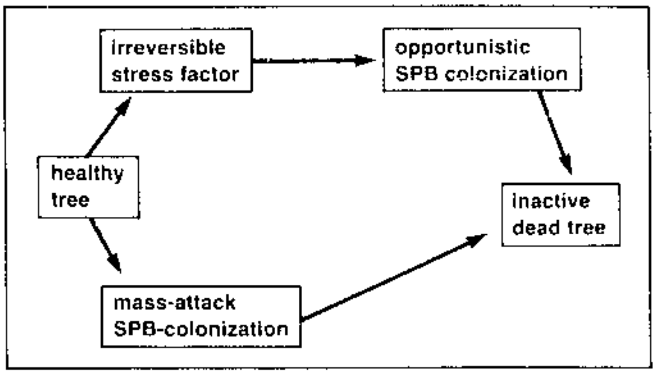


Figure 2.--State diagram for individual tree.

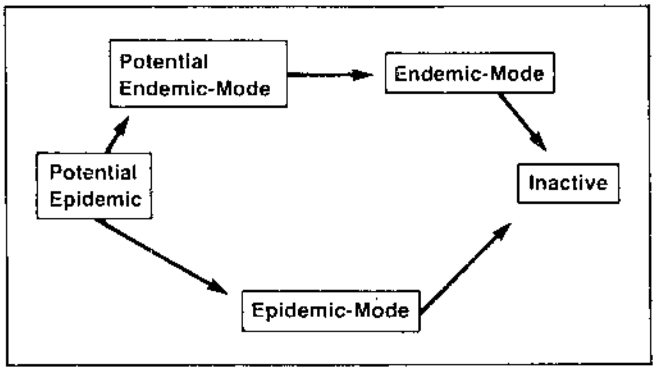


Figure 3.--Relabelled state diagram.

THE MODELING HIERARCHY

Level 1. Individual Tree

At the individual tree level, we define a difference between two modes of SPB attack:

Endemic mode: An effector has previously attacked the tree, substantially lowering its attack threshold as well as its productivity and capacity for beetle production. This chain of events permits SPB to enter as a secondary invader. The span of time over which beetles attack, and therefore over which the new brood emerges, is generally greater than in epidemic mode. (This timing factor is important in reducing the mass-attack potential of emergent brood.)

Epidemic mode: The tree is mass-attacked by SPB as primary invader. The beetle is then the primary agent inducing tree death.

For the individual tree, we then have the state diagram shown in figure 2, which corresponds, by relabelling, to the state diagram of figure 3. The probability of a transition between states will depend upon tree condition (genetic factors, developmental history, environmental stress), and upon local SPB activity (population density, genotype, pheromone level). Note that the local pheromone and beetle density will depend upon states and proximity of neighboring trees. Although the probability that a tree will be attacked depends explicitly upon beetle density, we propose to omit it as a part of the system description and to adopt an epidemiological approach, which refers the risk factor for each tree to the state and the proximity of its neighbors. The state transition probabilities for individual trees are therefore closely tied to *neighborhood* dynamics.

Level 2. Local Neighborhood

A neighborhood is a local group of trees. Two different *types* of neighborhoods may be defined for each individual tree: the *influencer*[3] neighborhood, consisting of all trees that influence the dynamics of the given tree, and the *influenced* neighborhood, consisting of all trees whose dynamics are influenced by a given tree. In a uniform symmetrical environment these neighborhoods would coincide. In the real world, they overlap but do not coincide, because of wind and other environmental factors.

In order to relate Levels 1 and 2, we propose to define four state variables and two parameters. Each of these six quantities is an attempt to summarize by a scalar the integrated effects of a large group of environmental, tree, edaphic, and population characteristics in terms of their effects on the dynamics of the beetle-tree interaction. That is, we propose to describe the dynamics of a system with a high dimensional state and parameter space in terms of its projection onto a six-dimensional hyperspace.

The two parameters relate to the attack threshold and potential brood productivity of the tree:

Threshold (T): Number of ambient adults necessary to attack the tree in order to initiate entry. The value to be assigned to *T* is an indicator of the maximum resistance the tree is capable of, and is determined by its genetic and developmental history. This quantity will be reduced by the stress state of the tree.

Potential Productivity (Q): Number of brood adults the tree is capable of supporting. It is also determined by the genetic and developmental history of the tree and is reduced by stress factors.

State variables are

Attractiveness (C): Relative attractiveness of a tree for potentially attacking SPB. It may be defined operationally by supposing a beetle to be released equidistant to two trees *i* and *j*. Letting p(i) be the probability that the beetle will attack tree *i*, DBH_i be its diameter at breast height, and C_i its relative attractiveness, then

$$\frac{C_i}{C_j} = \frac{p(i)/DBH_i}{p(j)/DBH_j} \tag{1}$$

This relation uniquely defines attractiveness up to a normalization factor. It is principally determined by local pheromone and tree volatile concentrations.

Stress (S): This is a scalar measure of tree stress, whose inverse will be used as a multiplier for both parameters *T* and *Q*. Its components include reversible damage, such as water stress, and irreversible damage, such as entry of blue-stain fungus. Its values may range from 1 to infinity (inverse ranges from zero to 1). Initially, its inverse will be used as a multiplier for both parameters *T* and *Q*, although at a later stage of the modeling effort, it may be desirable to differentiate the effect of stress on these two tree characteristics.

Attacking Adults (A): Rate at which attacking adults enter or reemerge. Its values may be either positive or negative.

Brood Adult Contribution (B): Rate at which brood adults are emerging.

Full specification of the state of the influencer neighborhood for any tree would require specification of the Cartesian coordinates of each tree, directional effects of wind and other environmental factors, and state description for each tree. For the purposes of simulation, it would be sufficient to specify a distribution of Euclidean distances (specific Cartesian coordinates for a *fixed* stand), the environmental effect, and the probability distributions of the state variables and parameters. Note that the number of trees in the neighborhood is taken to be a random variable and depends upon the distance over which a nonnegligible effect is exerted.

If the influencer neighborhood for any tree contains an epidemic-mode tree, that epidemic-mode tree will clearly have a major effect on the dynamics of the given tree. A neighborhood in which the dynamics is dominated by epidemic-

---

[3] The influence can involve exposure to emergent or reemergent adults or to pheromone cloud.

mode trees may be termed an *epidemic neighborhood*. In such a neighborhood, we would expect that the dynamics of the beetle-host relation would be approximated neglecting the contribution of endemically infested trees.

The union (set theoretic sense) of a contiguous group of such neighborhoods might reasonably be termed an *epidemic spot*. With such a definition, one may distinguish between a *collapsing epidemic spot* (in which trees become inactive faster than new trees are added) and an *expanding epidemic spot* (in which the reverse is true). For simulation and forecasting, we would wish a probability distribution for the change in the size of the spot.

It is important to note that a single epidemic-mode tree will not necessarily precipitate a local epidemic, i.e., an expanding epidemic spot. Pheromone and beetles will be exported from such a tree to nearby trees, but their densities will be diluted with distance.

Level 3. The Stand

A stand will be taken to be a quasi-uniform area (Daniels et al. 1979). Its state might be specified in a number of ways:

(1) Specification of the number and position of trees within the stand in each of the states shown in figure 2 or figure 3.

(2) Specification of a multinomial probability distribution over that set of states.

(3) Specification of a probability distribution within the stand for each of the state variables.

For many purposes, we will be interested only in the number of epidemic-mode trees within the stand, or in the probability distribution for this number. With this in mind, we introduce the following model assumptions:

(1) The probability of a zero to 1 transition (no epidemic-mode trees in the stand to one epidemic-mode tree in the stand) in some time interval Δt is a function of the probability distributions of the tree state variables and parameters, together with migrational interchanges with other stands. Therefore, the state of other stands in the locality must be considered.

(2) In dealing with endemic or low-level population, and a sufficiently small stand, the probability of a zero to n ($n > 1$) transition is $o(\Delta t)$; that is, negligible for short time intervals.

Level 4. Locality

It is convenient to regard the large geographical region as being partitioned into relatively small localities or subregions of specific geographical extent (Clark, Jones, and Holling 1977). These localities are taken to consist of a collection of stands that are contiguous in terms of SPB migration and risk. The state of such a locality is specified in terms of the component stands and their connectivity relations. Under conditions normally considered to be nonepidemic, we would expect the spatial distribution of such trees at any given time to be determined mainly by the distributional characteristics of a primary stable effector. If the locality is perfectly uniform as to edaphic, environmental, and stand characteristics, the spatial distribution defined on a single tree or small group of trees. Such uniformity is not to be expected in a locality but might be approximated in a stand.

An important part of the description of the locality is the number, size, and spatial relationships of epidemic spots. A small, single epidemic spot from which pheromone and beetles are exported is unlikely to produce a local epidemic because of dilution effects. As the epidemic spot density is increased, these spots will be expected to exert an increasing effect on the locality dynamics. A locality in which dynamics is dominated by the epidemic spots it contains would reasonably be referred to as an *epidemic locality*. The question of expansion or collapse of such a locality may be formulated in terms analogous to those for epidemic spots.

Level 5. Large Geographic Region

The geographic region might consist of a single State or it might be taken to be the entire southeastern range of the southern pine beetle. At one level of description, the instantaneous condition or state of the overall region would be decribed as the aggregate of component stand descriptions. However, for many purposes, it would be adequate to define an index of activities within each of the localities or subregions and to express the state of the overall region as the array of local indices. The dynamics of the regions would then be expressed in terms of a stochastic process which converts this array of indices in one time frame to another array in the succeeding time frame. Of particular interest in describing the large region are the number and distribution of localities with epidemic spots.

In this hierarchical description, the dynamics of a local neighborhood is determined by the states and interactions between the individual trees of which it is composed. The dynamics of a stand are determined by the states and interactions of the neighborhoods, thus allowing for the introduction of microheterogeneities as perturbation effects within the stand. And the dynamics of a locality would be determined by the states and interactions between the constituent stands, allowing at this level explicit consideration of small regional heterogeneities. At the level of the large geographical region, the heterogeneity dominates the description, which then is in terms of the time dynamics of the spatial distribution. The rest of this report will be primarily concerned with the link between the level of the locality and that of the large geographical region. The approaches used are adapted from the methodology of exploratory space-time pattern analysis.

The view we adopt is that in any locality, there is always a stochastic expectation of a nonzero endemic level of SPB. During "favorable" years, the expected endemic levels rise, while the distribution of threshold values shifts to lower levels, increasing the probability of epidemic outbreaks. Two extreme modes may be envisioned for the relation between local and regional dynamics:

(1) Outbreak probabilities in localities are correlated only by their common dependence on climatic conditions, but are otherwise independent. That is, migrational effects are negligible.

(2) Outbreaks spread from an initial epidemic locality, so that migrational effects are dominant.

Indeed, we expect neither extreme mode but some combination. The question of the relative contribution of these extreme modes is one that we hope to clarify through the use of these space-time analytical methods.

RELATION BETWEEN LOCALITY LEVEL AND GEOGRAPHICAL REGION

Methods Being Developed

In ecological studies, space-time patterns are often the only clues that exist as to the internal structure of the system under study. Experiments on ecosystems are always difficult to design, dangerous to implement, and largely irreproducible. Such manipulative studies should be, and generally are, approached with great caution, if at all. This inability to manipulate the chosen system freely is limiting but not prohibitive. Rather, it makes us shift emphasis to less traditional modes of analysis.

The model building process typically utilizes three major steps: exploratory analysis, model translation, and model confirmation (Getis and Boots 1975). For any complex (i.e., real) system, this process will be iterated and reiterated many times before researchers are satisfied. In this presentation, the focus will center on the exploratory analysis of data and some of its representative methods. However, it should be remembered that the latter two steps of the process are equally fundamental.

Tukey (1977) compares the confirmatory mode of statistics against the exploratory mode by analogy to the judicial and investigative branches of a criminal justice organization. Just as no court case would come to trial before extensive preliminary inquiry, the testing of hyoptheses must also be preceded by the discovery of what hypotheses to consider. Both aspects are fundamental and necessary, but the exploration naturally occupies a primordial position.

The exploratory statistical analysis of space-time patterns can be separated into three major branches: nonparametric, multivariate, and time-space series techniques. Although theory overlaps in these areas, particularly between multivariate methods and the other two types, practice does not. Most applications that deal in one branch of this classification scheme deal only with that branch. It is on the basis of three criteria that the distinction among these methods has been drawn: (1) commonality in certain literatures, (2) typical mathematical manipulations, and (3) consistent use of results.

Nonparametric Methods

Nonparametric statistics deals with procedures that give stable results under widely varying underlying populations. Hollander and Wolfe (1973) argue that nonparametric methods appeal for several reasons: they require less restrictive assumptions, they are easy to perform and understand, they generally use ranks, not magnitudes, and they remain efficient under normality. The first and fourth of these considerations are especially desirable in an exploratory phase. Ease of performance and understanding requires clarifications since the number of calculations can often be prohibitive despite the ease. Larger samples are almost universally handled through large sample (i.e., asymptotically normal) approximations because of this difficulty.

The fundamental objective of nonparametric space-time analysis is presented by Klauber (1974) as the elucidation of methods which will detect clustering of events as opposed to chance variation, but which will be insensitive to clumping in either coordinate frame alone. Typically a statistic relating pairs of space and time points is described; then its distribution is calculated, or estimated, under some loose assumptions, and this distribution served as a basis for future comparisions. The calculation of this theoretical distribution is accomplished through U-statistic theory (Hoeffding 1948), through graph theoretical techniques (Barton and David 1966), or through simulation (Siemiatycki and McDonald 1972). Most applications in biology are epidemiological in nature.

Several particular approaches are of special interest to the study of southern pine beetle dynamics. Haggett and Chorley (1970) devote a section to shape indices that might be helpful in spot growth models. Of a similar vein is the work of Bookstein (1978) on morphometrics. Join statistics and binary nearest neighbor statistics are two contributions of Cliff et al. 1975. The classic reference for *n*-phase mosaics is Pielou (1977) and for diversity, Pielou (1975) again. Mantel (1967) develops a generalized regression model for epidemiological uses, which permits estimation of contagion strength.

Multivariate Methods

Multivariate techniques deal with dependent variables and the individual entities upon which the measurements occur (Kendall 1975). Kendall remarks that there are at least four reasons for pursuing such methods: to reduce the complexity, to group individuals, to group variables, and to characterize the dependencies. Problems in applying classical multivariate analysis include the difficulty of justifying assumptions, the immensity of calculations, and the loose interpretation of results.

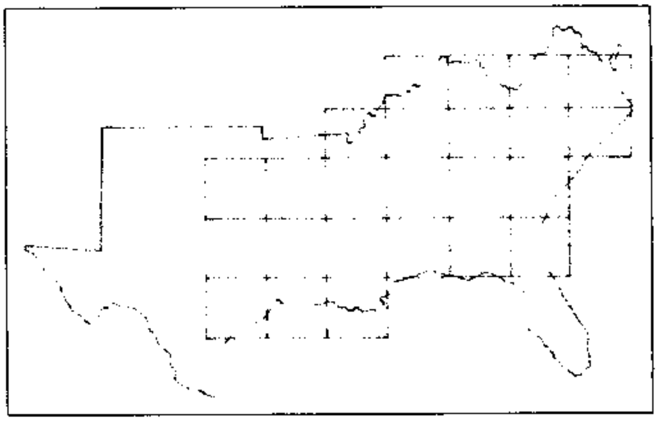


Figure 4.--Southeastern localities.

There are four central modes of multivariate space-time analysis: clustering, factor analysis, canonical correlations, and discrimination. One type of factor analysis, principal components analysis, is used quite often in ecological (Pielou 1977) and morphological (Blackith and Reyment 1971) work. Principal components seeks to simplify the dependencies in a set of data by choosing a new coordinate system, each axis of which is a linear combination of the old axes (McCammon 1975). Through this technique either the variables may be recoordinated (R-mode) or the individuals may be restructured (Q-mode). The new coordinates are usually chosen to be orthogonal, but the oblique rotation methods can remove this convention.

A specific form of principal components that has proven useful in the construction of the southern pine beetle hierarchical model is discussed by Sheth (1969). Beginning with a data matrix of N observations (times) and M subjects (areal units), the raw N by N cross products matrix is partitioned into the product of two matrices via eigenvalue decomposition. The two matrices (i.e., A and S) are then standardized for the sample size. The standardized matrices, V and P, contain the individual parameters (loadings) and the reference curves (scores). Finally certain hypotheses can be tested by axis rotation methods.

As an example, one stage of constructing the upper echelon submodel for the beetle hierarchical model consisted of partitioning the Southeastern United States into 24 localities (see fig. 4). Within each locality a measure of incidence intensity was defined for each of the 18 years of data given in Price and Doggett (1978). Several analyses of the data were performed, including a reference curve analysis. The purpose of this treatment is to isolate linear combinations of years, which might serve as

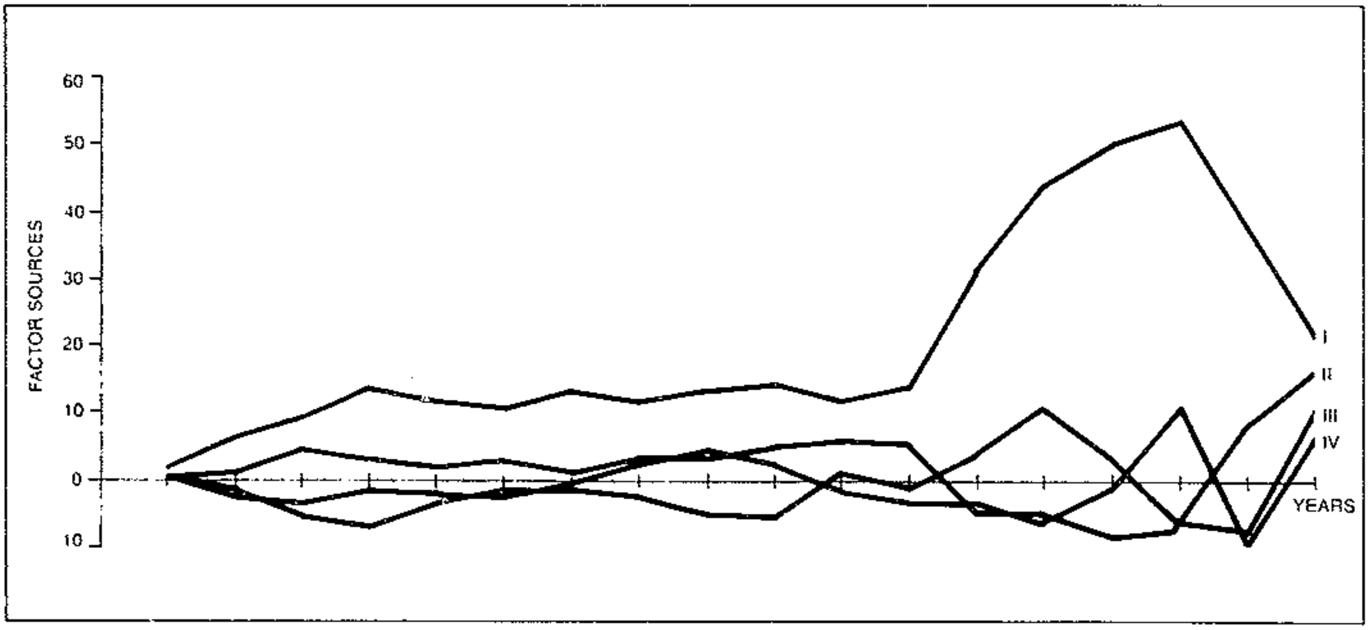


Figure 5.--Four major reference curves.

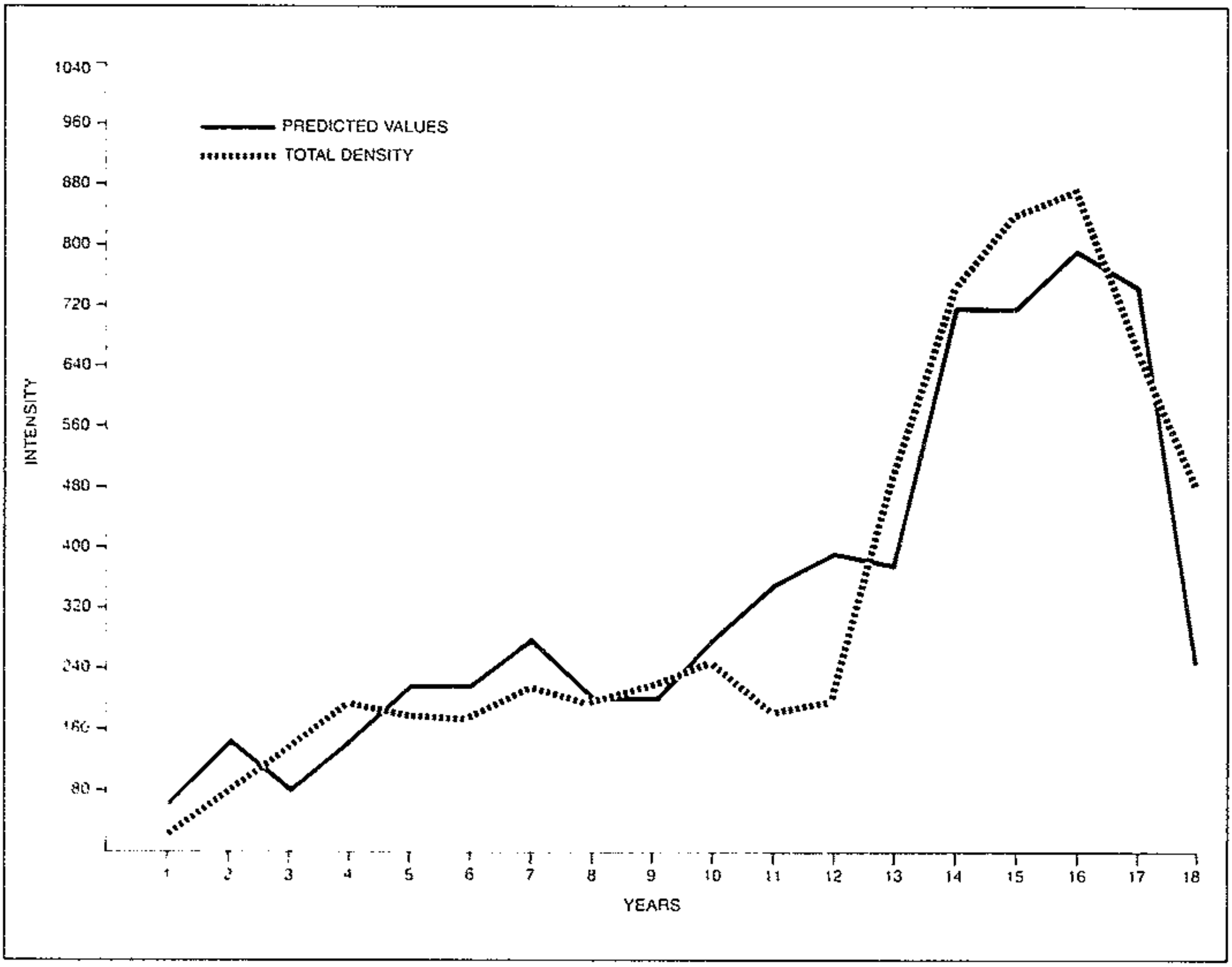


Figure 6.--Total intensity versus predicted values.

standards of behavior, and then to classify the localities according to which reference behavior they nearly followed.

The reference curve analysis of the raw data yielded four behavioral modes represented by eigenvectors, which together explain approximately 96 percent of the variation. Plots of these curves are given in figure 5. The largest eigenvector accounts for 85 percent of the variation by itself and is therefore likely to play a dominant role in all locality dynamics. This dominant reference curve is closely related to total intensity of the epidemic. Three of the 24 localities were classified as following this standard behavior. A simple linear regression of total intensity on the observations in one of these "first mode" localities is quite good (R^2 of .84), as figure 6 demonstrates. The other three modes of behavior were not linked strongly to any simple external variable in this analysis.

Time Series and Time-Space Methods

Time series is a rather recent elaboration of modern statistics, being traced to its conceptual beginnings with Udny Yule in 1927. The primary requirement of this approach is the ordered sequence of observations that behave nicely, i.e., are stationary or intrinsic. Included in this nice behavior is the existence of an autocovariance function which depends only on the distance between the observations. Analysis may be directed toward the correlogram (the graph of the autocorrelation function v. distance) or toward the spectrum (the Fourier equivalent of the correlogram).

The definition of a time series does not require that the spaced observations occur along the time axis, and extensions to spatial axes have been made. Cliff et al. (1975) have set the basic problems of spatial autocorrelation by examining a mosaic of cells, with observations within each cell. An example of an arbitrary mosaic is shown in figure 7. In defining the covariance one must account for the function used to compare pairs of cells, and one must weight the cell connections. The set of connection weights can be varied to emphasize certain interactions. General treatment of spatial lagging requires graph theoretical techniques (Ross and Harary 1952), and for structures allowing over ten lags is usually prohibitive.

A raw time series is usually conceived of as consisting of four pieces, a trend, regular fluctuations about the trend, seasonality, and a random effect (Kendall 1973). The isolation of the first three components is usually necessary before the random effect (i.e., the true time series) can be studied in full. Often the development of trends alone is a primary objective of the investigation. The random effect is assumed to be of an autoregressive nature (or equivalently a weighted average) of same order. The estimation of this autoregressive structure, especially its order, is a prime modeling ingredient.

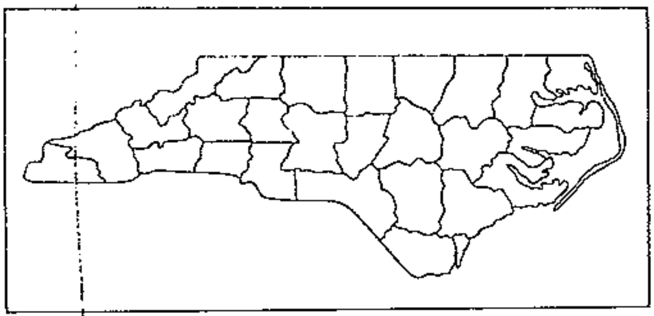


Figure 7.--Arbitrary spatial mosaic.

Time-space series is the next stage in the extension of time series methods, but the development is still elementary. Curry (1970) developed a univariate approach, but went no further. Cliff et al. (1975) also used a univariate scheme, but this time with weighted exponentials. More recent research by Matheron (1970) and others seems to be straying from the traditional idea and centers on random function theory instead. At present, a typical analysis would begin with a detrending followed by estimation of the order of spatial and temporal lag structure. Lastly, with the order specified, a simple model such as Cliff's would be estimated for projective purposes. Since the results are univariate, the total model would consist of some mixture of single areas.

For example, the 24 localities discussed above were subjected to a simple time and space series analysis. The raw data show great variability in behavior. Data for most years do not show any strong spatial autocorrelation, although all correlograms are of similar shape (fig. 8). A minor peak occurs in many spatial correlograms at five or six lags. These lags can be shown to be dominated by central locality which reflects the total epidemic behavior (see previous discussion of first mode localities). The temporal correlograms show nonstationary characteristics for numerous localities (fig. 9).

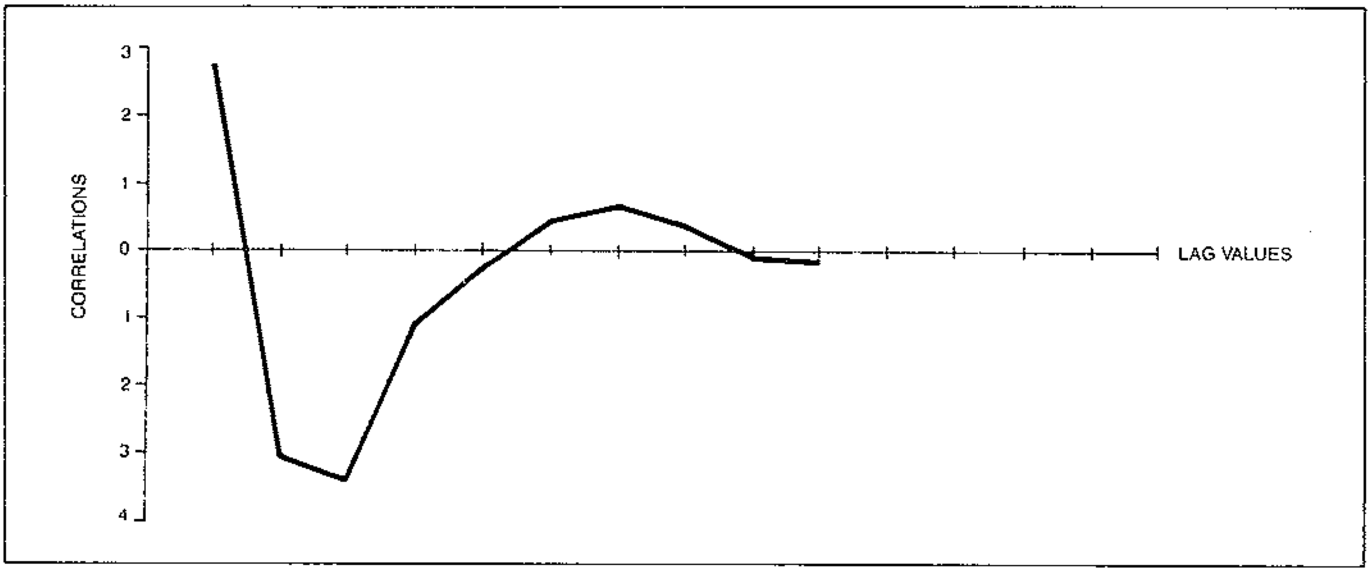


Figure 8.--Typical spatial autocorrelation for raw data.

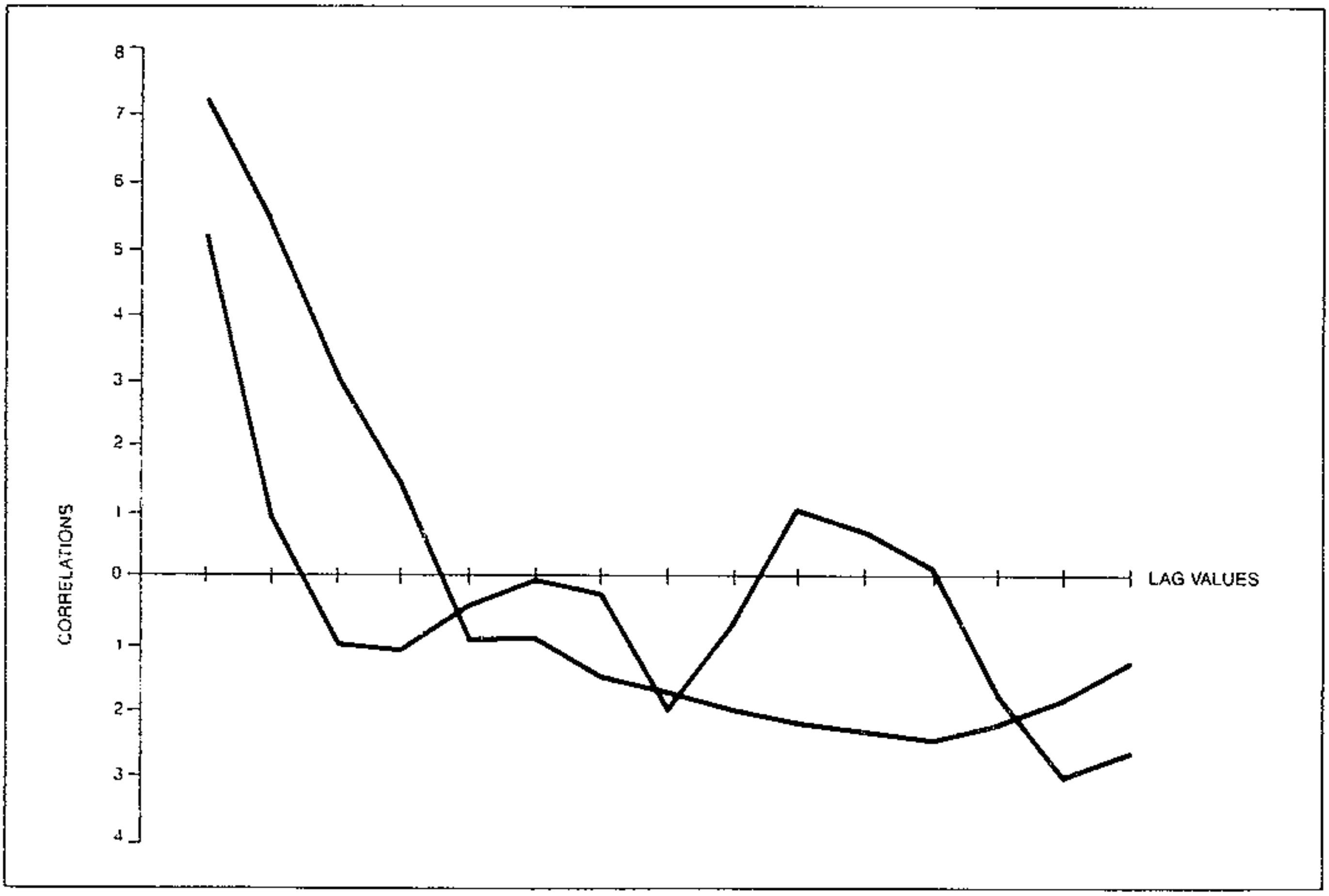


Figure 9.--Typical temporal autocorrelation functions for ray data.

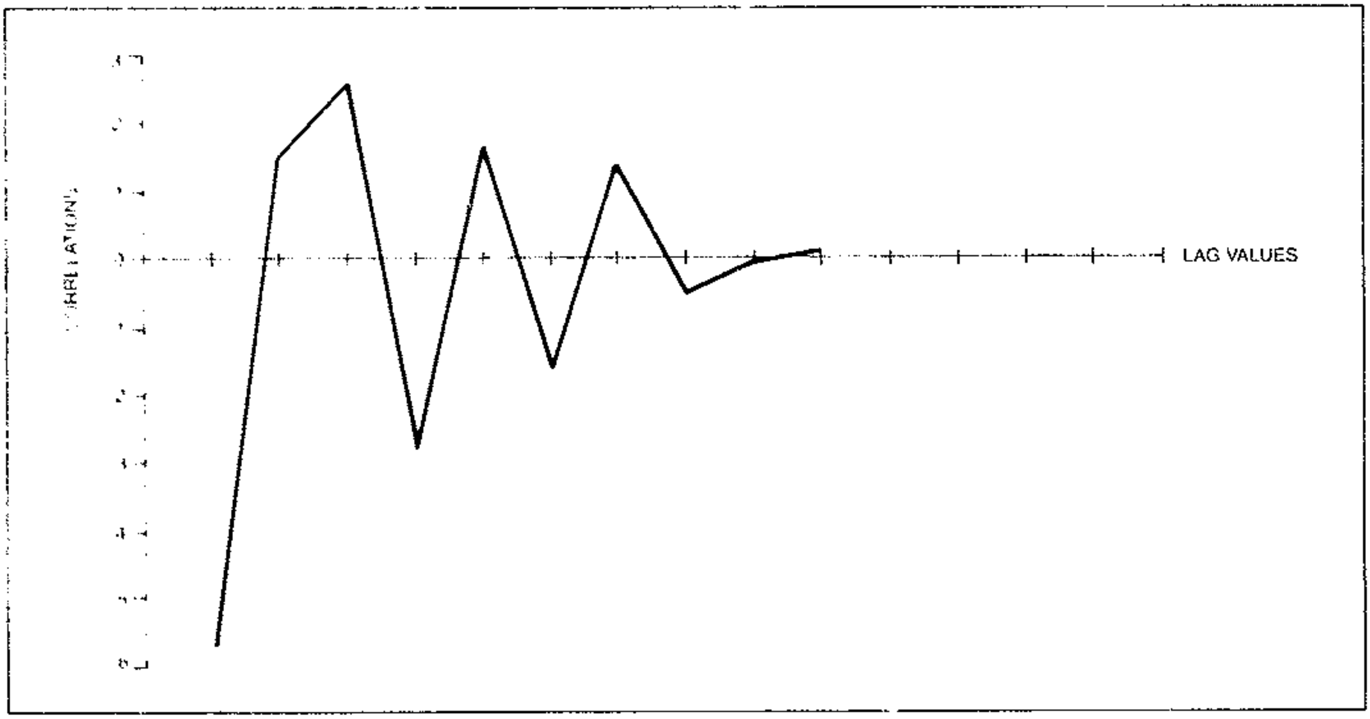


Figure 10.--Typical spatial autocorrelation function for detrended residuals.

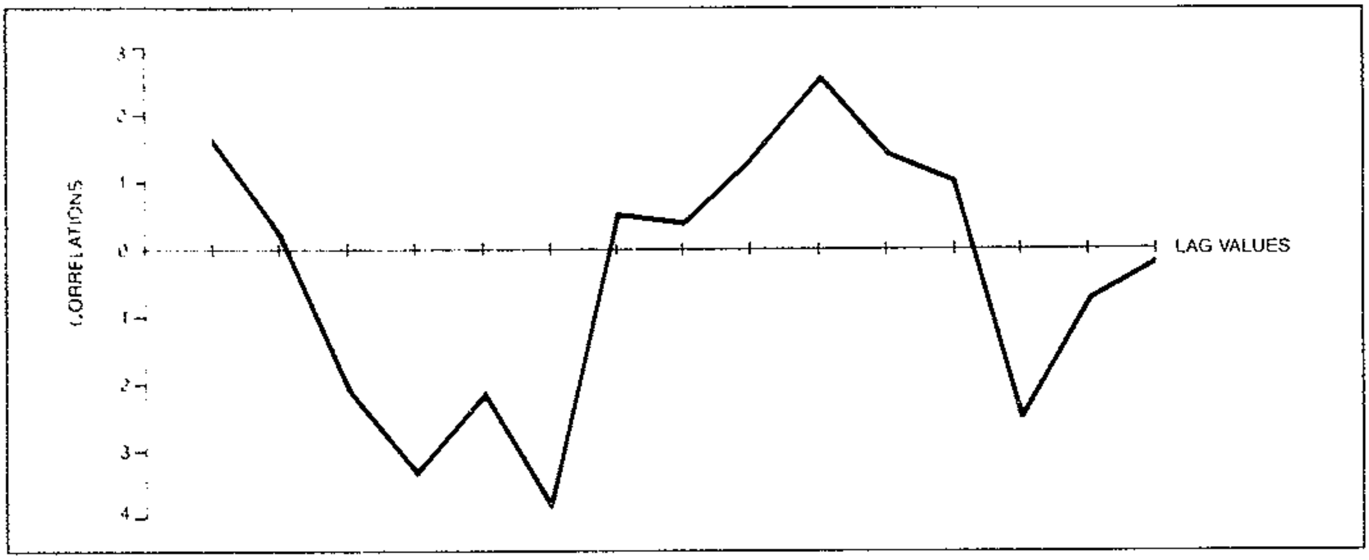


Figure 11.--Typical temporal autocorrelation function for detrended residuals.

Detrending in space and then again in time was chosen as a potential method for eliminating the nonstationary behavior of the time series. A cubic equation in space was first fitted to each year's data, followed by fitting a cubic equation in time to the residuals from the spatial regression. The residuals from the temporal regression were then examined for their autocorrelation properties (figs. 10 and 11). The spatial correlograms are of similar shape and show no unusual features; this generally indicates a low autoregressive spatial structure. The temporal correlograms, however, demonstrate some atypical behaviors. Data for nearly all of the localities show a complicated log structure, possibly extending to an order of four or five. There is also some indication of periodicity or seasonality, with perhaps an 8- to 12-year period.

SUMMARY

The intention in this report has been to describe the overall hierarchical modeling framework, to describe the basis upon which methods are being developed for exploring the relation between the upper levels, and to illustrate the use of these methods with some preliminary results.

LITERATURE CITED

Anderson, R. F. 1977. Dispersal and attack behavior of the southern pine beetle engraver, *Ips grandicollis* Eichh., Coleoptera, Scolytidae. Paper presented in the A. C. Hodson Lectures. 107 p. Univ. Minn. Agric. Exp. Stn., Tech. Bull. 310.

Barton, D. E., and F. N. David. 1966. Random intersection of two graphs. *In* Research papers in statistics. p. 445-461. F. N. David, ed. Wiley and Sons, New York.

Berryman, A. A. 1976. Theoretical explanation of mountain pine beetle dynamics in lodgepole pine forest. Environ. Entomol. 5:1225-1233.

Blackith, R. E., and R. A. Reyment. 1971. Multivariate morphometrics. 412 p. Academic Press, New York.

Bookstein, F. L. 1978. The measurement of biological shape and shape. *In* Lecture notes in biomathematics, No. 24. 191 p. S. Levin, ed. Springer-Verlag, New York.

Clark, W. D., D. D. Jones, and C. S. Holling. 1977. Patches, movements and population dynamics in ecological systems: a terrestrial perspective. *In* Spatial patterns in plankton communities. p. 385-432. H. J. Steele, ed. Plenum Press, New York.

Cliff, A. D., P. Haggett, J. K. Ord, K. A. Bassett, and R. C. Davies. 1975. Elements of spatial structure. 258 p. Cambridge Univ. Press, New York.

Curry, L. 1970. Applicability of space-time moving-average forecasting. *In* Regional forecasting. p. 11-25. M. Chisholm, A. E. Frey, and P. Haggett, eds. Twenty-second Symposium of the Colston Research Society at the University of Bristol, 1970. Butterworths, London.

Daniels, R. F., W. A. Leuschner, S. J. Zarnoch, H. E. Burkhart, and R. R. Hicks. 1979. A method for estimating the probability of southern pine beetle outbreaks. For. Sci. 25:264-269.

Gara, R. I., and J. P. Vité. 1962. Studies on the flight patterns of bark beetles (Coleoptera:Scolytidae) in second growth ponderosa pine forests. Contrib. Boyce Thompson Instit. 15:275-289.

Getis, A., and B. Boots. 1975. Models of spatial processes. 198 p. Cambridge University Press, New York.

Hain, F. P., and W. T. McClelland. 1980. Studies of low-level populations of southern pine beetle in North Carolina. *In* Population dynamics of forest insects at low levels: symposium proceedings. F. P. Hain, ed. North Carolina State Univ., Raleigh. [Raleigh, N.C., Aug. 1979.] [In press.]

Haggett, P., and R. J. Chorley. 1970. Network analysis in geography. 348 p. St. Martin's Press, New York.

Heikkenen, H. J. 1977. Southern pine beetle: a hypothesis regarding its primary attractant. J. For. 75:412-413.

Hoeffding, W. 1948. A class of statistics asymptotically normal distributions. Ann. Math. Stat. 19:293-325.

Hollander, M., and D. A. Wolfe. 1973. Nonparametric statistical methods. 503 p. John Wiley and Sons, New York.

Holling, C. S. 1973. Resilience and stability of ecological systems. Ann. Rev. Ecol. Syst. 4:1-23.

Kendell, M. G. 1973. Time-Series. 197 p. Charles Griffin, London.

Kendell, M. G. 1975. Multivariate analysis. 210 p. Charles Griffin, London.

Kennedy, J. S. 1973. Insect dispersal. *In* Insects, science and society. p. 103-120. D. Pimentel, ed. Academic Press, New York.

Klauber, M. R. 1974. Space-time clustering analysis: a prospective. *In* Epidemiology, SIMS Conference at Alta, Utah, 1974. p. 75-89. D. Ludwig and K. Cooke, eds. Society for Industiral and Applied Mathematics, Philadelphia.

Klovan, J. E. 1975. R- and Q-mode factor analysis. *In* Concepts in geostatistics. p. 21-69. R. B. McCammon, ed. Springer-Verlag, New York.

Mantel, N. 1967. Detection of disease clustering and a generalized regression approach. Cancer Res. 27:209-220.

Matheron, G. 1970. Random functions and their applications in geology. *In* Geostatistics: Proceedings of a colloquium on geostatistics. p. 79-87. D. F. Merrian, ed. Plenum Press, New York. [Univ. of Kansas, 1970.]

May, R. M. 1977. Thresholds and breakpoints in ecosystems with a multiplicity of stable states. Nature 269:269.

Namkoong, G., J. H. Roberds, L. B. Nunnally, and H. A Thomas. 1979. Isozyme variations in populations of southern pine beetles. For. Sci. 25:197-203.

Pielou, E. C. 1975. Ecological diversity. 159 p. John Wiley and Sons, New York.

Pielou, E. C. 1977. Mathematical Ecology, 2nd ed. 384 p. John Wiley and Sons, New York.

Price, T. S., and C. Doggett. 1978. A history of southern pine beetle outbreaks in the Southeastern United States. 31 p. Ga. For. Comm.

Ricker, W. E. 1954. Stock and recruitment. J. Fish. Res. Bd. of Can. 11:559-623.

Ross, J. C.. and F. Harary. 1952. On the determination of redundancies in sociometric chains. Psychometrilea 17:195-208.

Siemiatycki, J. U., and A. D. McDonald. 1972. Neural tube defects in Quebec: a search for evidence of 'clustering' in time and place. Brit. J. Prev. Soc. Med. 26:10-14.

Sheth, J. N. 1969. Using factor analysis to estimte parameters. J. Am. Stat. Assoc. 64:808-823.

Southwood, T.R.E. 1975. The dynamics of insect populations. *In* Insects, science and society. p. 151-200. D. Pimentel, ed. Academic Press, New York.

Takahashi, F. 1964. Reproduction curve with two equilibrium points: a consideration on the fluctuation of insect population. Res. Popul. Ecol. 6:28-36.

Thompson, W. A., I. P. Vertinsky, and W. G. Wellington. 1979. The dynamics of outbreaks: further simulation experiments with the western tent caterpillar. Res. Popul. Ecol. 20:188-200.

Tukey, John W. 1977. Exploratory data analysis. 688 p. Addison-Wesley, Reading, Mass.

Wagner, T. L., J. A. Gagne, P. C. Doraiswamy, R. N. Coulson, and K. W. Brown. 1979. Development time and mortality of *Dendroctonus frontalis* in relation to changes in tree moisture and xylem water potential. Environ. Entomol. 8:1129-1138.

Younan, E. G. 1979. Part I. Relative effectivenss of five trap designs for insects attacking severed shortleaf, Virginia, and loblolly pines. Part II. Sequence of arrival of insects associated with bark beetles at severed shortleaf, Virginia, and loblolly pines. Ph.D. thesis. No. Carolina State Univ., Raleigh. 119 p.

A REGIONAL SOUTHERN PINE BEETLE

DAMAGE PROJECTION SYSTEM

David D. Reed, Richard F. Daniels, Roy L. Hedden,

Harold E. Burkhart, and William A Leuschner[1]

Abstract.--Regional damages caused by the southern pine beetle can be simulated using two models, one representing spot incidence, or the initiation of infestations, and the other representing individual spot severity, or the spread of each spot. A spot incidence and a spot severity model were combined to form a regional damage projection system. This damage projection system was demonstrated on an example region in the Georgia Piedmont.

INTRODUCTION

In this paper we report on a regional damage projection system for southern pine beetle (SPB) (*Dendroctonus frontalis* Zimm.) with the capability to project SPB-caused damage for a multicounty area, such as a forest survey unit. We considered one major kind of damage: the physical losses in timber volume due to the SPB in the year of attack. We made no attempt to quantify the resulting loss in economic or social values. The object was to simulate the levels of SPB activity and to project the beetle's effect in terms of cubic feet of timber destroyed or the number of acres directly affected.

Our system considers the damages occurring in many individual spots. This requires developing methods of estimating both the number of infestations likely to occur and the eventual size of each individual spot. To accomplish this as efficiently as possible, it is necessary to use models that (1) provide accurate damage estimates for large numbers of spots, and (2) are computationally efficient.

We restricted variables in our model to those which are commonly available or easily measured for the large numbers of stand types occurring in a multicounty region. This allows application of the system without extensive, periodic data collection over and above that normally collected in conventional forest inventories.

SYSTEM COMPONENTS

The method of simulating regionwide damage levels can be divided into two models, one for spot incidence and the other for individual spot severity. These were considered separately for two reasons. First, variables and relationships important in the initiation of a spot may be different than those involved in the spot spread that follows. Thus, spot initiation and spread may require different variables and modeling techniques. Second, it is difficult to conceive of a general model of insect behavior that would account for the large numbers of stands without outbreaks and still explain the variability of damage levels within similar stands. The incidence and severity models will be reviewed and then the workings of the regional damage projection system will be examined.

Spot Incidence

The incidence model used in this paper was developed using methodology presented by Daniels et al. (1979). This model estimates a continuous measure of SPB incidence, which, under certain sampling conditions, may be interpreted as the probability of outbreak within a stand. A stand is defined as a contiguous forest condition in one forest type of similar origin, age, and stocking. An outbreak occurs if one or more trees in a stand succumb to SPB attack. An outbreak does not occur if the trees are not attacked or if they survive an attack. It is assumed here that there can be at most one outbreak in a stand in the specified time period, usually a year.

---

[1] The authors are, respectively, Graduate Research Assistant and Graduate Research Assistant, Dept. of Forestry, Virginia Polytechnic Institute and State University, Blacksburg; Associate Professor of Forest Entomology, Clemson University, Clemson, S.C.; Professor of Forest Biometrics and Associate Professor of Forest Economics, Virginia Polytechnic Institute and State University, Blacksburg.

This incidence relationship can be represented by a Bernoulli random variable, which takes the value zero if an outbreak is not initiated and the value 1 if an outbreak occurs. This variable will take the value 1 (indicating an outbreak has occurred) with a certain probability, P, and the value zero, indicating no outbreak, with the probability 1-P.

The probability P provides a bounded ($0 < P < 1$), continuous measure of the risk of southern pine beetle outbreak when applied to a given land area and time period. This probability is most useful for decisionmaking if it can be expressed in terms of site, stand, and insect variables that can be easily measured in the field or from aerial photographs. It may be estimated using a probability model such as the logistic function:

$$p = \frac{1}{1 + \exp(b_0 + b_1X_1 + b_2X_2 + \ldots + b_kX_k)}$$

where

p = the estimated value of P, $0 < p < 1$

X_i = the ith variable associated with outbreak probability, ($i = 0,1,2,\ldots k$)

b_i = the ith estimated regression coefficient, ($i = 0,1,2,\ldots k$)

This type of model is desirable because it gives a continuous measure of stand susceptibility. It also allows the determination of SPB attack on a stand-by-stand basis, information unavailable from a model that predicts the annual number of spots likely to occur in a region in a given time period. This model provides some idea as to where the spots are likely to occur and in what type of stand they are likely to be located. These features allow a more realistic estimate of the beetles' impact to a region.

Spot Severity

The individual spot severity model will be presented in detail later in this symposium. For this reason, the model and the relations between its component parts will only be briefly reviewed here.

In this study, the objective was to develop a model that used commonly available stand characteristics to predict damage caused by the southern pine beetle over a large number of spots. Highly precise individual spot damage estimates were not needed; only the cumulative damage over many spots was required. Thus, we took a stand-level approach in developing the model. In this approach, emphasis is placed on the forest stand and those stand characteristics that affect the spread of SPB infestations. It is probably possible to achieve more precise results on an individual spot basis by predicting spot spread based on insect-level variables. However, information needed to operate such models may be more expensive to collect and is generally less likely to be available on a regional basis than that required by a stand-level model. We used the stand-level approach here because it was better able to satisfy the objectives and meet the demands to be placed on the model.

The spot severity model contains a submodel for predicting the rate of spread, in terms of trees killed per day, and a function giving the probability of a spot becoming inactive within 30 days of observation. When combined, these produce a method of simulating the spread of infestations.

Spot Spread

The spot spread model predicts the rate of spread for southern pine beetle infestations. The following spot spread prediction equation was developed using standard multiple regression techniques from data collected in east Texas by Hedden and Billings (1979):

$$\begin{aligned} \ln(TK/D) = {} & 0.78099 + 0.96545 \ln AT \\ & - 2.84669 \ln DBH - 0.78786 \\ & TBA/DBH^2 + 0.016914\ TBA \\ & + 0.55764\ POP \end{aligned}$$

where

$\ln(TK/D)$ = the natural logarithm of trees killed per day

$\ln AT$ = the natural logarithm of the initial number of attacked trees

DBH = the mean d.b.h. of the stand (inches)

TBA = the total basal area of the stand (ft^2/acre)

POP = the number of spots per thousand acres of host type for the year being examined.

This equation has a coefficient of determination (R^2) of 0.73 and a standard error of estimates ($s_{y \cdot x}$) of 0.53.

Spot Inactivity

As time progresses, some spots become inactive for reasons not fully understood. Whatever the cause, in the simulation of spot growth it is necessary to allow for the cessation of beetle activity. An unpublished result of Hedden and Billings (1979) is a model describing the probability of a spot becoming inactive within a 30-day period, given the number of attacked trees at the beginning of the period. A logistic function predicting the probability of a spot becoming inactive within 30 days was developed. The prediction equation is

$$p = \frac{1}{1 + \exp(-1.04 + 0.06AT)}$$

where

p = the estimated probability of a spot becoming inactive within the next 30 days

AT = the number of attacked trees at the beginning of the 30-day period.

Simulating Spot Growth

Spot growth can be simulated with the spot spread model and the spot inactivity function if the stand characteristics and initial spot size are known. The combination of the spot spread model and the inactivity function make up the spot severity model (fig. 1).

Because the inactivity function gives the probability of a spot becoming inactive within 30 days, the simulation of spot growth is broken into 30-day periods. The discovery of a spot is considered to be the beginning of the first 30-day simulation period.

At the beginning of each 30-day period, the spot is tested to determine if it becomes inactive during that period. This is done by generating a uniform (0,1) random variate and comparing it with the probability of a spot becoming inactive from the inactivity function. If the uniform random variate is less than the probability of the spot becoming inactive, a discrete uniform (1,30) random variate is generated to indicate the number of days of the next 30-day period that the spot will continue to expand. The spot is then grown for this number of days and terminated. If the uniform (0,1) random variate is greater than the inactivity probability, the spot is judged to remain active throughout the entire period. The spread of the spot is then calculated for the entire 30-day period, the new number of attacked trees is found, and the next simulation period is entered. This procedure is continued until the spot is terminated or the end of the season of beetle activity is reached. The spots remaining active at the end of the last 30-day period are allowed to expand from 1 to 30 more days as before and then terminated. This allows for the cessation of beetle activity in individual spots while no new spots are beginning.

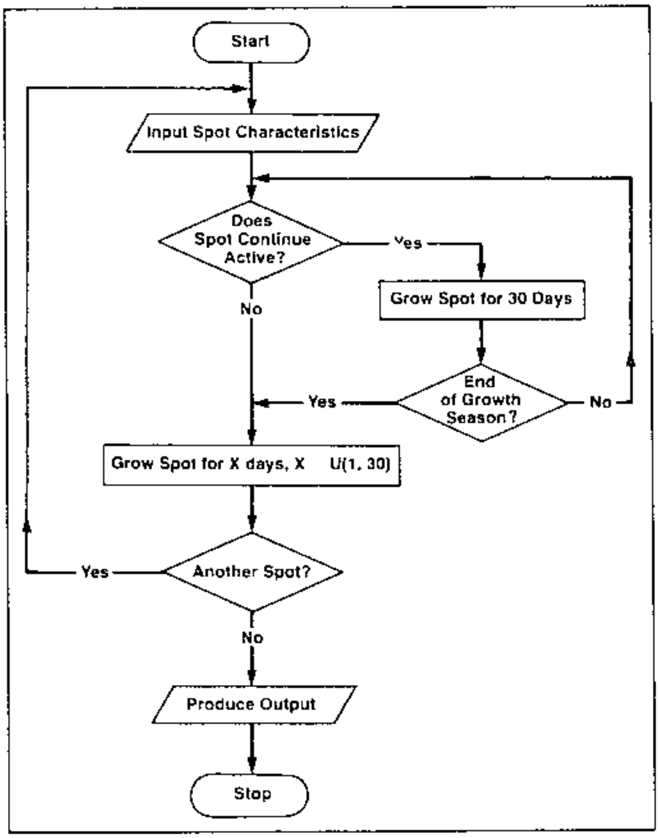


Figure 1.--Flow chart of the spot severity model.

THE DAMAGE PROJECTION SYSTEM

In order to understand the procedures and problems involved in formulating a regional damage projection system, it is probably best to look at an example region. The North Central Forest Survey Unit, Survey Unit Number 4, of Georgia (fig. 2) was chosen to demonstrate this methodology. This survey unit is located in the Georgia Piedmont. We chose it because of the availability of the many types of data required to develop the damage projection system. Data on the forest characterisitcs of the area were readily available from the Renewable Resource Evaluation Unit (formerly called Forest Survey) of the Southeastern Forest Experiment Station, U.S. Forest Service. These data were forest sample plot summary information from the survey unit.

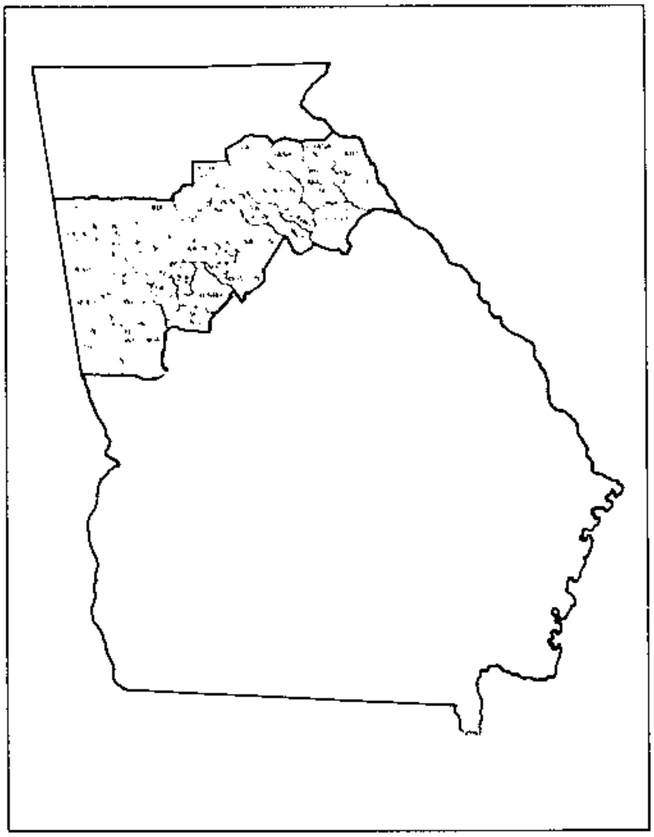


Figure 2.--The North Central Forest Survey Unit of Georgia.

Included were the sample plot forest type, age class, site class, BA, volume and growth data, and other variables such as physiographic class and stand origin. Also included was an acreage expansion factor for each plot. This allowed dividing the region into any combination of site or stand characteristics and determining acreage for each resulting stand type.

Records of southern pine beetle activity were available from aerial observations. The Georgia Forestry Commission collected this information for the years 1974-77. Flights were made on or about May 1, August 1, and October 1 for each year. Ground crews then verified these observations. The number of spots and their approximate sizes were summarized by county and year of observation along with the date of the flight.

Roger Belanger, of the U.S. Forest Service, has studied the relationships between the southern pine beetle and its hosts in this survey unit (Belanger, Osgood, and Hatchell 1979) and supplied data collected from both infested and noninfested stands. These data contained precise measurements of stand age, BA/acre, mean d.b.h., number of trees killed, and other variables such as average bark thickness and growth rate of the stand.

Forest Characteristics of the Region

The Renewable Resources Evaluation Unit of the Southeastern Forest Experiment Station provided data concerning the forest conditions of the area. This information was gathered during the last survey of the region, in 1972.

Forest Type

Three host types were identified--loblolly pine (*Pinus taeda*, L.) and shortleaf pine (*P. echinata*, Mill.), with loblolly pine further divided into planted and naturally regenerated stands. The standard U.S. Forest Service timber type definitions were used in this study. In these types, over 50 percent of the stand consists of either loblolly or shortleaf pine. The oak-pine type, which consists of stands containing 25 to 50 percent pine, was not considered to be a major host type.

Age

In 1972, stands were classified into 10-year age brackets. The exact ages were not recorded. Because of this, whenever age is required in a calculation, the midpoint of the age class is used rather than an exact age. In States now being surveyed, ages will be recorded to the nearest year. Thus, this categorization by age classes may not be necessary, unless desired, in a different region. When this unit was last surveyed, approximately 9 percent of the host type acreage was classed as uneven aged. This practice is also being phased out. For this region, the acreages reported as uneven aged were proportioned to the age classes according to the distribution of total acreage in stands classed as even aged.

Site Index

In the forest survey data, stands were classed into one of five site categories based on potential annual growth. The conversion of these classes to site index values varies from species to

Table 1.--Site index classes (base age of 25 years) for loblolly and shortleaf stands, based on U.S. Forest Service site quality classifications[1]

Site class	Productivity (ft^3/acre/year)	Site index class	
		Loblolly	Shortleaf
1	>165	>85	>75
2	120-165	75-85	65-75
3	85-120	60-75	52-65
4	50-85	45-60	40-52
5	<50	<45	<40

[1] The information in this table is taken from U.S. Department of Agriculture Forest Service (1977).

Table 2.--Acreages of shortleaf stands by age and site classes in the North Central Forest Survey Unit of Georgia

Age	Site Index$_{25}$ Class (ft)				
(years)	>85	75-85	60-74	45-59	<45
0-9	0	0	9068	80806	0
10-19	0	0	36588	124877	2287
20-29	0	4472	32457	63387	5551
30-39	0	479	31399	32833	4529
40-49	0	1752	2765	40029	4348
50-59	0	0	0	4787	0
60-69	0	0	0	9312	0
70-79	0	0	0	0	0

Total Acreage = 491,715

species. Table 1 indicates the basis for division into site classes and how these translate into site index, base age 25, for loblolly and shortleaf pine types. There is no distinction made in site curves between planted and natural stands of loblolly pine. We did not use the Forest Service's site index equations in this study; instead, we used a table look-up procedure to find the dominant height associated with stands of a given age and site class. In other situations, especially if there were a continuous measure of age, site index curves could be used to find the dominant height of stands, which is used in turn to find volume.

The forests of the region were divided into stand types based on the above three variables--forest type, age, and site class. We then calculated the acreages for each stand type using the acreage expansion factors. Table 2 illustrates the results for shortleaf pine. Similar arrays were developed for planted and natural loblolly stands. For each of these stand types, the total BA/acre and the average d.b.h. were needed for the incidence and severity models.

Total Basal Area

For each sample plot in the survey, the BA/acre of stems > 5.0 inches in d.b.h. was measured, and an estimate of the number of stems per acre from 1.0-4.9 inches in d.b.h. was calculated. The number of stems per acre in this size category was multiplied by the basal area of an average-sized stem (3 inches d.b.h.) and this is added to the basal area of stems > 5.0 inches d.b.h. to arrive at an estimate of the total BA/acre. The formula was

$$TBA = BA_{5+} + 0.005454\ (3)^2\ NLS$$

where

TBA = the total basal area of the stand (ft^2/acre)

BA_{5+} = basal area of all stems over 5.0 inches d.b.h. (ft^2/acre)

NLS = number of stems in the 1.0- to 4.9-inch d.b.h. category per acre.

Simplifying,

$$TBA = BA_{5+} + 0.049086\ NLS$$

Using the forest survey data, we found the average total BA for each cell of the forest type, age class, and site class array. This is the total BA that was used in later calculations. The error caused by using the average total BA for each category is probably less than the error which would be introduced by trying to fit a total BA distribution for each cell.

Mean d.b.h.

Mean d.b.h. is an important variable in the severity model, but it was not readily estimated from the Forest Survey data. Therefore, a regression was fitted with the Belanger data set to predict mean d.b.h. from the age, site index, and forest type of the cell. The model was of the form

$$DBH = b_0 + b_1AGE + b_2SITE + b_3TBA$$

where

DBH = the predicted mean d.b.h. (inches)

AGE = the midpoint of the 10-year age class (years)

SITE = the midpoint in terms of site index, of the site class (feet)

TBA = average total basal area of stands in the age and site class (ft^2/acre)

A separate regression was computed for each of the three timber types, natural loblolly, planted loblolly, and shortleaf. A relative *F* test was performed and indicated significant differences between the coefficients of the three regression equations. The coefficients and regression statistics for each of three equations are given in table 3.

Once the total BA and the mean d.b.h. have been found for each stand type in the region, the region's forest characteristics can be entered (fig. 3) into the regional damage projection system. The spot incidence model is then used to simulate the number of spots that occur in each stand type. The spot severity model is used to project the growth of each spot. The total damage occurring in the region is found by summing over all spots.

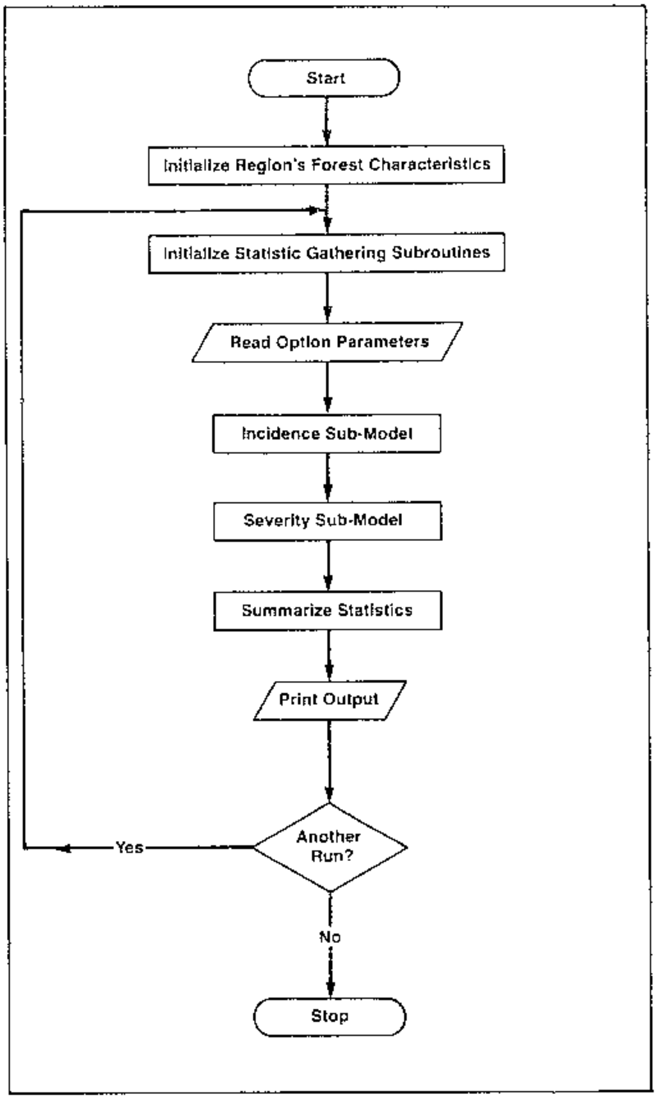


Figure 3.--Generalized flow chart of the damage projection system.

Table 3.--Regression equations for predicting the mean d.b.h. of a stand

Timber type	Coefficients[1] b_0	b_1	b_2	b_3	R^2	$S_{y \cdot x}$
Planted loblolly	-0.95102	0.21620	0.10180	-0.01394	0.647	1.111
Natural loblolly	-2.70930	0.07365	0.16750	-0.01825	0.594	1.831
Shortleaf	- .036013	0.07980	0.09756	-0.01354	0.574	1.326

[1] Model: $DBH = b_0 + b_1AGE + b_2SITE_{50} + b_3TBA$ where DBH = the mean d.b.h. of the stand; AGE = the age of the stand in years; $SITE_{50}$ = the site index of the stand, base age 50, in feet; and TBA = the total basal area of the stand (ft^2/acre).

Incidence

Because the factors affecting the occurrence of southern pine beetle infestations can vary greatly from region to region, it is desirable to fit the parameters of the incidence model to each region of interest. The following equations were developed for the Georgia Piedmont region.

For natural loblolly stands:

$$p = 1/(1 + \exp(4.76376 - 0.0106388\ \mathrm{SITE}_{50} - 0.039954\ \mathrm{TBA/AGE}))$$

For planted loblolly stands:

$$p = 1/(1 + \exp(-2.37849 + 0.0690323\ \mathrm{SITE}_{50}))$$

For shortleaf stands:

$$p = 1/(1 + \exp(3.15915 - 0.0071377\ \mathrm{AGE} - 0.00162082\ \mathrm{TBA/AGE}))$$

where

p = the probability of a stand with the given characteristics being attacked

SITE_{50} = the site index, base age 50 (feet)

TBA = the total basal area per acre (ft^2/acre)

AGE = the age of the stand in years.

In this set of equations, the same variables do not appear in each equation and the coefficients of SITE_{50} are of different sign in the planted loblolly and natural loblolly equations. These anomalies are probably caused by confounding among variables measured in the data set and possibly by the omission of relevant variables from the set of those chosen for measurement. This may be disconcerting, but these equations do perform reasonably well within the range of the measured variables. It should be noted that when these types of equations were applied to data from east Texas, satisfying results were achieved (Daniels et al. 1979).

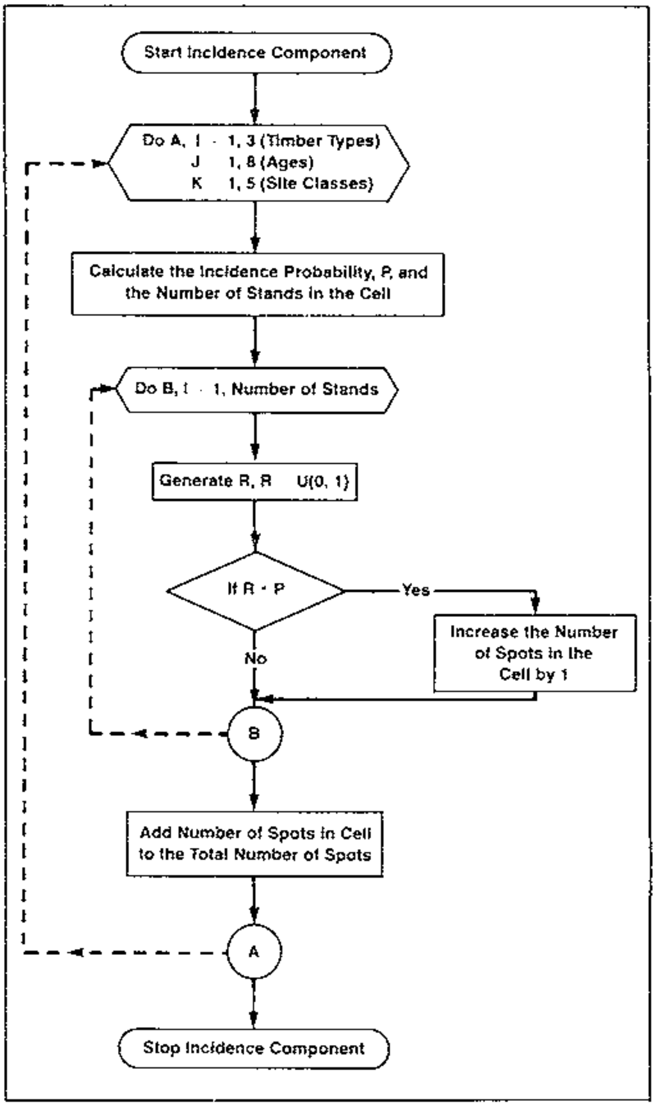


Figure 4.--Flow chart of the incidence component.

Once the region-specific forms of the incidence model are found, there are three steps in the application to the region (fig. 4). First, since the incidence model returns the probability of a stand being attacked, one must find the number of stands in each cell of the forest type, age, and site array. This is accomplished by dividing the acreage in each cell, known from the Survey data, by the average stand size for each timber type. Unfortunately, at the time the North Central Unit was last surveyed in 1972, no information on stand size was collected. However, in the 1977 survey of the neighboring South Carolina Piedmont, information on stand size was collected (Knight 1978). For pine plantations, the size of the average stand was about 15.7 acres. The average size of natural pine stands was about 10.8 acres. No distinction was made between stands of shortleaf pine and natural stands of loblolly pine. These averages from a neighboring region were rounded off to the nearest 5 acres, to 10 acres for natural pine stands and 15 acres for planted pine stands, for use in this survey unit.

Second, we calculated the number of spots occurring in each cell of the stand type array by defining a Bernoulli distributed random variable, X, such that:

$$X_i = 0 \text{ if } r > p$$

$$X_i = 1 \text{ if } r \leq p$$

where

X_i = the value for X in the ith stand in the cell

p = the probability of spot occurrence in a stand of the given characteristics

r = a uniform (0,1) random variate.

The number of spots in any particular cell is the sum of the X_i's over all stands in the cell. The number is recorded for each cell.

Finally, the total number of spots occurring in the simulation is found by summing, over all cells, the number of spots in each cell. The total number of spots in the region is then divided by the total acreage of SPB host type in the region (in thousands of acres) to formulate the SPB population level variable used in the severity model.

Severity

Before applying the severity model in the regional simulation, two distributions must be found: (1) the distribution of spot occurrence throughout the year, and (2) the distribution of initial spot size.

Time of Spot Occurrence

An empirical distribution of the time of spot occurrence was developed using data from the Georgia Forestry Commission. The spots observed on the first flight, made around May 1, were assumed to have initiated evenly throughout the previous 90 days. The spots observed on subsequent flights were assumed to have occurred uniformly through the time between flights. Table 4 indicates the empirical distribution of spot occurrence over a year. Because of the form of the available data, spot occurrence was assumed to commence on or about March 1 and cease on approximately October 11. This gives a period of 225 days for spot initiation. These dates do not seem unreasonable for the region of interest.

Table 4.--Distribution of spot occurrence through a year as observed over a 4-year period (1974-1977) in the North Central Forest Survey Unit of Georgia

Time period	Proportion of spots	Cumulative proportion of of spots
Mar 1-Mar30	0.15	0.15
Mar 31-Apr 29	0.15	0.30
Apr 30-May 29	0.14	0.44
May 30-Jun 29	0.13	0.57
Jun 29-Jul 27	0.12	0.69
Jul 28-Aug 27	0.12	0.81
Aug 28-Sept 26	0.12	0.93
Sept 27-Oct 11	0.07	1.00

Initial Spot Size

The simulation of spot growth begins on the date of spot detection. By the time an infestation is known to exist, several trees will have been killed. This initial number of trees killed must be generated for each individual spot. Such a distribution may have a similar form from region to region, but the parameter values may differ. Belanger's data set contained observations of initial spot size from 161 infestations in the North Central Forest Survey Unit of Georgia. Examination of these data revealed that there were many small spots, with the frequency decreasing as the number of affected trees increased. Besides having this general shape, the distribution chosen to model initial spot size should range from zero to infinity since no upper bound can be set on spot size and the initial number of trees affected must be greater than zero.

The generalized exponential or Pearson Type XI distribution was chosen to model the initial spot size distribution (table 5). This distribution is of the form

$$f(x) = ka^k(a + x)^{-(k+1)}$$

We chose this distribution over other alternatives because it allowed a better representation of the occurrence of large spots in the upper tail of the distribution.

A two-sample Kolmogorov-Smirnov test (Shannon 1975) indicated that the data from loblolly and shortleaf stands

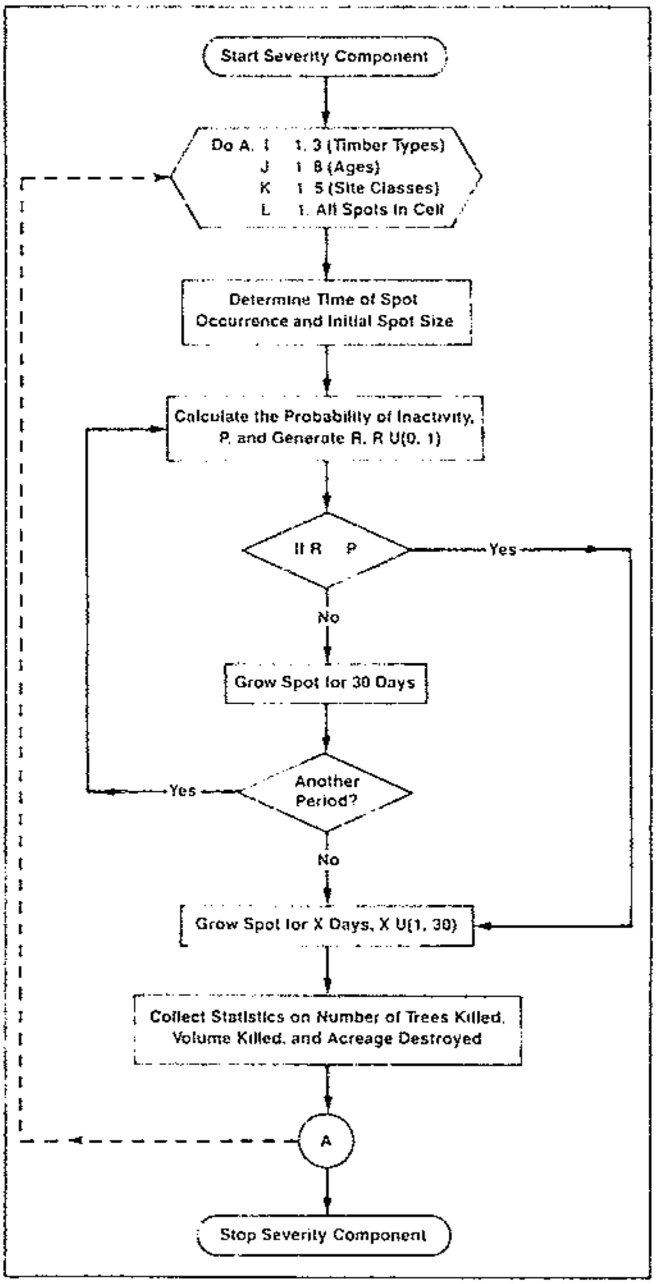


Figure 5.--Flow chart of the severity component.

Table 5.--Observed and predicted initial spot size distributions

Spot size class	Observed cumulative no. of spots	Predicted cumulative no. of spots
$0 < x \le 10$	50	46.61
$10 < x \le 20$	90	76.79
$20 < x \le 30$	105	97.20
$30 < x \le 40$	119	111.49
$40 < x \le 50$	127	121.80
$50 < x \le 60$	131	129.43
$60 < x \le 70$	134	135.20
$70 < x \le 80$	141	139.64
$80 < x \le 90$	143	143.11
$90 < x \le 100$	145	145.89
$100 < x \le 200$	155	156.88
$200 < x \le \infty$	161	161.00

could have come from the same underlying distribution. Because of this, we made no attempt to use separate initial spot size distributions for each timber type. The data were combined and one distribution was fit with this combined data and used for all timber types.

Determining Individual Spot Severity

To find the severity of an individual spot, the first thing that must be known is the date of spot detection (fig. 5). This is the date the spot is first known to exist and is generated from the empirical distribution of spot occurrence through time. This distribution generates the time period when the spot occurs. The date of spot occurrence is found by generating a discrete uniform random variable with range from 1 to 30 and adding this to the beginning of the time period. The length of time available for spot expansion can be found by subtracting the date of spot occurrence from the total time of simulation. For the example region, this total time of simulation is taken to be 225 days, from March 1 to October 11. After the date of spot detection is found, an initial spot size must be generated. Given this information, spot growth can be simulated with the spot severity model using the process described earlier.

Measures of Damage

The severity model returns the number of trees killed in each spot. To put the damage information in more meaningful units, this information is converted into cubic feet of timber killed and an estimate of the acreage lost to the SPB.

Acreage Destroyed

The acreage destroyed is estimated as follows:

$$ACRES = (TTK \cdot 0.005454\ DBH^2)/TBA$$

where

ACRES = the approximate acreage of the spot

TTK = the number of trees killed in the spot

DBH = the mean d.b.h. (inches) of the stand

TBA = the total basal area (ft^2/acre) of the stand

To use this measure of spot acreage, it must be assumed that the average d.b.h. of the trees killed is the same as the average d.b.h. of the stand. This must be regarded as a rough estimate since the tree of average diameter and the tree of average BA are seldom the same. In fact, since the tree of average BA is never smaller than the tree of average diameter, this estimate of acreage destroyed will always be biased low.

Volume Killed

The cubic feet of volume killed can be estimated by multiplying the number of acres destroyed by the cubic foot volume per acre. The volume per acre can be found using stand-level multiple regression yield equations such as those developed by Burkhart et al. (1972a and b).

For natural stands of loblolly pine:

$$\log_{10}VOL = 0.81129 - 8.23404/AGE + 0.18782\ H_d/AGE + 0.91938 \log_{10}TBA + 0.00191\ (AGE \cdot \log_{10} TBA) + 0.46069\ PBA/TBA$$

For planted stands of loblolly pine:

$$\log_{10}VOL = 2.37288 - 6.19378/AGE + 0.31876\ H_d/AGE + 0.00706\ TPA/100 + 0.00884\ AGE \cdot \log_{10}TPA$$

where

$\log_{10}VOL$ = the total stem volume in ft^3, inside bark per acre

AGE = the stand age (years)

H_d = the average height of dominants and codominants (feet)

TBA = the total basal area of the stand (ft^2/acre)

PBA = the pine basal area of the stand (ft^2/acre)

TPA = the stems per acre of the stand

Stems per acre is found by dividing the trees killed by the number of acres destroyed. It was assumed that in this region, in the average natural stand, 80 percent of the total BA was pine. The equation for natural stands of loblolly pine was also used for shortleaf stands since shortleaf pine occurs in stands similar to natural loblolly stands.

Another method is to find the volume of the "average" tree and multiply this by the number of trees killed to estimate the volume killed in the stand. An equation relating tree volume to tree diameter and the height of dominant and codominant trees in planted loblolly stands is given by Burkhart and Strub (1974). A similar equation was developed for natural loblolly stands for use in the damage projection system.

For natural loblolly stands:

$$VOL = -.864615 + 0.00218\ DBH^2H_d$$

For planted loblolly stands:

$$VOL = -.63136 + 0.00187\ DBH^2H_d$$

where

VOL = the total ft^3 volume, inside bark

DBH = d.b.h. (inches)

H_d = the average height of dominants and codominants in the stand (feet).

The natural loblolly equation was also used in shortleaf stands as in the previous method of volume estimation.

RESULTS AND CONCLUSIONS

The program output is summarized in four types of tables. The first type (table 6) contains a summary of beetle

Table 6.--Damage projection system output--summary of beetle damage to natural loblolly stands

Damage measure	Number of spots	Total damage	Average damage	Standard deviation	Range Min	Range Max
Trees killed	879.00	219977.50	250.26	485.52	0.01	6425.64
Acres destroyed	879.00	596.61	0.68	1.61	0.00	26.64
Volume lost	879.00	881491.06	1002.83	4065.98	0.01	88841.25

Table 7.--Damage projection system output--distribution of acres destroyed by timber type and date of spot occurrence

Date of detection	Timber type: Natural loblolly	Plantation loblolly	Shortleaf	All host types
Mar 1-Mar 30	83.6	117.5	117.3	318.4
Mar 31-Apr 29	93.4	61.5	134.1	289.0
Apr 30-May 29	77.3	90.3	97.9	265.5
May 30-Jun 28	65.9	90.8	86.6	243.2
Jun 29-Jul 28	69.6	101.2	97.9	268.8
Jul 29-Aug 27	92.1	96.5	79.1	267.7
Aug 28-Sept 26	91.1	85.1	131.2	307.4
Sept 27-Oct 11	23.7	56.2	60.5	140.4

damages for a given timber type. Included are the number of spots in the timber type and the total and average damages for the three measures of damage--trees killed, acres destroyed, and volume lost. Also included are the standard deviation and the range of damages observed for the forest type.

The second type (table 7) summarizes the damage distribution by the time of spot occurrence. A table is printed for the number of spots occurring and each of the three damage measures. The damages in each table are further grouped by timber type.

The third type of table (table 8) presents the acreage destroyed in a timber type by the age class of the stand where the spot occurs. The damages are further grouped according to the size in acres of the infestation. This information is useful in the economic analysis of beetle damage.

The last table type (table 9) summarizes, by timber type, the damages occurring by the average diameter of the infested stand.

The system will project the expected damages given the forest conditions of the region. It may be reasonable to assume that a region's forest characteristics will remain approximately the same for a few years after they are measured, but they cannot be expected to remain constant over many years. For this reason, care should be taken in applying the damage projection system to years that may have different forest conditions than those input into the system, to insure that the conditions input are not significantly different than those in the field.

Unfortunately, there are no data available concerning the actual damages caused by the southern pine beetle in this region; thus, the regionwide system cannot be validated. The individual components can be validated, however. Even though we cannot make a statement of the absolute validity of the damage projection system, it seems that since

Table 8.--Damage projection system output--acreage destroyed by spot size and age class for shortleaf stands

	SPOT SIZE IN ACRES							
Age	Under 0.10	0.10-0.25	0.25-0.50	0.50-0.75	0.75-1.00	1.00-5.00	5.00-10.00	10.00 and over
5	5.2	7.2	21.8	21.6	18.0	55.6	16.1	17.0
15	15.1	24.8	23.6	12.6	5.1	18.6	0.0	0.0
25	9.0	10.5	31.6	22.1	22.4	77.1	15.7	0.0
35	7.1	8.9	10.8	7.4	8.3	37.2	14.6	0.0
45	3.7	5.6	13.3	18.6	11.3	71.0	10.7	12.6
55	0.4	0.6	0.9	1.4	3.3	2.9	12.0	0.0
65	0.8	1.2	1.7	3.7	3.5	53.8	11.4	15.0
75	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0

Table 9.--Damage projection system output--southern pine beetle damages by spot d.b.h. class

d.b.h. class	Number of spots	Trees killed	Acres destroyed	Volume killed
5	2532.	468510.	863.9	425102.
6	855.	233539.	518.0	879911.
7	286.	76031.	163.9	365734.
8	307.	99541.	366.7	692718.
9	85.	30074.	113.5	283454.
10	26.	13586.	64.1	192396.
11	8.	2313.	10.3	36370.
12	0.	0.	0.0	0.
13	0.	0.	0.0	0.
14	0.	0.	0.0	0.
15	0.	0.	0.0	0.
16	0.	0.	0.0	0.
17	0.	0.	0.0	0.
18	0.	0.	0.0	0.
19	0.	0.	0.0	0.
20 and over	0.	0.	0.0	0.

the components of the system have been validated, the relative damage levels observed under various options in the system would be reasonable.

We believe that the methodology of developing a regional southern pine beetle damage projection system has successfully been demonstrated for the North Central Forest Survey Unit of Georgia. Further information on the options available in the system and copies of the program are available from the authors upon request.

LITERATURE CITED

Belanger, R. P., E. A. Osgood, and G. E. Hatchell. 1979. Stand, soil, and site characteristics associated with southern pine beetle infestations in the Southern Appalachians. 7 p. U.S. Dep. Agric. For. Serv., Res. Pap. SE-198. Southeast. For. Exp. Stn., Asheville, N.C.

Burkhart, H. E., and M. R. Strub. 1974. Dry weight yield estimates for loblolly pine: a comparison of two techniques. *In* IUFRO biomass studies. H. E. Young, ed. College of Life Sciences and Agriculture, Univ. of Maine at Orono.

Burkhart, H. E., R. C. Parker, and R. G. Oderwald. 1972a. Yields for natural stands of loblolly pine. 63 p. Div. For. and Wildlife Resour., Pub. FWS-2-72. Va. Polytech. Inst. and State Univ., Blacksburg.

Burkhart, H. E., R. C. Parker, M. R. Strub, and R. G. Oderwald. 1972b. Yields of old-field loblolly pine plantations. 51 p. Div. For. and Wildlife Resour., Pub. FWS-3-72. Va. Polytech. Inst. and State Univ., Blacksburg.

Daniels, R. F., W. A. Leuschner, S. J. Zarnoch, H. E. Burkhart, and R. R. Hicks. 1979. A method for estimating the probability of southern pine beetle outbreaks. For. Sci. 25:265-269.

Hedden, R. L., and R. F. Billings. 1979. Southern pine beetle: factors influencing the growth and decline of summer infestations in east Texas. For. Sci. 25:547-556.

Knight, H. A. 1978. Sizes of timber stands in the Piedmont of South Carolina. U.S. Dep. Agric. For. Serv., Res. Note SE-267. Southeast. For. Exp. Stn., Asheville, N.C.

Shannon, R. E. 1975. Systems simulation: the art and science. 387 p. Prentice-Hall, Inc., Englewood Cliffs, N.J.

U.S. Department of Agriculture Forest Service. 1977. Field instructions for South Carolina. U.S. Dep. Agric. For. Serv., Southeast. For. Exp. Stn., Asheville, N.C.

SOUTHERN PINE BEETLE: FACTORS INFLUENCING THE GROWTH AND DECLINE OF SUMMER INFESTATIONS

Roy L. Hedden and David D. Reed[1]

Abstract.--A model has been developed to simulate the spread of southern pine beetle infestations using stand-level variables. The model consists of two principal functions: (1) a function to predict the rate of spread, in terms of trees killed per day, and (2) a function to predict the probability of a spot becoming inactive. Spot growth can be simulated with these two relatively simple functions.

INTRODUCTION

Seasonal behavior of the southern pine beetle (SPB), *Dendroctonus frontalis* Zimm. (Coleoptera:Scolytidae), is characterized by dispersal and initial infestation establishment in spring to early summer (Billings and Kibbe 1978) followed by spot growth and decline. Initial spot establishment is influenced by stand disturbances such as lightning, logging damage, and flooding, and by the presence of low-vigor pine trees (Coulson, Hain, and Payne 1974; Ku, Sweeney, and Shelburne 1976; Lorio 1968 and 1978). The number of trees attacked during the infestation establishment phase is determined by the weather, the proximity and number of brood sources producing dispersing beetles, and to a lesser extent, the prevailing stand conditions (Hedden and Billings 1979). During the summer, beetle immigration into spots declines (Billings 1979). And the beetle population within the infestations must establish and maintain synchrony between emergence and attack in order for spot growth to continue (Gara 1967). When the synchronization between brood emergence and pheromone production (attack) is interrupted, infestation growth ceases and beetle dispersal occurs (Gara 1967, Gara and Coster 1968).

The purpose of this study was (1) to identify site and stand factors related to southern pine beetle summer spot growth and decline, and (2) to use these factors in the development of submodels for predicting the rate of infestation growth (spot growth) and for predicting the probability of an infestation ceasing to expand (spot inactivity).

PROCEDURES

Data Collection and Analysis

Details on spot selection and data collection have been explained elsewhere (Hedden and Billings 1979). The independent variables included

pine BA/ha, in m^2

hardwood BA/ha

total BA/ha (pine + hardwood)

mean pine BA/tree

mean d.b.h. per pine, in cm

percent pine by number of stems

percent pine by BA.

Additional variables derived from the periodic measurement of active trees were the basal area and number of

active (brood) trees at the initial visit,

active trees at a subsequent visit,

new infested trees since the last visit, and

previously infested trees vacated by beetles (inactive) since the last visit.

Infestation growth rate was expressed as the number of new trees killed per day (TK) for each spot where

$$TK = \frac{\text{number of new trees killed between visits}}{\text{time lapse (days) between visits}}$$

Using the number of trees killed per day (TK) as the dependent variable, we conducted regression analyses with

---

[1] The authors are, respectively, Associate Professor, Dept. of Forestry, Clemson University, Clemson, S.C.; and Graduate Research Assistant, School of Forestry and Wildlife Resources, Virginia Polytechnic and State University, Blacksburg.

data from 1975, 1976, and 1977 combined. In addition to the variables previously described, we included the total number of beetle spots detected in east Texas for the appropriate year (POP) as a covariate to account for annual differences in areawide beetle population levels. Both linear and nonlinear regression equations were generated. For the linear models Mallow's C_p, the total squared error, was used as a criterion for preliminary screening of candidate variables (Daniel and Wood 1971, Seber 1977). Parameters included in the final model were selected on the basis of simplicity and ease of interpretation. Criteria for selection of the nonlinear model included predictive ability and behavior of residuals. Only data from infestations that continued to expand were used in the nonlinear analysis.

Lastly, we derived a logistic function (Cox 1970) predicting the probability of a spot becoming inactive. Three models were developed. Model I predicts the probability of a spot going inactive within 30 days after the initial visit. This function was based upon data from 1975 and 1976. The second equation (Model II) predicts the probability that a spot will contain fewer than 20 active trees at day 30. This model was based upon 62 spots monitored from 1975 through 1977. Model III was derived from operational data on 1,386 spots aerially detected from June to December 1975 by the Texas Forest Service (1976). This model predicts the probability of a spot being inactive when ground checked within 30 days of detection.

RESULTS AND DISCUSSION

Data suitable for regression analysis were collected from 28, 24, and 10 active infestations during the summers of 1975, 1976, and 1977, respectively. Spots monitored during 1975 were relatively small (mean = 36 active trees at the first visit) and occurred in stands with a mean total BA of 35 m^2/ha. During 1976, sampled spots were larger (mean = 66.5 active trees at the first visit) and were located in stands with lower BA (mean = 29.6 m^2/ha). In the 10 spots monitored in 1977, the mean number of active trees was 47.6 while the mean BA at the spot origin was 38 m^2/ha.

During this time, beetle population levels varied greatly--first increasing, then decreasing. In 1975, 4,000 SPB infestations with 10 or more trees were reported in east Texas. In 1976, the number of spots reported increased to 11,000. Only 4,300 spots were detected in 1977, and in 1978 the total number reported statewide delcined to 37 spots. Just two spots were detected in 1979.

Infestation Growth and Decline

Spot Growth

Two models for infestation growth were developed. The first was a linear model:

$$TK = 1.78627 + 0.02475\ AT + 0.02765\ TBA + 0.01182\ POP$$

where

TK = trees killed per day

AT = initial number of active trees at the first visit

TBA = total BA at the spot origin (m^2/ha)

POP = number of spots per 1,000 ha of host type.

This equation has coefficient of determination (R^2) of 0.80 and a standard error of the estimate of 0.68. This model works well when fitted to data from any one year but predicts too great a rate of spread for years when population levels are low.

In order to develop a better predictor of spot growth we computed a nonlinear equation:

$$\ln(TK) = 3.43457 + 0.96545 \ln(AT - 2.84669 \ln(DBH) - 22.13668\ TBA/DBH^2 + 0.07366\ TBA + 0.22567\ POP$$

where

ln(TK) = natural logarithm of trees killed per day

ln(AT) = natural logarithm of the initial number of active trees

DBH = mean d.b.h. of the stand (cm)

TBA = total BA of the stand (m^2/ha)

POP = number of spots per 1,000 ha of host type.

This equation has an R^2 of 0.73 and an $S_{y.x}$ of 0.53. In fitting the model, we used only those spots that expanded.

There were six spots in 1975, three in 1976, and three in 1977 that did not expand and were not included. This model predicts spot growth better during years when population levels are low than does the linear model.

Spot Inactivity

We developed a logistic function (Cox 1970) predicting the probability of a spot becoming inactive. The model is

$$p = \frac{1}{1 + \exp\,(a+Bx)}$$

where

p = probability of a spot becoming inactive

x = number of initially active trees or the natural logarithm of AT.

Three equations were derived (table 1). Model I predicts the probability of a spot going inactive within 30 days after the initial visit. This function was based upon data from 1975 and 1976. The second equation (Model II) predicts the probability that a spot will contain fewer than 20 active trees at day 30. This model is based upon 62 spots monitored from 1975 through 1977. Model III was derived from operational data on 1,386 spots aerially detected from June to December 1975 by the Texas Forest Service (1976). This model predicts the probability of a spot being inactive when ground checked within 30 days of detection. Table 2 presents predicted probabilities of inactivity for selected initial numbers of active trees.

Model Behavior

This discussion will be limited to the behavior of the spot inactivity model derived from the 1975 and 1976 data (Model II, table 1), and the nonlinear model of spot growth.

The probability of a spot going inactive is inversely related to the initial number of active trees (table 2). A high number of brood trees insures that a population of beetles is available for continuation of spot growth. A large number of active trees also increases the probability of synchrony between pheromone production and SPB emergence. In the absence of an active pheromone source, emerging beetles will disperse and the spot will go inactive (Gara 1967, Hedden and Billings 1979).

Of the various stand factors measured, only total basal area (TBA), diameter at breast height (d.b.h.), and the ratio TBA/d.b.h.^2 were significantly

Table 1.--Parameter estimates for the models to predict spot inactivity.

Model[1]	a	SD[2]	B	SD[2]	Dependent variable (x)
I[3]	- 1.144	0.653	0.069	0.023	AT
II[4]	-11.314	3.141	3.617	0.946	ln(AT)
III[5]	- 0.640	0.124	0.092	0.010	AT

[1] The model has the form $p = \frac{1}{1 + \exp\,(a+Bx)}$.

[2] SD = the asymptotic stand deviation.

[3] p = probability of a spot going inactive after 30 days.

[4] p = probability of a spot containing fewer than 20 trees after 30 days.

[5] p = probability of a spot being inactive when ground checked within 30 days of detection.

Table 2.--Predicted probabilities (p) of spot inactivity for selected initial numbers of active trees.

Initial number of active trees (AT)		Model	
	I[1]	II[2]	III[3]
5	.69	.54	1.00
15	.53	.32	.82
25	.36	.16	.42
35	.22	.07	.18
45	.12	.03	.08
55	.07	.01	.04

[1] $p = \frac{1}{1 + \exp\,(-1.144 + .069\ \text{AT})}$;
p = probability of a spot going inactive after 30 days.

[2] $p = \frac{1}{1 + \exp\,(-11.314 + 3.617\ \ln\text{AT})}$;
p = probability of a spot containing fewer than 20 trees after 30 days.

[3] $p = \frac{1}{1 + \exp\,(-.640 + 0.92\ \text{AT})}$;
p = probability of a spot being inactive when ground checked within 30 days of detection.

Table 3.--Behavior of the spot growth model.[1] Trees killed per day when the population level (POP) is 3.05 spots per thousand hectares of host type.

d.b.h. (cm)	TBA (m^2/ha)			
	15	25	35	45
		AT (number) = 10		
20	.1485	.1784	.2142	.2573
35	.0528	.0921	.1605	.2799
50	.0220	.0420	.0803	.1535
		AT (number) = 50		
20	.7024	.8436	1.10132	1.2170
35	.2498	.4355	.7593	1.3238
50	.1039	.1986	.3800	.7261
		AT (number) = 150		
20	2.0287	2.4366	2.9265	3.5149
35	.7214	1.2578	2.1930	3.8235
50	.3001	.5737	1.0969	2.0971

[1] $\ln(TK) = 3.43457 + .96545 \ln(AT) - 2.84669 \ln(DBH) - 22.13668\ TBA/DBH^2 + 0.73662\ TBA + .22567\ POP$

related to spot growth. For a given average diameter, the rate at which new trees are killed increases as TBA increases (table 3). Trees will be more closely spaced in stands of high TBA than in stands of lower BA, assuming the trees in the stands have the same diameter distribution. Trees in dense stands will experience greater competition for resources (Hedden 1978a) and will grow at a slower rate than under less crowded conditions (Schumacher and Coile 1960). High stand density, low radial growth, and reduced tree vigor are characteristic of SPB infestations (Lorio 1968 and 1978, Coulson et al. 1974, Ku et al. 1976).

Wide tree spacing, regardless of tree vigor, can also limit spot growth. Gara and Coster (1968) have shown experimentally that spot growth ceases when the distance between a tree currently under attack and the nearest unattacked pine is greater than 6 to 9 m. Johnson and Coster (1978) indicate that this phenomenon may only apply in small to moderate infestations (< 100 active trees) with a single pheromone source. In large spots (> 100 active trees) with multiple pheromone sources, the probability of attack is more dependent upon the size of the resident beetle population than upon tree spacing (Johnson and Coster 1978) or stand conditions (Hedden unpublished).

As average d.b.h. or the ratio TBA/DBH^2 increases, the rate of spot growth decreases (table 3). In a stand of fixed basal area, as d.b.h. increases, distance between trees increases. This increase in spacing has the effect of reducing both intertree competition and the probability that an unattacked neighbor tree will come under the influence of an active pheromone source.

Spot growth also increases as the number of spots detected per year increases. This variable is probably related to SPB brood production per tree, beetle brood developmental rates, and possibly beetle immigration from nearby spots--variables not measured in this study.

Simulation of Infestation Growth

Spot growth can be simulated with the spot spread model and the spot inactivity function if the stand characteristics and initial spot size are known. The combination of the spot spread model and the inactivity function make up the spot severity model.

Because the inactivity function gives the probability of a spot becoming inactive within 30 days, the simulation of spot growth is broken into 30-day periods. The discovery of a spot is considered to be the beginning of the first simulation period.

At the beginning of each 30-day period, the spot is tested to determine if it becomes inactive during that period. This is done by generating a uniform (0,1) random variate and comparing it with the probability of a spot becoming inactive from the inactivity function. If the uniform random variate is less than the inactivity probability, the spot is grown for an additional 15 days as a best estimate of when activity would cease. If the uniform random variate is greater than the inactivity probability, the spot is judged to remain active throughout the entire period. The spread of the spot is then calculated for the entire 30-day period, the new number of attacked trees is found, and the next simulation period is entered. This procedure is continued until the spot is terminated or the end of the season of beetle activity is reached. The spots remaining active at the end of the last 30-day period are allowed to expand for 15 days more before termination. This allows for the termination of beetle activity in individual spots while no new spots are beginning.

Table 4.--Results of the validation test of the severity model on data from north Georgia.

	Number of attacked trees					
	Observed		Predicted		Predicted	
Plot	Initial	Final	Final[1]	Residual	Maximum	Minimum
C- 1	20	24	25.67	+ 1.67	37.0	21.9
C- 4	12	18	22.88	+ 4.88	34.5	15.1
C- 7	10	18	16.92	- 1.08	24.3	11.4
C- 8	8	29	18.95	-10.05	36.3	10.2
C- 9	17	30	30.06	+ 0.06	54.8	20.4
C-10	14	50	30.85	-19.15	52.3	17.2
C-11	20	27	24.90	- 2.10	31.5	21.4
C-12	14	25	18.28	- 6.72	23.6	15.6
C-13	4	4	5.01	+ 1.01	6.1	4.2
C-14	22	23	29.76	+ 6.76	41.3	25.1
C-15	22	22	29.22	+ 7.72	45.0	25.6
Totals		270	252.6	-17.40		

[1] Average of ten simulation runs.

Model Validation

Validation Data

The spot spread model and the inactivity function were developed from east Texas data, but no data from that region were available for validation. Dr. G. E. Moore, of the United States Forest Service, supplied data collected in north Georgia for the purpose of validating the severity model. This data set consists of 11 infestations that had been visited in June 1977 and revisited in October of the same year. The necessary stand variables (total BA and mean stand d.b.h.), the population level, and two measurements of the number of attacked trees, taken about 4 months apart, were available for each spot.

Procedure

The number of attacked trees in each of these 11 spots had been initially observed in June and then again in October, a period of about 120 days or four 30-day periods. For simplicity of simulation, each spot was assumed to have been discovered on the first day of June. Spots were followed through four simulation periods. If a simulated spot was active at the end of the fourth period, it was grown for an additional 15 days and terminated. This was done because 120 days from June 1 is September 29, and the extra 15 days caused the spots to be active into October, when they were actually remeasured.

Validation Results

The results of the validation procedure are contained in table 4. The growth for each spot was simulated 10 times and averaged. The severity model predicted that there would be 6.45 percent fewer trees killed than were observed. The total number of trees killed on individual runs bracketed the observed number of trees killed. Spot number C-12 was the only spot that expanded significantly after the first measurement in which the predicted number of trees killed from individual simulation runs did not bracket the observed number of trees killed. For spot number C-10, 3 of 10 simulation runs predicted slightly more trees killed than were observed and the other 7 predicted significantly fewer trees killed than were observed. If this underprediction is interpreted as meaning that spot C-10 behaved abnormally, and this spot is therefore removed from the validation data set, then the new observed number of trees killed is reduced to 220 and the new predicted total to 221.75, an overprediction of 0.8 percent. Spots C-13, C-14, and C-15 did not expand significantly after the initial observation. In the simulation, if a spot became inactive within 30 days, it was grown for 15 days and terminated. Evidence suggests that spots C-13, C-14, and C-15 did not expand for 15 full days after detection. Thus, the final predicted number of trees killed in these spots was higher than the observed number of trees killed.

These simulation results are especially encouraging when it is noted that the models were developed from data gathered in east Texas while the test data were collected in north Georgia.

Models for predicting southern pine beetle infestation growth and decline are useful in the development of regional SPB damage projection systems (Reed et al. 1980). Such systems assist planners and policy makers in developing regional programs of pest management and in allocating funds to carry out these programs.

Models of southern pine beetle spot growth and inactivity are also important to land managers in developing programs of prevention as well as direct suppression. Silvicultural manipulation of overstocked stands has been recommended to minimize the occurrence of SPB infestations (Hedden 1978b). The same practices should serve to reduce timber losses from summer spot growth during most years. When new spots are detected in early summer, immediate control is recommended for larger spots (100 or more active trees) as excessive timber losses may occur in even sparse stands. In moderate-size spots (20 to 100 active trees), high priority should be assigned to spots in dense stands. Small spots with less than 20 active trees should be given lowest priority. These spots, especially those without signs of fresh attacks, will probably be inactive in a few weeks with little or no additional timber loss.

LITERATURE CITED

Billings, R. F. 1979. Detecting and aerially evaluating southern pine beetle outbreaks--operational guides. South. J. Appl. For. 3:50-53.

Billings, R. F., and C. A. Kibbe. 1978. Seasonal relationships between southern pine beetle brood development and loblolly pine foliage color in east Texas. Southwest. Entomol. 3:89-95.

Coulson, R. N., F. P. Hain, and T. L. Payne. 1974. Radial growth characteristics and stand density of loblolly pine in relation to the occurrence of the southern pine beetle. Environ. Entomol. 3:425-428.

Cox, D. R. 1970. The analysis of binary data. 142 p. Chapman and Hall, London.

Daniel, C., and F. S. Wood. 1971. Fitting equations to data. 342 p. Wiley-Interscience, New York.

Dixon, W. J., and M. B. Brown, eds. 1979. BMDP-79: Biomedical computer programs P-series. 879 p. Univ. of California Press, Berkeley.

Gara, R. I. 1967. Studies on the attack behavior of the southern pine beetle I. The spreading and collapse of outbreaks. Contrib. Boyce Thompson Inst. 23:349-354.

Gara, R. I., and J. E. Coster. 1968. Studies on the attack behavior of the southern pine beetle III. Sequence of tree infestation within stands. Contrib. Boyce Thompson Inst. 24:77-86.

Hedden, R. L. 1978a. Host tree spatial pattern in southern pine beetle infestations. Southwest. Natural. 23:71-76.

Hedden, R. L. 1978b. The need for intensive forest management to reduce southern pine beetle activity in east Texas. South. J. Appl. For. 2:19-22.

Hedden, R. L., and R. F. Billings. 1979. Southern pine beetles: factors influencing the growth and decline of summer infestations in east Texas. For. Sci. 25:547-556.

Johnson, P. C., and J. E. Coster. 1979. Probability of attack by southern pine beetle in relation to distance from an attractive host tree. For. Sci. 24:574-580.

Ku, T. T., J. M. Sweeney, and V. B. Shelburne. 1976. Site and stand characteristics associated with southern pine beetle infestations in Arkansas. Ark. Farm Res. 24:2.

Lorio, P. L., Jr. 1968. Soil and stand conditions related to southern pine beetle activity in Hardin County, Texas. J. Econ. Entomol. 61:565-566.

Lorio, P. L., Jr. 1978. Developing stand risk classes for the southern pine beetle. 9 p. U.S. Dep. Agric. For. Serv., Res. Pap. SO-144. South. For. Exp. Stn., New Orleans, La.

Reed, D. D., R. F. Daniels, R. L. Hedden, H. E. Burkhart, and W. A. Leuschner. 1980. A regional southern pine beetle damage projection system. *In* Modeling of southern pine beetle populations: symposium proceedings. [Asheville, N.C., Feb. 1980.] F. M. Stephen, J. L. Searcy, and G. D. Hertel, eds. U.S. Dep. Agric. For. Serv., Tech. Bull. 1630. Comb. For. Pest Res. Develop. Prog., Pineville, La.

Seber, G.A.F. 1977. Linear regression analysis. 465 p. John Wiley and Sons, Inc., New York.

Schumacher, F. X., and T. S. Coile. 1960. Growth and yield of natural stands of the southern pines. 115 p. T. S. Coile, Inc., Durham, N.C.

Texas Forest Service. 1976. Texas forest pest activity 1974-1975 and Forest Pest Control biennial report. 19 p. Tex. For. Serv., Circ. 226. College Station.

LONG-TERM, REGIONAL PROJECTION OF SOUTHERN PINE BEETLE DAMAGES

David D. Reed, Harold E. Burkhart, and William A. Leuschner[1]

Abstract.--We made long-term projections of damages caused by southern pine beetle by incorporating an SPB-specific mortality component into the Timber Resource Analysis System (TRAS). Regional damages are simulated using variables available from the stand table projection used by TRAS to predict future forest resources. Options are available for examining various management strategies for controlling the southern pine beetle.

INTRODUCTION

In planning management activities to control southern pine beetle (SPB) (*Dendroctonus frontalis* Zimm.) damages, it is necessary to project probable long-term damages. Damages occurring without any control efforts and damages occurring with various control efforts should be projected and compared. The benefits gained by control efforts are the difference between damage levels occurring when the control measures are applied and those occurring if no control is attempted. Control effort costs can then be compared to projected benefits of those efforts in an economic analysis of control activities.

This discussion will be centered upon methods to project SPB-caused damages over long time periods (25 or more years) for a multicounty area. The program provides information to decision-makers developing long-term, regional pest management strategies rather than projecting consequences of management decisions for a particular spot at a particular time.

SYSTEM CHARACTERISTICS

Any system designed to project long-term damages must also incorporate changing forest conditions over that time period and account for the changes in the forest that occur as a result of both man's and the beetle's activity. Taking into account the changing forest is necessary because the forest characteristics of a region can be considered constant only if the object is to project short-term damage levels and/or to examine the consequences of specific types of control strategies to be applied to existing situations. In the long term, the conditions of the forests of a region are subject to change and the activity of the beetle can influence the changes.

The Timber Resource Analysis System (TRAS), developed by the U.S. Forest Service, projects long-term timber supply under various assumptions regarding removal rates and management practices (Larson and Goforth 1970, 1974). In the existing TRAS program, mortality rates are specified by the user and applied to each year of the projection. This study developed an SPB-specific mortality component to adjust total mortality to reflect control efforts and insect behavior.

TRAS

TRAS is a FORTRAN language computer program used by the Renewable Resource Evaluation Unit (formerly called Forest Survey) to make long-term timber inventory projections, among other things. A stand table projection method is used to project changes in the forest structure through time. In this method, the forests on a large acreage are classified according to stand and/or site characteristics such as species composition or site class. The stand type classifications are up to the user and may be as broad or as narrow as desired. The projections are then made separately for each stand type.

To run the program for a stand type, an estimate of the number of trees for each diameter class (in 2-inch increments) is entered. This information is available from the forest survey data collected periodically in each State.

---

[1] The authors are, respectively, Graduate Research Assistant, Professor of Forest Biometrics, and Associate Professor of Forest Economics, Virginia Polytechnic Institute and State University, Blacksburg.

The user also specifies removal, mortality, and ingrowth rates for each size class, as well as the volume per tree in each class. The program then calculates the change in the stand structure by applying these rates to each size class and determining the net change in the number of trees in the class in a year. A new stand table is computed, and, if desired, the process can be repeated. Users can request output, which contains the current inventory and the net growth, removals, and mortality of the year by 2-inch diameter classes, at the end of any year.

There are several options available to the user regarding removal and ingrowth rates that account for various types of forest management. However, once these initial rates and options have been entered, they cannot be changed during the projection period. Detailed information on the program and the options available can be found in Larson and Goforth (1970, 1974).

SOUTHERN PINE BEETLE MORTALITY

Originally, TRAS calculated annual mortality in each 2-inch diameter class by multiplying a user-supplied mortality rate by the number of live trees in the class. No effort was made to distinguish mortality totals by cause of the mortality. The methods discussed here estimate the amount of mortality due to the SPB. All other mortality is handled as before, by multiplying the number of live trees in each class by a mortality rate. This mortality rate can be a total mortality rate, as it is in the original TRAS program. In this case, the SPB mortality is calculated and subtracted from the total mortality, to leave mortality due to other causes. Another option is that the mortality rate represents non-SPB mortality. If so, the total mortality can be found by summing the SPB mortality and non-SPB mortality.

Southern pine beetle mortality estimation can be broken into two parts. First, the number of spots that occur in the entire acreage included in a run is estimated. Second, the growth of each spot is simulated and the number of trees killed in a year by the SPB is found. Volume killed is then found using the number of trees killed and a local volume table supplied by the user.

Estimating the Number of Spots

The number of spots occurring in the forest or stand type of interest is estimated by first finding the probability of an outbreak occurring in the stand type. There are two options in the program involving this probability. In the first option, the user supplies a single probability of stand attack for the stand type of interest. This probability remains constant for the entire projection period, acting as an average outbreak probability. In the second option, the probability of stand attack is found by using a model of the type described by Daniels et al. (1979). The outbreak probability is estimated by a logistic equation using stand, site, and/or insect variables. This equation takes the form

$$p = \frac{1}{1 + \exp(b_0 + b_1X_1 + b_2X_2 + \ldots + b_kX_k)}$$

where

p = the estimated outbreak probability

X_i = the *i*th variable associated with outbreak probability.

Daniels et al. (1979) developed equations for estimating outbreak probabilities that contain only stand and site variables such as age or basal area. These variables change slowly; thus, estimated outbreak probabilities do not change much from year to year. The number of spots occurring in a given region can vary greatly from year to year, however. So it appears that the true outbreak probabilities depend on more than stand or site variables. Efforts are underway to find variables that can account for the annual fluctuations in outbreak probabilities, but the efforts are restricted to using variables from TRAS or which are easily observed or predicted from year to year. One alternative is to include a function of the number of spots occurring in each of the previous 2 years as a predictor variable for the outbreak probability in the current year. If improved equations can be developed, they will be used when the system is calibrated for east Texas. Otherwise, the equations given by Daniels et al. (1979) will be used.

Once the outbreak probability has been determined for a stand type, the number of spots occurring in a year is estimated. This is accomplished by first finding the number of stands in the region and then stochastically testing each stand to determine if an outbreak will occur. The number of stands of a given type in the region is estimated by dividing the acreage in the stand type by the average size of a stand of the given type. The acreages of various stand types are available from periodic Forest Survey data and must be entered in TRAS whenever a projection is to be made. Data on average stand sizes of different timber types is now being collected by the Renewable Resource Evaluation Unit of the U.S. Forest Service in its periodic inventories of the forests of the Southeast (Knight 1978).

After the probability of outbreak, *p*, has been found and the number of stands estimated, each stand must be tested to determine if it contains an outbreak in the current year of simulation. To do this, a uniform (0,1) random variate is generated for each stand in the stand type of interest. If the uniform random variate is less than the probability of outbreak, an outbreak is judged to occur in that stand. If the random variate is greater than the probability of outbreak, an outbreak is not initiated and no mortality occurs in the stand as a result of SPB activity.

Simulating Spot Growth

If an outbreak is determined to occur in a stand, the growth of the spot is simulated using a spot spread model and a spot inactivity model (Hedden and Reed 1980). Once a stand has been identified as being attacked, the time of the year when the spot appears and the initial spot size are generated. The methods for doing this are identical to those described by Reed et al. (1980).

Briefly, the spot inactivity function predicts the probability of a spot becoming inactive within a 30-day period, given the number of trees at the beginning of the period. It is a logistic function with the form

$$p = \frac{1}{1 + \exp(-1.04 + 0.06\ AT)}$$

where

p = the estimated probability of a spot becoming inactive within the next 30 days

AT = the number of affected trees at the beginning of the 30-day period.

The spot spread model describes the natural logarithm of the number of trees killed per day as a function of the initial number of attacked trees, the mean stand d.b.h., total stand BA, and the number of spots per thousand acres of host type in the region in the year of interest. This model has the form

$$\begin{aligned} \ln(TK/D) = {} & 0.78099 + 0.96545\ \ln AT \\ & - 2.84669\ \ln DBH - 0.78786\ TBA/DBH^2 \\ & + 0.016914\ TBA + 0.55764\ POP \end{aligned}$$

where

$\ln(TK/D)$ = the natural logarithm of trees killed per day

$\ln AT$ = the natural logarithm of the initial number of attacked trees

DBH = the mean stand d.b.h. (inches)

TBA = the total BA of the stand (ft^2/acre)

POP = the number of spots per thousand acres of host type for the year being examined.

The variables needed for these models are either generated or are available in the stand table, which is annually updated by TRAS. The initial number of attacked trees is generated for the first 30-day period. If the spot exists for more than one period, the number of attacked trees is updated at the end of each 30-day period. This new number of attacked trees is used in the inactivity function and the spot spread model in the following simulation period. The mean stand d.b.h. and the total BA are available from the stand table carried by TRAS. The number of spots per thousand acres of host type (POP) presents a problem because in TRAS, projections must be made by stand type and cannot be made for all of the stand types of the region simultaneously. Thus, spots on contiguous, but different, stand types are unknown. There is an option in the program allowing the number of spots per thousand acres of host type in the region (POP), which includes the spots in all stand types, to be either a constant or estimated using the information available in a stand type for each year. If POP is given as a constant, it will represent an average value over the years.

If POP is to be calculated each year, the user must specify the proportion of the region's total number of spots that occur in the stand type of interest. This proportion is assumed to remain constant over time and can be estimated by simulating a large number of spots using a set of spot incidence equations as described earlier and the forest characteristics of the area. The number of spots occurring in the stand type in N years of simulation can be divided by the total number observed in the N years of simulation to estimate the desired proportion, that is:

$$p_i = N_i/N$$

where

p_i = average proportion of the total number of spots which occur in stand type i

N_i = the number of spots occurring in stand type i over N simulated years

N = the total number of spots occurring in the region in N simulated years.

The number of spots occurring in a year in the stand type of interest is multiplied by the reciprocal of this proportion to estimate the region's total number of spots. Dividing by the total acreage in the region gives an estimate of POP for use in the spot spread model:

$$POP \cong n_i/(p_i * ACRES)$$

where

n_i = the number of spots in stand type i

p_i the proportion of the total number of spots which occur in stand type i

ACRES = thousands of acres of host type in the region.

The number of trees killed for a year in the stand type is found by summing the number of trees killed in each spot over all spots. This total number of trees killed is then proportioned to all diameter classes larger than 4 inches in proportion to the number of living trees in each class. The number of trees killed in each diameter class is subtracted from the number of living trees in the class. After other mortality and removals have been subtracted and the ingrowth added, the resulting stand table is the inventory in the stand type at the start of the next year.

Control Options

We incorporated the artificial termination of spot activity into the system to represent control efforts. This treatment consists simply of not allowing a spot to expand for longer than a specified number of simulation periods. The specified number of periods until the spot is controlled represents the maximum length of time that would pass between detection and control of the spot. A spot is considered controlled if no more trees are killed in the spot in the year. Spots terminating naturally prior to the end of the control period are allowed to terminate as if no control efforts were underway. This gives a conservative estimate of the control effects since spots not naturally terminating prior to the end of the control period terminate on the last day of the period. In practice, spots would be controlled at various times within the control period and not just on the last day. This method of representing control does not model any particular control method, but rather it measures the impact of any method which is 100 percent effective in not allowing the spot to expand any longer. The effect of controlling a spot within, say, 30 days after detection can be compared to no control or controlling the spot within 60 or 90 days after detection.

The maximum length of time the spot will be allowed to expand before it is artificially terminated can be specified for all spots in the simulation or just those occurring at certain times of the year. The user can request that control efforts initiate with spots beginning in any simulation period and cease with spots beginning in any later period. Thus, it is possible to examine the controlling of only those spots occurring before, say, June 1 and allowing other spots to expand naturally. Also, for example, it is possible to control spots beginning between March 1 and August 1 and allow other spots to expand as they will.

DISCUSSION

If the forests of a region consist of several distinctive stand types, TRAS must be run for each stand type to make long-term projections for the region. This is true whether or not the SPB mortality component is in effect. The finer the distinctions made between stand types, the more reliable the projections from the SPB mortality component will be. However, the cost of acquiring the data and running the program will increase as the number of stand types increases. The user must ultimately decide how to divide up the region based on data availability, precision requirement for estimation, and economic consideration. Unfortunately, the more reliable the projection, the greater the data requirements and the greater the cost.

When the system has been calibrated for a specific region and has been applied to that region, there will undoubtedly be portions of the system identified where improvement or refinement is needed. Until the system is in practical use, it is difficult to identify the areas that need modification. But once the system is in operation and its weaknesses are identified, data can be collected, if they are not already available, for model improvement. Many of the models in the SPB mortality component were developed from data collected in only 2 or 3 years of observations. Improved estimates will undoubtedly result when more extensive data become available.

LITERATURE CITED

Daniels, R. F., W. A. Leuschner, S. J. Zarnoch, H. E. Burkhart, and R. R. Hicks. 1979. A method for estimating the probability of southern pine beetle outbreaks. For. Sci. 25:265-269.

Hedden, R. L., and D. D. Reed. 1980. Southern pine beetle: factors influencing the growth and decline of summer infestations. *In* Modeling southern pine beetle populations: symposium proceedings. F. M. Stephen, J. L. Searcy, and G. D. Hertel, eds. [Asheville, N.C., Feb. 1980.] U.S. Dep. Agric. For. Serv., Tech. Bull. 1630. Comb. For. Pest Res. Develop. Prog., Pineville, La.

Knight, H. A. 1978. Sizes of timber stands in the piedmont of South Carolina. U.S. Dep. Agric. For. Serv., Res. Note SE-276. Southeast. For. Exp. Stn., Asheville, N.C.

Larson, R. W., and M. H. Goforth. 1970. TRAS--a computer program for the projection of timber volume. 24 p. U.S. Dep. Agric. For. Serv., Agric. Handb. 377.

Larson, R. W., and M. H. Goforth. 1974. TRAS--a timber volume projection model. 15 p. U.S. Dep. Agric. For. Serv., Tech. Bull. 1508.

Reed, D. D., R. F. Daniels, R. L. Hedden, H. E. Burkhart, and W. A. Leuschner. 1980. A regional southern pine beetle damage projection system. *In* Modeling southern pine beetle populations: symposium proceedings. [Asheville, N.C., Feb. 1980.] F. M. Stephen, J. L. Searcy, and G. D. Hertel, eds. U.S. Dep. Agric. For. Serv., Tech. Bull. 1630. Comb. For. Pest Res. Develop. Prog., Pineville, La.

MODELS FOR SOUTHERN PINE BEETLE HOST DYNAMICS

Harold E. Burkhart and Richard F. Daniels[1]

Abstract.--We developed stand models for loblolly pine that use individual trees as the basic growth unit. These models (one for planted stands, the other for seeded stands) "grow" tree diameters and heights annually as a function of tree size, site quality, competition from neighbors, and a stochastic component representing genetic and microsite variabilty. We then determined individual tree mortality stochastically through Bernoulli trials. Subroutines were added to each model to simulate the effects of selected silvicultural practices. These models provide a method for evaluating a wide range of silvicultural treatments that might be used to help control southern pine beetle (SPB) population levels and have the potential to be linked with SPB population models.

INTRODUCTION

Stand models have been used extensively for production forecasting and evaluation of silvicultural alternatives. More recently, there has been increasing interest in the use of stand models when assessing the impact of catastrophic events such as southern pine beetle (*Dendroctonus frontalis* Zimm.) infestations. Most stand models developed in the past provide little detail regarding stand structure and are limited to a very small number of treatment alternatives. When looking ahead at the wide range of silvicultural treatments that might be used to help control SPB population levels and the potential for linking stand models with SPB population models, we concluded that an approach with more detailed information about the size distributions, growth, and mortality of individual trees in stands would be appropriate. Consequently, we developed individual tree-based models for loblolly pine (*Pinus taeda* L.) stands. A model was developed and tested for planted stands (Daniels and Burkhart 1975) first and later extended to seeded stands (Daniels et al. 1979b). The purpose of this paper is to discuss the overall structure and application of these two loblolly pine stand models. Details on the derivation of components of the models, as well as complete FORTRAN source listings, are contained in Daniels and Burkhart (1975) and Daniels et al. (1979b).

PLANTED STAND MODEL

The plantation model, PTAEDA (Daniels and Burkhart 1975), consists of two main subsystems--one dealing with the generation of an initial precompetitive stand and another with the growth and dynamics of that stand. Management subroutines were added to this framework to simulate site preparation, fertilization, and thinning.

Initial Stand Generation

A number of options are available for creating rectangular spatial patterns in PTAEDA. Users may specify the distance between trees and between rows in a conventional manner (e.g., 6 ft × 8 ft, 6 ft × 12 ft), allowing the program to compute the planted number of trees. Alternatively, the number of trees may be specified along with the ratio of planting distance to row width (e.g., 3:4, 1:2). If this ratio is omitted, square spacing is assumed.

From this information, a plot of 100 trees is generated with ten rows of ten trees each. A fixed number of trees was chosen rather than a fixed plot size so that, in effect, plot size would increase with decreasing density.

From this point, the juvenile stand is advanced to an age where intraspecific competition begins. Strub, Vasey, and Burkhart (1975) found that over a wide range of sites and planting densities, the age at which average diameter in

---

[1] The authors are, respectively, Professor and Graduate Research Assistant, Dept. of Forestry, Virginia Polytechnic Institute and State Univ., Blacksburg.

plantations first differs from that of open-grown trees is consistently 1 year after Crown Competition Factor (CCF) reaches 100. This relationship is used to compute the end of the precompetitive growth stage. CCF is predicted as a function of surviving number of trees per acre (TS), height of the dominant stand (HD) (average height of dominant and codominant trees), and age, using the equation developed by Strub et al. (1975). This equation is evaluated each year after age 5 until CCF is greater than or equal to 100. HD is predicted using the site index curves of Burkhart et al. (1972), while TS is estimated from the survival function of Smalley and Bailey (1974).

At this point the predicted juvenile mortality is assigned at random. Individual tree dimensions are then generated for the residual stand.

Diameter at breast height (d.b.h.) is generated from a two-parameter Weibull distribution with a cumulative distribution function as follows:

$$F(y) = 1 - e^{-ay^b} \qquad 0 < y < \infty$$

The inversion technique was used for generating random variates from this distribution. Parameters *a* and *b* are estimated from minimum and average d.b.h. as follows (Strub and Burkhart 1974):

$$b = \frac{\ln(TS/10)}{\ln DAVE - \ln DMIN}$$

$$a = \left[\frac{\Gamma(1 + 1/b)}{DAVE}\right]^b$$

where

DMIN = minimum d.b.h. (inches)

DAVE = average d.b.h. (inches)

TS = surviving number of trees per acre.

DMIN and DAVE are predicted from stand age, HD, and TS.

Height is generated for each tree based on a prediction equation involving d.b.h., HD, TS, and age. Crown length is then calculated as total height minus clear bole length, where clear bole length is a function of total height, d.b.h., TS, and age.

After assigning dimensions to each tree, the competition effect of neighboring trees is calculated as:

$$CI_i = \sum_{j=1}^{n} (D_j/D_i)/DIST_{ij}$$

where

D = d.b.h.

DIST = distance between subject tree *i* and *j*th competitor

CI_i = Competition Index of the *i*th tree

n = the number of neighbors "in" with a BAF10 sweep centered at the *i*th tree

Growth and Dynamics of Stand

After generation of the precompetitive stand, competition is evaluated and trees are grown individually on an annual basis. In general, growth in height and diameter is assumed to follow some theoretical growth potential. An adjustment or reduction factor is applied to this potential increment based on a tree's competitive status and vigor, and a random component is then added representing microsite and/or genetic variability.

Height Growth

The potential height increment for each tree is the change in average height of the dominant and codominant trees, obtained as the first difference with respect to age of the following expression, transformed from the site index equation in Burkhart et al. (1972):

$$HD = SI\ 10^{b(1/A - 1/25)}$$

where

HD = average height of dominant stand (feet)

SI = site index (feet) at base age 25 years

A = stand age (years)

A tree may grow more less than this potential, depending on its individual attributes.

We believe that crown ratio is an expression of a tree's photosynthetic potential. So we used it in conjunction with competition index in the adjustment factor for height growth. The final form of the height growth adjustment was:

$$(b_1 + b_2 CR^{b_3}\ e^{-b_4 CI - b_5 CR})$$

where

CR = crown ratio

CI = competition index

b_i = constants to be estimated from data

An equation relating actual and potential height increment by this factor was fitted by nonlinear least squares. It can be seen that as competition increases, the realization of potential height growth decreases. Holding competition index constant, the adjustment factor has a maximum value when crown ratio is roughly 0.25. It gradually decreases with increasing crown ratio, but decreases rapidly as crown ratio approaches zero. It should be noted that the height growth adjustment factor may attain values > 1, so that, under favorable conditions, individual tree height growth may be greater than the change in average dominant stand height. A normally distributed random component is added to the final height growth determination.

Diameter Growth

The maximum d.b.h. attainable for an individual tree of given height and age was considered to be equal to that of loblolly pines grown in the open. We developed an equation describing this relationship from open-grown tree data:

$$D_0 = b_0 + b_1 H + b_2 A$$

where

D_0 = open-grown d.b.h. (inches)

H = total tree height (feet)

A = age from seed (years)

The first difference of this equation with respect to age was thought to represent a maximum potential diameter increment:

$$PDIN = b_1 \, HIN + b_2$$

where

$PDIN$ = potential diameter increment (inches)

HIN = observed height increment (feet)

This potential diameter increment is adjusted by a reduction factor of the form

$$(b_1 + b_2 CL^{b_3} e^{-b_4 CI})$$

where CI represents competitive effects and CL (crown length in feet) is a measure of photosynthetic potential. The multiplier decreases with increasing competition and increases with increasing crown length. An equation relating actual and potential diameter growth by this factor was developed using nonlinear least squares. A normally distributed random component is added to diameter growth determinations.

The inclusion of measures of photosynthetic potential in the above models plays a key role in determining thinning response. Other investigators have included only competitive effects in such adjustment factors. However, when a tree is released by removing neighboring trees, its response will depend not only on the reduction in competition for resources but also the potential it has for using those resources. Both crown length and crown ratio reflect this potential.

Crown length is modified each year as the difference between height increment and change in clear bole length. Clear bole length is predicted annually as a function of height, d.b.h., age, and number of trees per acre.

Mortality

We assumed the probability that a tree remains alive in a given year to be a function of its competitive stress and individual vigor as measured by photosynthetic potential. Accordingly, we developed an equation describing the probability using nonlinear least squares and methodology proposed by Hamilton (1974) for fitting probabilities to dichotomous (0,1) data. The probability of survival equation took the form

$$PLIVE = b_1 CR^{b_2} e^{-b_3 CI^{b_4}}$$

where PLIVE = probability that a tree remains alive and CR and CI are as defined previously.

PLIVE increases with increasing crown ratio and decreases with increasing competition. When crown ratio is 1 and competition index is 0, PLIVE takes on its maximum value, b_1 (1.08635). That this "probability" is > 1 is of no practical concern in predicting PLIVE under stand conditions.

In PTAEDA, survival probability is calculated for each tree and used in Bernoulli trials to determine annual mortality stochastically. The calculated PLIVE is compared to a uniform random variate between 0 and 1. If PLIVE is less than this generated threshold, the tree is considered to have died.

Management Routines

After PTAEDA was initially developed for old-field, unmanaged plantations, we added management subroutines to simulate the effects of site preparation, fertilization, and thinning.

Site Preparation

The efficiency of a site preparation method is modeled as the degree to which a cutover site approaches old-field conditions. We assumed that growth reductions on cutover land were due solely to competing vegetation since changes in site quality caused by site preparation practices could be described by initially specifying an appropriately adjusted site index. Under these assumptions, we developed a subroutine including a competition adjustment factor, which is multiplied times both competition index and trees per acre to reflect the increased number of stems on cutover land and an age at which the stand will be released to old-field conditions. The user must specify the number of loblolly pine equivalent competitors and the age at which the stand will be released to old-field conditions.

Fertilization

Response to fertilizer treatments is simulated by increasing the site index. A site adjustment factor acts as a multiplier on site index for fertilized stands.

Of course, the true nature of fertilizer response depends on many factors, such as the element applied, the application rate, mode of application, time of year of application, physiographic province, drainage, and soil texture, origin, and fertility. We did not have enough data to aggregate these effects and their interactions into a reliable model of fertilization response. Thus, it was not possible to calibrate site adjustment factors with actual fertilizer treatments. Instead, three parameters were included which specify, respectively, the maximum response in site quality, the length of time (from application) in years to attain this maximum response, and the total length of time of the response. Site index increases linearly from the age of fertilization until maximum response is reached. From that time, the site adjustment factor decreases linearly until site quality, at the end of the response period, is the same as the original site quality prior to fertilization. Linear functions were chosen as initial approximations in the absence of actual data. Users must specify values for the maximum response, length of time to attain this maximum, and total length of time of the response.

Thinning

A user may thin by rows, from below, or by a combination of these methods by specifying the thinning type. Thinning from below includes two options--thinning to an upper diameter limit, or to a specified basal area. In either case, a lower diameter limit may be specified, below which trees will not be removed. When a combination of thinning types is used, the row thinning occurs first and the residual stand is then thinned from below as specified.

Testing and Validating the Model

Validation of simulation models is a difficult problem, involving many practical, theoretical, and philosophical complexities. The testing and validation of PTAEDA was largely restricted to empirical comparisons and analysis of residuals with published and historical data.

First, PTAEDA was used to generate and grow stands over a wide range of stand conditions and silvicultural treatments. These trials gave reasonable results, suggesting that logical and functional relationships were generally in good order. However, we saw an illogical height response due to thinning in these initial trials. Consequently, we derived an expression for maximum height growth from plot data and incorporated it into the model. Subsequent trials showed more realistic thinned stand volumes. Further validation of the thinning option was pursued by comparing PTAEDA-generated thinning yields with those published by Coile and Schumacher (1964) and by Goebel, Warner, and VanLear (1974). These comparisons indicated that the refined thinning option works satisfactorily.

Yield predictions from PTAEDA were originally evaluated with the plot data of Burkhart et al. (1972). (NB: These data were used in computation of some of the components of PTAEDA and are thus not a completely independent data set.) In general, plot yields predicted by PTAEDA were in close agreement with the observed values. Subsequently, an evaluation has been conducted with independent plot data (Daniels, Burkhart, and Strub 1979a). This test indicated that PTAEDA provides accurate estimates of merchantable cubic-foot yield.

SEEDED STAND MODEL

The basic modeling philosophy and framework used by Daniels and Burkhart (1975) for loblolly pine plantation was adopted in constructing model components for seeded loblolly pine stands. In this approach, stand development is divided into two stages. The first stage involves the generation of an initial stand of trees at the onset of competition. The second deals with the annual growth and development of that stand by simulating the growth, mortality, and competitive interaction of individual trees. Added to this structure are routines to simulate intensive management practices, such as thinning and fertilization.

In this discussion of the seeded stand model (Seed-PTAEDA), we will discuss only the aspects unique to quantifying components of seeded stands. Many of the components are identical to those of the planted stand model and will not be reiterated here.

Initial Stand Generation

The initial stand generation stage involves the complete specification of the stand spatial pattern and size distributions, including the assignment of individual tree coordinate locations, d.b.h., height, and crown length. Realistic specification of early stand structure is crucial to subsequent simulation of stand dynamics. The aggregated spatial patterns found in seeded stands are much more complex to model than the simple rectangular patterns of plantations. Size distributions are also more varied. Daniels and Burkhart (1975) employed a prediction of the age at which competition begins to affect stand structure in plantations, to determine the age to generate tree sizes and to begin annual growth computations. This approach was questioned for seeded stands due to the higher degree of variability in tree sizes and spatial relationships in these stands. These considerations prompted intensive investigations into methods for realistically generating size and spatial relationships in young seeded stands.

Spatial Patterns

Daniels (1978) used point-to-plant distance methods and Pielou's (1969) index of nonrandomness to quantify spatial patterns in 40 even-aged loblolly pine stands of seed origin, ranging from 5 to 12 years old. His work indicated that aggregated, or clumped, patterns were prevalent in all seeding methods studied, including natural (old-field), seed tree, broadcast, and aerial methods. Further, nonrandomness index values were not found to be related to seeding method or stand attributes such as age, site index, or stand density.

Distance frequencies were further described by Daniels (1978) using distribution methods. By using squared distance as the variate, he derived a form of the Pearson type XI distribution from the aggregated distribution proposed by Eberhardt (1967). The Pearson type XI distribution fit observed values well and was used as a spatial model for seeded stands. Using this distribution, we developed a routine to generate seeded stand spatial patterns, given stand density and nonrandomness index values.

Size Distributions

After generating the initial stand spatial pattern and assigning tree coordinates, tree sizes are assigned. We used a two-parameter Weibull function, with methods akin to those used in the planted stand model, to model the diameter distribution of the initial stand.

A fixed age of 10 was chosen for generating the initial stand because of the difficulties involved with determining an age when intraspecific competition begins. We think that competition already has begun to affect growth at age 10 in typical seeded stands. To reflect this influence, initial diameters are assigned as a function of competition at age 10. For each tree in the stand, d.b.h. is temporarily set equal to the average diameter and the competition index is evaluated to provide an index of tree growing space. Actual diameters are then generated, sorted largest to smallest, and assigned to tree locations so that the largest d.b.h. is associated with the smallest competition value, etc. Correlations between tree sizes and spatial measures in young seeded stands were shown by Daniels (1978) to be negligible, but these methods should ensure logical spatial-size relationships.

Total height (H) is assigned for each tree using a prediction equation based on diameter at breast height (d.b.h.), height of dominants and codominants (HD), surviving number of loblolly pine trees per acre (TS), and age (A). Crown length is determined as total height minus clear bole length (CBL) where CBL is predicted as a function of H, d.b.h., TS, and A.

Stand Growth and Development

After generation of the juvenile stand, competition is evaluated and trees are grown individually on an annual basis. As before, growth in height and diameter is assumed to follow some theoretical growth potential. An adjustment of reduction factor is applied to this potential increment based on a tree's competitive status and vigor, and a random component is then added representing microsite and/or genetic variability.

Height increment, diameter increment, and mortality models in Seed-PTAEDA are the same as those in the plantation model.

Management Routines

Subroutines to simulate hardwood control, fertilization, and thinning are included in Seed-PTAEDA. These subroutines are similar in structure and operation to their counterparts in the plantation model PTAEDA.

Initial Tests

We performed initial tests of the seeded stand model. These tests indicated that the overall model structure appears adequate for simulating seeded stands, but complete calibration will require further data on growth and survival of individual trees. Data requirements and calibration procedures are discussed in Daniels et al. (1979b).

APPLICATIONS

The two models described offer detailed information for analyzing growth and dynamics of loblolly pine stands over a wide range of regeneration and cultural alternatives. These models may be incorporated into projection systems to estimate regional SPB losses. By projecting host dynamics, given estimates of SPB incidence and severity for different stand conditions, we could estimate expected SPB losses. Because of the flexibility of the growth models for simulating various cultural regimes, proposed silvicultural programs aimed at reducing SPB losses can be evaluated vis-a-vis current practices.

Because these stand models incorporate the spatial patterns and dimensions of individual trees, they may be useful in the study of SPB populations and SPB/host interactions at the tree and stand level. SPB population and behavior models that use intertree distances or measures of tree stress and vigor could be tested and linked with the PTAEDA models, thereby incorporating host dynamics. Such a link would provide an opportunity to study relationships between SPB population levels and the future host dynamics for a wide range of conditions.

LITERATURE CITED

Burkhart, H. E., R. C. Parker, M. R. Strub, and R. G. Oderwald. 1972. Yields of old-field loblolly pine plantations. 51 p. FWS-3-72. Virginia Polytechnic Inst. and State Univ., Blacksburg.

Coile, T. S., and F. X. Schumacher. 1964. Soil-site relations, stand structure, and yields of slash and loblolly pine plantations in the southern United States. 296 p. T. S. Coile, Inc., Durham, N.C.

Daniels, R. F. 1978. Spatial patterns and distance distributions in young seeded loblolly pine stands. For. Sci. 24:260-266.

Daniels, R. F., and H. E. Burkhart. 1975. Simulation of individual tree growth and stand development in managed loblolly pine plantations. 69 p. FWS-5-75. Virginia Polytechnic Inst. and State Univ., Blacksburg.

Daniels, R. F., H. E. Burkhart, and M. R. Strub. 1979a. Yield estimates for loblolly pine plantations. J. For. 77:581-583, 586.

Daniels, R. F., H. E. Burkhart, G. D. Spittle, and G. L. Somers. 1979b. Methods for modeling individual tree growth and stand development in seeded loblolly pine stands. 50 p. FWS-1-79. Virginia Polytechnic Inst. and State Univ., Blacksburg.

Eberhardt, L. L. 1967. Some developments in distance sampling. Biometrics 23:207-216.

Goebel, N. B., J. R. Warner, and D. H. VanLear. 1974. Periodic thinnings in loblolly pine stands: growth, yield, and economic analysis. 11 p. Clemson For. Res. Ser. No. 28. Clemson Univ., Clemson, S.C.

Hamilton, D. A. 1974. Event probabilities estimated by regression. 18 p. U.S. Dep. Agric. For. Serv., Res. Pap. INT-152. Intermountain For. Range Exp. Stn., Ogden, Ut.

Pielou, E. C. 1969. An introduction to mathematical ecology. 286 p. John Wiley and Sons, Inc., New York.

Smalley, G. W., and R. L. Bailey. 1974. Yield tables and stand structure for loblolly pine plantations in Tennessee, Alabama, and Georgia highlands. 81 p. U.S. Dep. Agric. For. Serv., Res. Pap. SO-96. South. For. Exp. Stn., New Orleans, La.

Strub, M. R., and H. E. Burkhart. 1974. Approximating forest diameter distributions using the Weibull density function. (Abstr.) Va. J. Sci. 25:119.

Strub, M. R., R. B. Vasey, and H. E. Burkhart. 1975. Comparison of diameter growth and crown competition factor in loblolly pine plantations. For. Sci. 21:427-431.

ATTACK:EMERGENCE RATIO AS AN INDICATOR OF AREA SOUTHERN PINE BEETLE POPULATION TRENDS AND EXPECTED TIMBER MORTALITY IN THE PIEDMONT OF GEORGIA

George W. Ryan, William A. Carothers, Gordon E. Moore, and Helen Bhattacharyya[1]

Abstract.--The use of attack:emergence (A:E) ratios to predict southern pine beetle (*Dendroctonus frontalis*) population trends and as a factor in a model to predict related timber mortality has proven effective in past studies on individual spots. This study represents an expansion of the methodology to predict insect population trends and expected timber mortality on areas of 826 acres. Data from 77 southern pine beetle spots in 39 sample areas have been collected and are currently being analyzed. This data from the Piedmont of Georgia will be used to develop (on 26 sample areas) and validate (on the 13 remaining areas) a linear regression model that predicts southern-pine-beetle-related timber mortality from June through October. Population trends will be predicted from A:E ratios and evaluated by using aerial photography and ground sampling.

INTRODUCTION

It has become clear that forest managers need to be able to predict accurately the population trends and expected timber mortality associated with damaging forest insects. The amounts of money budgeted for suppression projects and determining control priorities point up our sense of urgency on this matter.

In the past, the basis for southern pine beetle (*Dendroctonus frontalis* Zimm.) population trend predictions ran the gamut from "gut feelings" of the evaluator to elaborate and time-consuming considerations of the many variables, real and often imagined, that determine the ebb and flow of the population. The interactions of parasites and predators on the SPB population, as well as climatic influences and site-stand conditions, have been considered.

With the advent of the Expanded Southern Pine Beetle Research and Applications Program (ESPBRAP), the development of predictive systems and models accelerated. Many different, and at times opposing, approaches have been taken. The approach to the problem is of little consequence as long as it is based on factual evidence and the ultimate goal of consistently accurate predictions is reached.

One such approach is the use of ratio estimates. Researchers have investigated a number of ratios, including emergence/attack, attack/emergence, emergence/egg, and a variety of similar comparisons, for use in predicting SPB population trends. The main advantage in using this kind of predictive tool is that the ratios are fairly easy to determine. To date the most promising appears to be the ratio of attack to emergence (Moore 1978 and Moore et al. 1979 unpublished).

Moore's methodology compares the number of attacking adults to the brood which subsequently emerge, i.e., the attack emergence (A:E) ratio of a 3.1 dm^2 bark sample. A prediction of spot growth or decline is then made based on the calculated A:E ratio. (If necessary, several secondary factors may be incorporated in conjunction with the A:E ratio.) This methodology was used operationally for 2 years on declining populations (Morris 1975 and 1976). The results of a study of 22 SPB spots in North Carolina indicate that predictions made using the A:E ratio compared favorably (average: 95 percent with the actual trends) (Hain 1979 unpublished). We must emphasize that until our study, only declining populations in individual spots served as samples on which predictions and evaluations were made.

---

[1] The authors are, respectively, Statistician, USDA Forest Service, Southeastern Area, State and Private Forestry, Atlanta, Ga.; Entomologist, USDA Forest Service, Aerial Survey Team, Southeastern Area, State and Private Forestry, Doraville, Ga.; Entomologist, USDA Forest Service, Southeastern Forest Experiment Station, Research Triangle Park, N.C.; and Statistician, USDA Forest Service, Southeastern Forest Experiment Station, Research Triangle Park, N.C.

Because of the consistently accurate predictions which have been made using Moore's methodology, we initiated our study to (1) determine if Moore'e methodology could be modified to successfully predict SPB population trends on an areawide basis, and (2) develop and validate an area model to predict expected timber mortality (SPB-related) during the period of June through October.

PROCEDURES

Spot Selection

The results of routine aerial detection surveys conducted by the USDA Forest Service Aerial Survey Team (Carothers 1979 and Dull 1979) indicated an expanding southern pine beetle population in the Georgia Piedmont. In particular, the Oconee National Forest, Hitchiti Experimental Forest, and Piedmont National Wildlife Refuge experienced an increase in the numbers and sizes of spots. Largely because of Federal ownership, we sought and gained permission to conduct our study on these areas.

True color aerial photography (9" × 9" format) at a scale of 1:8,000 was obtained from flights conducted during late May and early June of 1979. Initial photo interpretation delineated areas of dead and dying pines. A probability proportional to size (PPS) sampling scheme was employed to select four spots in each sample area of 826 acres (approximately the area covered by one aerial photo at a scale of 1:8,000).

A sampling scheme that one might be tempted to use within each area is stratified random sampling, in which the stratification is by level of intensity, or spot size. However, stratification within an area is not appropriate, because sampling within an area cannot be sufficiently intensive. The structure of our areas negates the use of stratification, but it is still important to maintain the area concept in the model. That is, the model is supposed to be developed to apply to geographic units (areas).

Since the level of infestation is proportional to spot size, PPS sampling can be effectively used. This would be tantamount, or at least analogous, to stratifying by level of infestation. Small spots show a greater tendency to collapse than larger ones (Hedden and Billings 1979). Therefore, it is appropriate to use a sampling scheme where spots are selected with unequal probability.

The purpose of an unequal probability sampling scheme is an increase in the precision of the estimate. A simple random sample of spots within areas could be used, but the precision of the resulting estimators would in all likelihood be inferior to stratified random sampling. And as remarked above, stratification is not feasible within an area.

Since ratio estimates are going to be used for many of the estimates, the increase in precision by use of PPS sampling compared with any equal probability sampling or stratified sampling may be considerable (Cochran 1977).

We selected four spots in each area in the event that some agent other than southern pine beetle (*Ips*, fire) was responsible for the pine mortality or the spot was inactive. Only two spots per area were actually sampled. Our initial goal was to sample 90 spots in 45 areas. Due to constraints of time and the land managers, only 77 spots in 39 areas were sampled (in one area only one spot was sampled).

Data Collection

Ground crews visited spots within each sample area in the priority designated by the PPS sampling scheme, using aerial photos as maps. The crews determined the cause of the pine mortality in each spot. If SPB was the cause, the crews determined the number of active trees (those containing SPB brood or attacking adults by chipping and examining the bark at breast height. Each active tree was marked with paint and tallied. All vacated trees (those from which all SPB brood had emerged and which contained no attacking adults) were also tallied. An estimate of number of freshly attacked (containing only attacking adults) was recorded.

The crews measured total basal area and pine BA 6 m in front of the advancing head of the spot. If the workers found more than one active head, they took basal area measurements in front of each.

One bark sample (3.1 dm^2) was removed from two to five recently vacated pines (no SPB brood remaining, but with larval galleries intact) at breast height. Five samples per spot is optimum, but in many cases fewer than five were collected. Each bark sample was tagged for identification, placed in a plastic bag, and transported to our temporary headquarters.

Field A:E ratios were determined by counting the total number of holes on the outside of the bark, subtracting the sum of attack holes and air holes from the total, and applying the number of attack holes to this number of emergence holes:

$$A{:}E = \frac{\text{No. attack holes}}{\text{Total no. holes} - (\text{no. attack holes} + \text{no. air holes})}$$

Laboratory A:E ratios were determined by X-raying each sample and determining the number of attacks, air holes, emergences, living brood still in the sample, dead brood, and the cause of death if known (parasite, predator, or disease):

$$A{:}E = \frac{\text{No. attacks}}{\text{No. SPB emerged} + \text{no. healthy SPB brood in sample}}$$

The field and laboratory A:E ratios will be compared, but trend predictions will be made only from laboratory A:E ratios.

Further photo interpretation was necessary to determine the total number of infested trees per sample area (based on crown color), acres of susceptible host type ($\geq$ 25 percent pine composition) per area, and acres of infested pine per area. This data will be considered as inputs in the development of the model to predict expected timber mortality.

In October, we began the second phase of the study. Again, aerial photographers surveyed the Oconee National Forest, Piedmont National Wildlife Refuge, and Hitchiti Experimental Forest. These photos are currently being interpreted to determine the subsequent tree mortality since the first flight in June. This data will be used to determine the accuracy of our predictions of trend and to evaluate the timber mortality model.

Upon completion of the second photography mission, the field crews revisited 76 of the sample spots (one spot could not be relocated). In each spot the number of additional pines killed by SPB since the first ground sampling was recorded. Volume measurements were collected on 10 representative trees in each spot in the event that we might need to determine mortality on a volume rather than a tree basis.

STATISTICAL ANALYSIS

Model

Definition of Model

The model being developed concerns the prediction of N_2/N_1; that is, the ratio of subsequent mortality (additional trees killed) between the time of predictions and time of evaluation to the number of infested trees at the time of prediction. The model is in the form

$$N_2/N_1 = b_0 + b_1X_1 + b_2X_2 + b_3X_3 + b_4X_4 + b_5X_5$$

where N_1 and N_2 have been previously defined and the independent variables are defined for each area as follows:

X_1 = mean E:A ratio,

$X_2 = p_s\,(1 - p_s)\,A_s$, where

p_s = ratio of the number of acres of infested land in the area to the number of acres of susceptible host type in the area,

A_s = size (in acres) of the area,

X_3 = number of spots/100 acres of susceptible host type,

X_4 = mean basal area,

X_5 = mean number of fresh attacks;

and where $b_0, b_1, \ldots, b_5$ are the regression coefficients.

Rationale for Using N_2/N_1, as Dependent Variable in the Model

The ratio was used (instead of mean per unit) because ratio estimators are superior to mean per-element estimators if the two variables making up the ratio are highly correlated. In stratified random sampling, the mean per element may be of poor precision if the means per unit vary little from spot to spot. A ratio estimator in which N_1 is the auxiliary variate will have greater precision. Also, the use of a ratio estimator in which the denominator is proportional to spot size will accomplish, in part, stratification by level of intensity of infestation.

Note that the units of measurement of both N_1 and N_2 are trees; therefore, the ratio is dimensionless (similar to a coefficient of correlation). The quantity, although computed from spot data, applies to the total area by virtue of being divided by N_1. Hence, no inflating or "blowup" factor is needed.

Method of Computing A:E Ratio for Spot

The average of the A:E ratios for the sampled trees in each spot is used as the A:E ratio for the spot. This amounts to use of a separate ratio estimator instead of a combined estimator, which would have been the ratio of overall attack to overall emergence. Even though combined ratio estimators may be appropriate statistically, since the sample size within each spot is not large enough to apply separate ratio estimators, the separate estimator is valid for biological reasons. The number of trees per spot being sampled may not be large enough to apply the variance formulas for separate ratio estimators. This does not mean the separate estimator cannot be used. The small sample size may prevent any hypothesis testing concerning the A:E ratio, but the main interest lies in the estimation of N_2/N_1, not A:E ratio.

The mean A:E ratio for the area is the average of the A:E ratios of the two spots sampled.

Estimating Number of Freshly Attacked Trees

Since freshly attacked trees are not directly detectable on aerial photography, ground data from the two spots sampled per area is used to estimate the number of fresh attacks. We are doing this by means of photo interpretation factors being developed using the data from the ground checks. A factor is computed for each area and applied to the total number of infested trees in the entire area to obtain an adjusted number to be used in the model development. This is done for both N_1 and N_2.

Variable Selection and Model Validation

If some terms do not contribute significantly to the model's effectiveness, as determined by appropriate statistical analyses, they will be deleted. Transformations will be considered depending on the nature of the data. Hopefully, the simplest but most effective equation for predicting expected timber mortality will be revealed.

In order to validate the model, the 39 study areas have been divided into three blocks of 13 areas each, NE, NW, and SW. The model will be developed using two of the blocks and tested by use of the third. That is, the model will be validated on the areas of the third block by comparing the values of N_2/N_1 it gives with the actual values measured.

The model will be predictive in the sense that it may be used in a new area of the Georgia Piedmont with the constants developed. By using the third block of land for model validation, we will test the hypothesis that the model can be used in new areas.

Applicability and Extension of Model

After the evaluation period, the results of the study will be analyzed and reported. We will assess the practicality of using the A:E ratio as a guideline for SPB management decisions. If the results indicate that use of the A:E ratio is accurate for areawide prediction of expected timber mortality in the Georgia Piedmont, this technique should be tested in other geographic areas.

An extension of the design to a larger block of land (e.g., 100,000 acres) could be handled by means of a two-stage sampling procedure in which the primary units (first stage) would be the "areas" as discussed previously, except that only a portion of all the areas in the block would be selected. The areas would be chosen by some unequal probability scheme with probabilities proportional to percent host type (i.e., analogous to stratified random sampling). The model development here would be applied to the sampled areas, and an estimate of N_2/N_1 computed for the large block.

LITERATURE CITED

Carothers, W. A. 1979. Aerial detection report on the Oconee National Forest, Piedmont National Wildlife Refuge, and Hitchiti Experimental Forest. 2 p. U.S. Dep. Agric. For. Serv. Aerial Survey Team Rept. 79-3-2. Doraville, Ga.

Cochran, W. G. 1977. Sampling techniques. Third Edition. 428 p. John Wiley & Sons, Inc., New York.

Dull, C. W. 1979. Aerial detection report on the Oconee National Forest and Hitchiti Experimental Forest. 2 p. U.S. Dep. Agric. For. Serv. Aerial Survey Team Rept. 79-3-1. Doraville, Ga.

Hedden, R. L., and R. F. Billings. 1979. Southern pine beetle: factors influencing the growth and decline of summer infestations in east Texas. For. Sci. 25(4):547-566.

Moore, G. E. 1978. Factors for determining population trends in southern pine beetle spots. Environ. Entomol. 7:335-342.

Morris, C. L. 1975. A preliminary report on the effectiveness of bark sampling to predict population trends of the southern pine beetle in Virginia. 4 p. Va. Div. For., Blacksburg.

Morris, C. L. 1976. Follow-up report on the effectiveness of bark sampling to predict population levels of the southern pine beetle in Virginia. 2 p. Va. Div. For., Blacksburg.

UNPUBLISHED LITERATURE CITED

Hain, F. P. 1979. The dynamics of endemic southern pine beetle populations. Progress report (Jan. 1-June 30, 1978). 16 p. Expanded Southern Pine Beetle Research and Applications Program, Pineville, La.

Moore, G. E., G. D. Hertel, and H. Bhattacharyya. 1979. Southern pine beetle attack:emergence ratio and stand factors for predicting spot trend. 25 p. Final Report. Expanded Southern Pine Beetle Research and Applications Program, Pineville, La.

EMERGENCE:ATTACK RATIO[1] AS A PREDICTOR OF SOUTHERN-PINE-BEETLE-CAUSED TREE MORTALITY

Gordon E. Moore, Gerard D. Hertel, and Helen T. Bhattacharyya[2]

Abstract.--Several predictive models based on E:A ratio are developed to estimate the 4-month tree mortality in individual spots. A least-squares fit based on E:A ratio alone resulted in the equation $N = -3.81 + 1.54Q$ with $R^2 = 0.77$ and $s^2 = 14.82$.

INTRODUCTION

Forest managers and pest control foresters have attempted to predict the trend of southern pine beetle (SPB), *Dendroctonus frontalis* Zimmermann, infestation in the past with limited success. Yet, understanding the dynamics of spot growth is vital in determining where suppression efforts should be applied. Continued SPB-caused losses of growing stock have been attributed to several factors. Hedden (1978) implicates increasing basal area of pine per acre in east Texas, while Belanger, Osgood, and Hatchell (1979) pinpoint correlation with slow radial growth and high percentage of live crown. Several studies that led to pest population dynamics or prediction models have been funded by the Expanded Southern Pine Beetle Research and Applications Program. These were based on within-tree and within-stand sampling models such as those of Coulson et al. (1976) and Foltz et al. (1977).

Spot growth or decline has been related to the vigor of the beetle population as expressed by a trend prediction model using the emergence:attack ratio (Morris 1975, 1976; Moore 1978; and Moore, Hertel, and Bhattacharyya[3]) and to the number of trees and basal area of pine in the stand (Hedden and Billings 1979; Twardus, Hertel, and Ryan 1978). This study was carried out to examine further the usefulness of a continuous model using the E:A ratio in predicting tree mortality in individual beetle spots over a 4-month period.

MATERIALS AND METHODS

Study Locations

In June 1977, 14 spots were located in the Piedmont (3 in North Carolina, 11 at the Chickamauga and Chattanooga National Military Park near Oglethorpe, Georgia). The original design was to select the same number of spots of low (< 5), medium (5 to 10), and high (> 10) E:A ratio in each location. However, this was not feasible as the SPB population was beginning to decline.

Sampling Procedure

In each spot where samples were collected, our field crews performed the following tasks:

(1) The infested trees and recently vacated trees were counted.

(2) Up to five recently vacated trees near the expanding head of the infestation were sampled. Recently vacated trees (those with few to no brood in the bark at breast height, but unspoiled by borers) were chosen because bark samples from these trees give a complete record of the SPB activity over the course of the infestation. Two 310-cm^2 bark samples were cut from each sampled tree at heights of 2.0 and 5.5 m. Bark samples were then packaged, and returned to the laboratory to make radiographs, from which

---

[1] The name of the ratio has been changed from attack:emergence to emergence:attack because the new term better expresses the number actually used.

[2] The authors are, respectively, Research Entomologist, USDA Forest Service, Southeastern Forest Experiment Station, Research Triangle Park, N.C.; Research Coordinator, USDA Expanded Southern Pine Beetle Research and Applications Program, Pineville, La.; and Mathematical Statistician, USDA Forest Service, Southeastern Forest Experiment Station, Research Triangle Park, N.C.

[3] Moore, G. E., G. D. Hertel, and H. T. Bhattacharyya. 1979 Unpublished. Southern pine beetle attack:emergence ratio and stand factors for predicting spot trend. 25 p. Final report, Expanded Southern Pine Beetle Research and Applications Program.

the number of attacks and emerged beetles plus the few live beetles in the bark were counted.

(3) Four months later, in October 1977, we again went to the same spots and counted the number of trees infested by SPB since June.

RESULTS

Preliminary Analysis

A *t* test was performed comparing the E:A ratios at 2.0 m and the E:A ratios at 5.5 m. It was found that there was no significant difference at 0.05 level between counts at these two heights.

Regression Equation Based on E:A Ratio

It was our belief that the number of new trees infested by southern pine beetle in a spot between June and October should, to great extent, depend on the "vigor" of the SPB population. A measure of the vigor of the population is the E:A ratio, the ratio of the number of SPB emerged and the number of SPB attacks on a typical, recently vacated tree. The simplest model we tried to fit was

$$N = a + bQ \tag{1}$$

where

N = number of trees at the spot infested between June and October,

and

Q = the E:A ratio.

Using the data from Table 1, the least squares fit resulted in the equation

$$\hat{N} = -3.81 + 1.54Q$$

With $R^2 = 0.77$ and s^2 the residual error square. The predicted values and 95 percent confidence intervals are given in the last two columns of table 1.

Table 1.--Summary of data and results from SPB study at Chickamauga and Chattanooga National Military Park

Spot	Q	N_1	N	$\hat{N}$	95% CI
C_1	5.1	20	4	4.02	0-13
C_4	6.8	12	6	6.63	0-16
C_7	8.3	10	11	8.93	0-18
C_8	11.5	8	21	13.84	4-23
C_9	9.7	17	13	11.08	2-20
C_{10}	14.7	14	21	18.76	8-29
C_{11}	7.7	20	7	8.01	0-17
C_{12}	16.0	14	13	20.75	10-31
C_{13}	3.9	4	0	2.17	0-12
C_{14}	3.2	22	1	1.10	0-11
C_{15}	3.6	22	0	1.71	0-11

Q = E:A ratio

N_1 = number of infested and newly vacated trees in June

N = number of trees infested between June and October

$\hat{N}$ = predicted value of N using model (1)
$\hat{N} = -3.81 + 1.54Q$

$$95\%\ CI = \hat{N} \pm ts\sqrt{1 + \frac{1}{11} + \frac{(Q - \bar{Q})^2}{\Sigma(Q - \bar{Q})^2}},\ \text{where } t = t(0.975,\ 9df) = 2.26,\ s^2 = 14.82$$

Although the value $R^2 = 0.77$ was quite high, we felt the fit may be improved by taking into account N_1, the number of SPB-infested and recently vacated trees in June, and by exploring a possible better linear relationship between log(N) and log(Q) than between N and Q. Some other models we tried to fit were

$$\log(N) = a + b\log(Q), \tag{2}$$

$$\log(N/N_1) = a + b\log(Q) \tag{3}$$

$$\log(N) = a + b\log(Q) = c\log(N_1), \tag{4}$$

resulting in R^2 values of 0.87, 0.81, and 0.90, respectively. It should be noted, however, that in making the logarithmic transformation two observations, where N = 0, were deleted.

The logarithmic models appear to give the best fit, although it is evident from the R^2 values that all four models may serve as excellent predictors.

The results of this study clearly demonstrated E:A ratio to be a good indicator of short-term spot trend. However, we are fully aware these results were obtained from the data of one contiguous region, and more data are needed to validate our findings.

LITERATURE CITED

Belanger, R. P., E. A. Osgood, and G. E. Hatchell. 1979. Stand, soil, and site characteristics associated with southern pine beetle infestations in the southern Appalachians. 7 p. U.S. Dep. Agric. For. Serv., Res. Pap. SE-198. Southeast. For. Exp. Stn., Asheville, N.C.

Coulson, R. N., P. E. Pulley, J. L. Foltz, and W. C. Martin. 1976. Procedural guide for quantitatively sampling within-tree populations of *Dendroctonus frontalis*. 29 p. Texas Agric. Exp. Stn. MP-1267. College Station, Tex.

Foltz, J. L., P. E. Pulley, R. N. Coulson, and W. C. Martin. 1977. Procedural guide for estimating within-spot populations of *Dendroctonus frontalis*. 27 p. Texas Agric. Exp. Stn. MP-1316. College Station, Tex.

Hedden, R. L. 1978. The need for intensive forest management to reduce southern pine beetle activity in East Texas. South. J. Appl. For. 3:19-22.

Hedden, R. L., and R. F. Billings. 1979. Southern pine beetle: factors influencing the growth and decline of summer infestations in east Texas. For. Sci. 25:547-556.

Moore, G. E. 1978. Factors for determining population trends in southern pine beetle spots. Environ. Entomol. 7:335-342.

Morris, C. L. 1975. A preliminary report on the effectiveness of bark sampling to predict population trends of the southern pine beetle in Virginia. 4 p. Va. Div. For., Blacksburg.

Morris, C. L. 1976. Follow-up report on the effectiveness of bark sampling to predict population levels of the southern pine beetle in Virginia. 2 p. Va. Div. For., Blacksburg.

Twardus, D. B., G. D. Hertel, and G. W. Ryan. 1978. Southern pine beetle infestation, growth, and decline--1977. 13 p. U.S. Dep. Agric. For. Serv., Rep. 78-2-8. Forest Insect and Disease Mgt., Pineville, La.

SUMMARY REMARKS AND EVALUATION

Jerry L. Stimac and Robert W. Campbell[1]

We accepted the responsibility of evaluating and summarizing this symposium because we believe that outside reviewers have greater freedom to be objective and because we believe objectivity to be a prerequisite to formation of constructive criticism. Our purpose is neither to pat backs nor to point the finger. Rather our job is to evaluate the SPB-related models that have been developed and presented and to suggest some further approaches that might be taken.

We will start by making some comments on the models and modeling approaches presented. These comments will be followed by a comparison of SPB modeling to similar work in another forest insect program. We will then share some ideas on the relationship between modeling activities and acceptance and use of these models by forest managers. We conclude with comments on the usefulness of this symposium.

COMMENTS ON MODELS PRESENTED

In ESPBRAP, three levels of modeling activities appear to be directed toward spot performance. These range from simple empirical representations (descriptive regression models) to detailed representation of biological processes (mechanistic or process models). A fourth type of modeling activity is directed at the transition from endemic to epidemic population status and is intended to have ultimate application at each of several levels of spatial resolution (tree, spot, and stand locality and large region). All four categories of modeling activity appear to have an important role in the ESPBRAP overall. Likewise, each model has potential utility in forest management.

Descriptive Models

Descriptive models such as those presented by Reed and Hedden will be the easiest and fastest to apply in forest practice. These regression models use information available from forest surveys to make short-term projections of spot spread and damage resulting from spot growth, but their empirical nature limits their ability to make robust projections in space and time. Descriptive regression models usually have coefficient values that are estimated from data sets collected over a narrow range of environmental variation. These models will be difficult to validate; they must be examined over a wide range of environmental conditions to see if values of empirically determined coefficients remain constant. Models based on biological processes, rather than statistical description of a particular data set are generally more appropriate for making predictions over a wide range of environmental conditions. However, descriptive regression models do offer a logical first step in improving the decisionmaking capability of forest managers.

Arkansas Model

The Arkansas model presented by Hines, Taha, and Stephen is a deterministic simulation model, driven only by temperature. SPB development is dynamic with respect to temperature, but neither development nor mortality is dynamic with respect to feedback from host trees or natural enemies of SPB. Stand composition parametrically influences SPB mortality rates, but the stand is actually considered as a "super tree" that is colonized by a pool of SPB. The utility of the Arkansas model lies in the fact that the model is user-oriented and can make short-term (60- to 90-day) predictions of timber losses in terms of dollars. Although a user may not understand the details of how this model works, all forest managers will be able to relate to the projected dollars lost.

Before forest managers can use the Arkansas model, they must satisfy information requirements for model initialization (see Hines, Taha, and Stephen 1980, table 3). Presently, the model requires a measurement of d.b.h. of each infested tree plus other tree and stand data. The necessary d.b.h. measurements will probably not be available from forest inventory survey data. If they are not, provisions must be made to obtain them.

---

[1] The authors are, respectively, Assistant Professor, Dept. of Entomology and Nematology, University of Florida; and Research Entomologist, U.S. Forest Service, Corvallis, Oregon.

inventory survey procedures could be supplemented with additional sampling procedures that would be used within SPB-infested spots. A possible alternative would be to provide additional structure to the Arkansas model so that information available from forest inventory surveys could be translated into d.b.h. measurements needed to run the model.

The model requires values for six SPB stage-specific mortality rates, which are difficult to estimate. Forest Service personnel or other model users will not have to make these estimates as they have been preset to time-dependent parameters based on previous SPB population sampling data. Although the values may not now be applicable Southwide, if researchers choose to set the values to conservatively low levels, the Arkansas model can provide liberal estimates of timber losses from SPB.
Such conservative values will sacrifice precision of the prediction and will sometimes suggest a need to apply controls in situations where none are really needed. Prior to implementation, the Arkansas model should be validated over a wide area, covering various stands with a range of tree species mixes. Perhaps running the Arkansas model for spots in Texas and Georgia could provide necessary validation.

TAMBEETLE Model

The TAMBEETLE model presented by Feldman, Curry, and Coulson is a detailed, process-oriented model. As a result, this model is best suited for longer range projections and potentially for evaluation of spot control tactics (especially if a more extensive tree and stand model is added to current structure). However, the present form of TAMBEETLE is a research model that probably could not be used by a forest manager because of the amount and detail of required information. For example, the predominant SPB life stage at breast height is an initial condition that must be specified even for the simplified option. The detailed option, for which the model has been validated, requires disc sample counts of SPB or selected trees. The data requirements for TAMBEETLE execution are stringent, but for some applications the potential robustness of this model appears to outweigh the inconvenience of these requirements. If forest managers want to evaluate potential spot control strategies, TAMBEETLE (with some additional model structure) appears to be the best candidate. TAMBEETLE considers the effects of tree quality and spatial dispersion of trees within a stand. Thus, TAMBEETLE also provides a method for considering the effects of host tree feedback on rates of SPB development and mortality.

Endemic-Epidemic Transition Model

The conceptual model presented by Gold is different from the other models in that it is not oriented only at the spot dynamics of SPB and host trees. Rather, the Gold model is aimed at describing the transition of SPB populations from endemic to epidemic levels for a stand, locality, or even larger regions. The key to understanding SPB outbreaks and resulting damage may be in discovering the "trigger" that releases SPB populations. Gold's approach, although only conceptual at this time, offers encouraging promise for gaining an understanding of the essence of SPB problems. But until this conceptual model is developed into a mathematical representation, applications cannot be realized.

MODELING EFFORTS ON FOREST INSECT PROBLEMS

Recently, the CANUSA (West) program held a modeling workshop on the western spruce budworm. This intensive, week-long group effort by about 30 researchers, modelers, pest and forest managers, and facilitators was a major step toward a principal objective of the budworm program: to develop a comprehensive budworm/forest growth model. The model is critically needed for two reasons. First, it will ultimately provide forest and pest managers with the likely short- and long-range consequences of both untreated budworm populations and any management tactics--direct and indirect, single or combined--they may wish to consider. During the remaining life of the formal program, the model will also be used by program management to redirect and focus available program resources in the most promising, productive, and critical areas. For both reasons, the model is being structured to facilitate incorporation of the anticipated modifications that will maintain it to reflect as close to state-of-the-art knowledge as possible.

We know relatively little about the western spruce budworm--particularly when we compare that knowledge base with the monumental body of information now available on the life system of a critter like the southern pine beetle. Consequently, our first approximation model was rife with guesses. In any case, the facilitators managed to have a coupled model up and running by the last day of the workshop.

By all accounts, virtually every participant in this workshop considered the effort a gratifying and encouraging success. We'll come back to this workshop after sharing some thoughts on the uses forest managers will, or could, make of SPB-related models.

MODELING ACTIVITIES

Frankly, we are greatly concerned at the apparent lack of meaningful dialogue between modelers and managers. We haven't been able to get a firm handle on just what decision-support system is expected to emerge from the models you have described. Consequently, we have felt frustrated in our role here. Bluntly put, we have concluded that there is no clear, mutual understanding of how forest and pest managers will use these models. In our judgment, your next order of business should be the development of a comprehensive decision-support package. We are also concerned that the likelihood of ultimate operational implementation of this package will be greatly reduced unless users are included as more active participants in this development.

In a landmark book titled *Adaptive Environmental Assessment and Management*, Holling and his colleagues (1978) describe an approach through which the essential attributes of the scientific method can be extended from individual or small groups of investigators to a much larger, heterogeneous group including researchers, decisionmakers, land managers, and others. The development of a process model of whatever system may be in question lies at the heart of this approach: and holding a series of intensive modeling workshops, such as the one mentioned earlier for the spruce budworm, is crucial to model development. In our judgment, the approach described in Holling's book is a blueprint for developing the comprehensive decision-support system you need for the southern pine beetle.

MODELING APPROACHES IN THE ESPBRAP

To our knowledge, the ESPBRAP is the only project in which numerous different modeling approaches have been pursued simultaneously. In any large program with a great diversity of problems to be solved, numerous models may be needed to address different categories of questions. Therefore, it is necessary to diversify modeling efforts to address a range of user needs. ESPBRAP's administration and scientists are to be highly commended for providing models that are potentially sufficient to address this range. As a result, models developed in the Program can offer forest managers greater diversity of short- and long-range applications.

In this Program, close interaction between modelers and experimentalists has obviously been the rule, not the exception. Scientists involved in the modeling efforts deserve to be congratulated for working together to generate products that may not be equaled by any other programs for many years. However, to assure justly deserved recognition for their efforts, we hope researchers will play an *active* role in working with applications personnel to provide a vehicle for transfering technology to end users. After all, who understands new technology better than those who develop it?

USEFULNESS OF THE SYMPOSIUM

Just before this session started, Fred Stephen wondered if we would share some thoughts on the usefulness of this symposium. That's easy. The program is more than the simple sum of a series of unrelated studies precisely because you are sharing and synthesizing your knowledge. Without workshops like this, that sort of intergroup activity just wouldn't happen.

You've done a fantastic job, we agree, in exploring the wonderful world of the southern pine beetle. We salute you, one and all. The job isn't quite over, but you're very close to seeing your efforts put into practice.

LITERATURE CITED

Hines, G. S., H. A. Taha, and F. M. Stephen. 1980. Model for predicting southern pine beetle population growth and tree mortality. *In* Modeling southern pine beetle populations: symposium proceedings. [Asheville, N.C., Feb. 1980.] F. M. Stephen, J. L. Searcy, and G. D. Hertel, eds. U.S. Dep. Agric. For. Serv., Tech. Bull. 1630. Comb. For. Pest Res. Develop. Prog., Pineville, La.

Holling, C. S. 1978. Adaptive environmental assessment and management. 377 p. Wiley Interscience, New York.

END