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A REFERENCE CURVE AND SPACE-TIME SERIES ANALYSIS OF THE REGIONAL POPULATION DYNAMICS OF THE SOUTHERN PINE BEETLE (*DENDROCTONUS FRONTALIS* ZIMMERMANN)[1]

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INTRODUCTION

The southern pine beetle, *Dendroctonus frontalis* ZIMMERMANN, has done considerable damage to southeastern United States pines in the last 23 years of recorded information. During this interval the insect has undergone tremendous fluctuations in its population levels, ranging from near undetectability to the destruction of some 401004 cords of wood in 1975 (PRICE and DOGGETT, 1978). Because of its destructiveness this beetle has been the object of intense investigation by many researchers over the last decade (PAYNE, 1980). However, nearly all of this work falls into two categories, either stand-hazard rating (HICKS, 1980) or population dynamics on the local infestation (spot) level (COULSON, 1980). These local infestations or spots are clusters of trees which are undergoing beetle colonization. Spots may contain one tree or thousands of trees and can grow over several years. New attacks within the spot are under pheromone control. However, information and analysis on the crucial aspects of inter-spot dispersal and large-scale population dynamics has remained virtually zero.

Several authors have previously described the southern pine beetle (SPB) as possessing a multi-level population dynamics, i.e. several distinct levels of organization in behavior. COULSON (1979) discusses two dynamic levels, the single spot and the multiple spots situations. Each level is presumed to be a complex blend of site conditions, evnironmental stresses, and competitor/predator effects. GOLD, MAWBY and HAIN (1980) extend this two level system to a formal five-level hierarchy which includes tree, spot neighborhood, patch, subregion, and region. Furthermore this same set of authors ascribe a two phase dynamic structure to each of the five separate levels. Such two phase systems occur frequently in the dynamics of most organisms. Migratory behavior and feeding preference behavior are some common entomological examples. In particular many forest

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insects are believed to show a behavioral transition on the basis of environmental or genetic cues (McNamee et al., 1981). In the case of the SPB these two phases represent distinct low-level (endemic) and high-level (epidemic) behaviors with the threshold between phases being parametrized (possibly stochastically) by the local conditions. Under drought conditions, for example, this threshold may be lowered substantially and thus increase the liklihood of a population outbreak. This framework builds heavily upon the work of Berryman (1978) and Berryman (1979) in which the author suggests that a multiple equilibrium approach is advisable for modelling bark beetle dynamics. These three equilibria represent a low level maintained by host defensive capabilities, a high level bounded by host availability, and an unstable threshold lying between the levels.

The present work assumes that the full five level hierarchy, complete with the two distinct intra-level phases at each level is a satisfactory description of the system. Furthermore, it considers that primary importance should be placed on elucidating and describing the function relating the probability of a population exceeding the threshold in any given circumstance. This function measures the risk of sustaining an SPB epidemic on a specific area given a set of conditions such as previous SPB activity, moisture extremes and host resistance level. The present investigation restricts itself to one hierarchical level (the region) and to a rough formulation of the required function.

Methods and Materials

Only one set of adequate data exists for the regional level of the SPB hierarchy (the 13 states represented in Fig. 1). Price and Doggett (1978) are the sources of this information, which consists of a county-by-county enumeration of the presence or absence of SPB activity during each of 18 consecutive years from 1960–1977. It was decided that the best way of utilizing this information was to examine the areal coverage of the infestations. Towards this end a rectangular mosaic of 24 blocks was superimposed over the portion of the region which had experienced beetle activity in the 18 year interval. Figure 1 shows the placement of these blocks which were designed merely for similarity of size and nearly complete coverage of the range of the SPB. For each block and for each

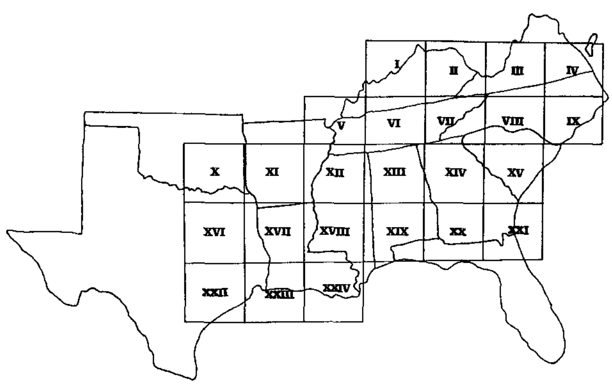

Fig. 1. Definition and location of the twenty four block system on the effective southern pine beetle range.

year the areal coverage by SPB infestations was calculated in two steps. First, a grid of 64 square units was placed over each block. Then the number of grid squares which were predominantly infested (colored in the maps) were counted and converted to a percentage, i.e. the areal coverage value. MAWBY (1980) has a more detailed explanation of the procedure and its justification.

Given the lack of knowledge about the large-scale aspects of the system, it was decided that an exploratory data analytic approach should be adopted. In adopting such an approach TUKEY (1977) suggests that extra information may be gained through the combination of several independent analytic techniques. The fact that each technique examines a different feature of the system enables the investigator to form a broader view of the situation. Two techniques appeared eminently suitable for the SPB regional system, the reference curve analysis of SHETH (1969) and the space-time autocorrelation analysis of CLIFF et al. (1975). Their suitability stems primarily from the former's "top-down" viewpoint being complementary to the "bottom-up" manner of the latter. The blocked data was analyzed through the two complementary techniques with the hope that the resulting information could be used to sketch out a form for the threshold function. In particular, the analyses were expected to illuminate the spatial-temporal dependencies of the function, the flexibility needed in its form to cover different areas, and the nature of interplay between the functions in neighboring blocks.

Reference curve analysis is a variant of factor analysis which differs in using the raw cross products matrix rather than the correlation matrix at the initial stage. Because the data consists of homogeneous units (equal sized areas observed at yearly intervals) standardization is not necessary and the analysis retains the essential level and scatter of the data. Following SHETH's notation the initial matrix of n observations over m times is called Y. The objective is to resolve the matrix into two matrices P and V such that $Y=PV$. The decomposition follows in several steps. First $Z=YY'$ is formed where Y' is the transpose of Y and hence Z is square and real symmetric. Thus the decomposition $Z=UG^2U'$ is possible. The matrix U contains the eigenvectors of YY' and G^2 contains the eigen-values in appropriate order. Thus $Y=AS$ where $A=UG$ and $S=G^{-1}U'Y$. After scaling A and S by a diagonal matrix N with all entries equal to the square root of the sample size, the formulation is $Y=PV$ where $P=AN^{-1}$ and $V=NS$. An approximate matrix Y_r may be obtained by selecting only the r largest eignvalues to yield $Y_r=P_rV_r$ where $P_r=U_rG_rN_r^{-1}$ and $V_r=G_r^{-1}U_r'Y$. This reduction in dimension is an essential feature of this analysis. The matrix P_r contains the approximating reference curves and the V_r matrix contains the individual coefficients. Both P_r and V_r are standardized by sample size.

Spatial series analysis as discussed in *Cliff* et al. (1975) utilizes the kth spatial autocorrelation which is defined by $I_k=(n/W)(\sum_{i=1}^{n} w_{ij}Z_iZ_{i,k})/\sum_{i=1}^{n} Z_i^2$ where $Z_{i,k}=X_{i,k}-\bar{x}$, $n\bar{x}=\sum_{i=1}^{n} x_i$, $W=\sum_{i=1}^{m}\sum_{j=1}^{n} w_{ij}(i\neq j)$, and w_{ij} is the weight assigned to the i to j connection. The $x_{i,k}$ represent the areal coverage value for any block precisely k blocks away from block

i. Potentially there are m of these blocks at spatial lag k. Thus the Z_i and $Z_{i,k}$ values represent mean standardized forms of the areal coverage values. The use of $\bar{x}$ rather than $\bar{x}_k$ is recommended by CLIFF et al. (1975) to ensure lag-to-lag comparability. In general, the w_{ij} values may be non-symmetric and arbitrarily chosen for testing particular hypotheses about the system.

Time series analysis (Box and JENKINS, 1976) defines the kth temporal autocorrelation as $I_k = C_k/C_o$ where $C_k = \frac{1}{n}\sum_{t=1}^{n-k}(X_t - \bar{x})(X_{t+k} - \bar{x})$ with $\bar{x} = \frac{1}{n}\sum_{t=1}^{n} x_t$. A rough estimate of the order of the autoregressive process is obtained by BARTLETT's formula, $var\ (r_k) = \frac{1}{n}\left(1 + 2\sum_{i=1}^{n} I_i^2\right)$ with $k > q$ and q is an order at which all further autocorrelations may be assumed zero. The approximate normality of the autocorrelations then allows one to test for significant values and hence approximate the process order. Autocorrelation functions of nonstationary processes drop off in a linear fashion and preempt the order estimation process.

RESULTS

Four reference curves were found sufficient to account for over 95% of the system variability (Table 1) where variability in this context refers to the sum of squares. In an effort to keep the number of curves to a minimum, the 95% limit was accepted as an adequate approximation to the system. The shapes of these curves (Fig. 2) are important indications of their interpretation. Note particularly that the dominant curve is highly positively correlated with the average areal coverage calculated over all 24 blocks at each year ($r^2 = .99$). Table 2 lists the correlation of each block with the primary curve and with the total areal coverage (i.e. 24 times the average areal coverage) and suggests that several blocks might serve as adequate bellwethers in a surveillance system for the region. The best choice for such a purpose appears to be block #7 (see Fig. 1) with an r-square

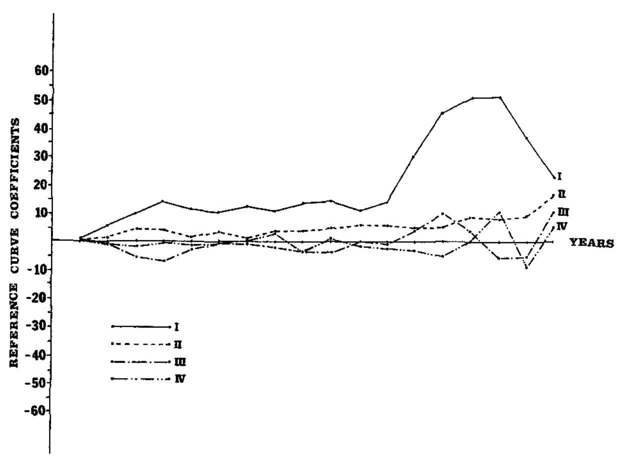

Fig. 2. Reference curves for the original reference curve analysis with I representing curve one, II representing curve two and similarly on through curve four.

Table 1. The breakdown of variability by reference curve.

Reference Curve Number	Per cent Variability Explained	Cumulative Per Cent Variability Explained
1	85. 2	85. 2
2	5. 0	90. 2
3	3. 6	93. 8
4	2. 3	96. 1

of .84. Figure 3 plots the predictions of a linear regression equation based on block #7 against the total areal coverage values on which it is fitted.

The adequacy of the primary reference curve in accounting for system variability can be used to rate each block by its summed weight on the component (KENDALL, 1975). If Y represents the observation matrix and P is the dominant reference curve written as a column vector then $Y'P$ is this rating. This measure is a projection of each block history onto the dominant reference curve and reflects their closeness. A high risk block demonstrates a coordination in direction and magnitude between the block and the total areal

Table 2. Correlations of blocks with total intensity and with the primary reference curve.

Block Number	Correlation with First Component	Correlation with Total Intensity
1	.474	.508
2	.540	.569
3	.913	.898
4	.551	.556
5	.463	.528
6	.773	.820
7	.922	.914
8	.847	.822
9	.699	.685
10	.288	.368
11	.572	.642
12	.767	.810
13	.908	.880
14	.908	.892
15	.722	.709
16	.687	.743
17	.890	.914
18	.899	.895
19	.877	.877
20	.908	.908
21	.574	.575
22	.548	.548
23	.646	.646
24	.697	.697

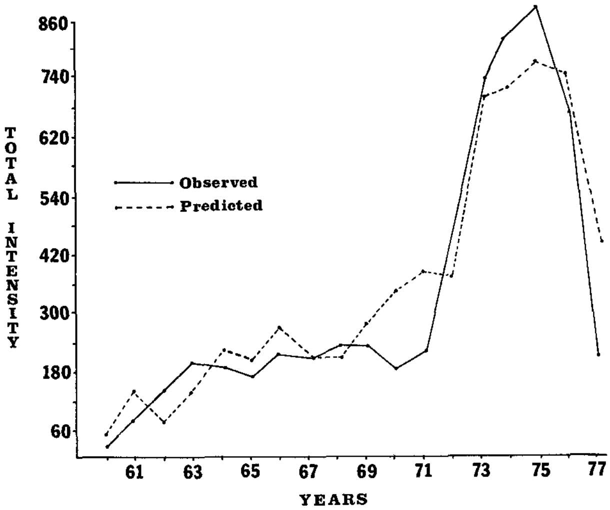

Fig. 3. Predicted values of the linear regression of total southwide intensity on the block number seven subtotal.

coverage of the region. Figure 4 illustrates such a rating system where ranks have been assigned to indicate low, medium and high risk areas. SHETH suggests using the relative dominance of the coefficients for each of the four curves to rate the blocks. A block with a relatively dominant coefficient on curve one, for example, would behave similarly to this curve and thus, similarly to the average behavior of all twenty four blocks. Likewise curves two, three, and four will have their associated blocks as well. In this manner the 24 blocks can be classified into 4 groups for simplification purposes. Figure 5 illustrates the rating system derived from this interpretation.

The temporal autocorrelation function for each of the 24 blocks was individually estimated using procedure AUTOREG (HELWIG and COUNCIL, 1979) of the Statistical Analysis System and the order s estimated using BARTLETT's formula. Table 3 lists these estimated orders and typical temporal autocorrelation functions are shown in Figure 6.

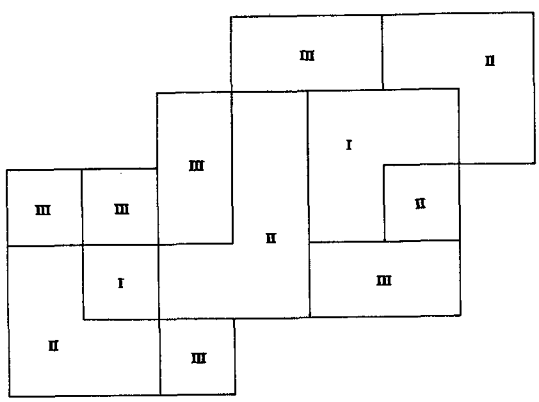

Fig. 4. Classification of the 24 blocks into high (I), medium (II), and low (III) risk based upon only the dominant curve.

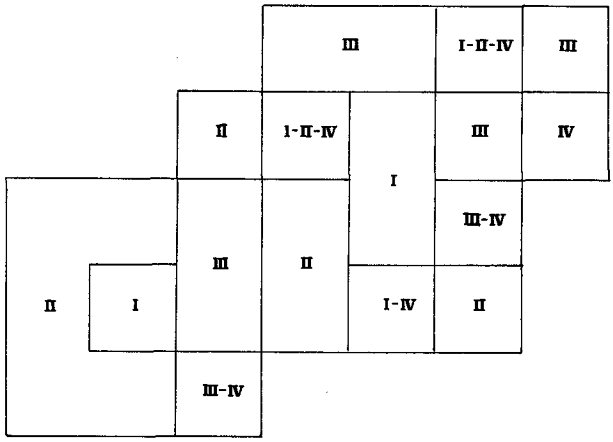

Fig. 5. Classification of the 24 blocks according to the curve or mixture of curves that each follow must closely with curve one represented by the numeral I and similarly on through curve four.

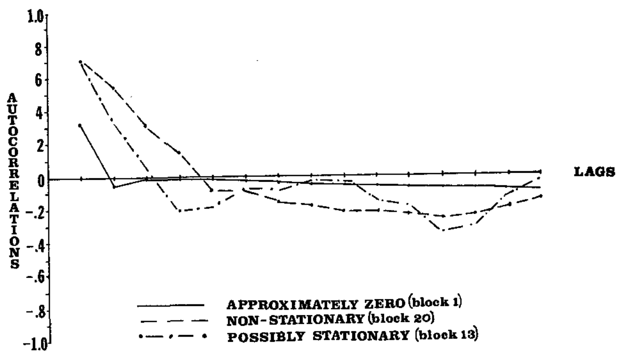

Fig. 6. Some examples of temporal autocorrelation functions for the original analyses. Note that block 13 is possibly stationary but is assumed to be not so for the purposes of Table 3.

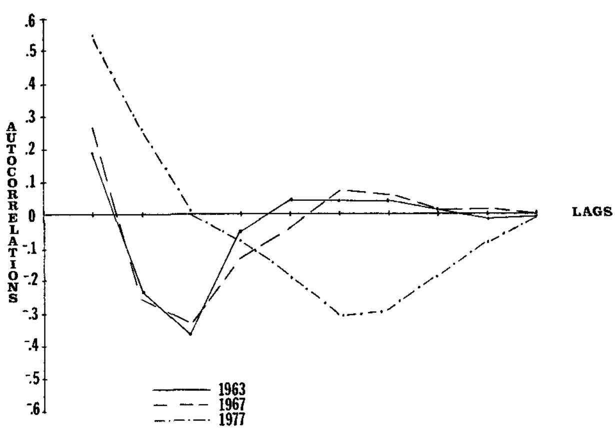

Fig. 7. Some examples of spatial autocorrelation functions for the original analyses.

Table 3. Order estimation for the raw temporal autocorrelation functions.

Block Number	Order	Block Number	Order
1	1	13	ns
2	2	14	ns
3	ns	15	1
4	1	16	ns
5	1	17	ns
6	ns	18	ns
7	ns	19	ns
8	1	20	ns
9	1	21	1
10	1	22	ns
11	ns	23	ns
12	ns	24	ns

ns=nonstationary

Table 4. Order estimation for the raw spatial autocorrelation functions.

Year	Order	Year	Order
1960	0	1969	0
1961	2	1970	0
1962	0	1971	0
1963	0	1972	2
1964	0	1973	2
1965	0	1974	2
1966	0	1975	0
1967	0	1976	2
1968	3	1977	1

Table 5. Order estimation for the "detrended" temporal autocorrelation functions.

Block Number	Order	Block Number	Order
1	5	13	4
2	0	14	0
3	0	15	0
4	2	16	5
5	0	17	5
6	5	18	2
7	0	19	0
8	0	20	4
9	7	21	3
10	2	22	3
11	0	23	0
12	0	24	2

Table 6. Order estimation for the "detrended" spatial autocorrelation functions.

Year	Order	Year	Order
1960	1	1969	1
1961	0	1970	0
1962	0	1971	1
1963	0	1972	0
1964	1	1973	1
1965	1	1974	0
1966	1	1975	0
1967	1	1976	1
1968	1	1977	0

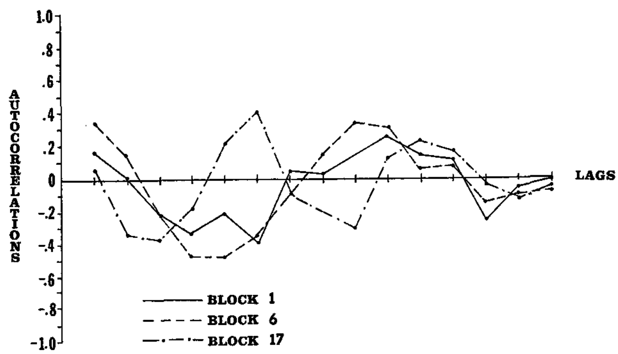

Fig. 8. Some examples of temporal autocorrelation functions for the analyses occurring after detrending the data.

The spatial autocorrelation function for each of the 18 years was calculated by an author-written Fortran program and the orders estimated by BARTLETT's formula. Table 4 lists the orders and Fig. 7 graphs the typical spatial autocorrelation functions. Due to the presence of non-stationarity in some of the blocks it was deemed necessary to remove it through fitting of a "trend" function.

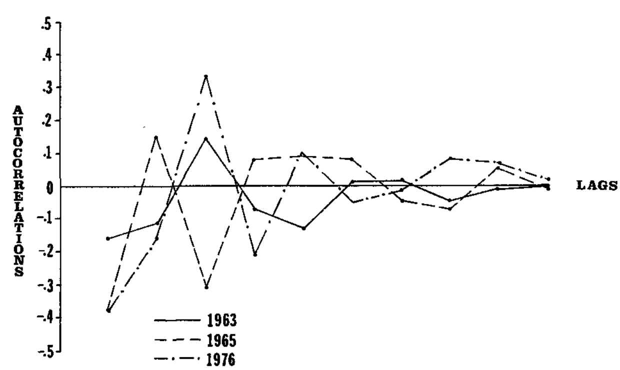

Fig. 9. Some examples of spatial autocorrelation functions for the analyses occurring after detrending the data.

A set of x and y coordinates was established over the block centers and a cubic regression of the coordinates $(x, y, x^2, y^2, xy, x^2y, xy^2, x^3, y^3)$ was performed for each year. The residuals from these regressions were themselves regressed on a cubic function of time after being grouped by block. The year 1960 was labelled as year 1. The residuals from this double regression were then analyzed for their temporal and spatial orders in a similar manner to the prior analysis. Tables 5 and 6 show the estimated orders while Figs. 8 and 9 illustrate the curves themselves. Note that the temporal autocorrelation functions suggest a possible periodicity which couldn't be isolated due to data limitations.

Discussion

The estimated orders of the initial space series indicate only low autocorrelation between blocks during most years. The 7 non-zero order years are not associated with overall decrease or increase of the total intensity. One possible explanation is that these non-zero years tend to occur when spatially separated clusters of infestations tend to coalesce. After "trend" removal the orders are reduced and are concentrated in the 1964–1969 range with no apparent reason.

The inital time series orders (and nonstationarity) indicate that 15 blocks are "trend" controlled. The blocks that exhibit low order stationary are all located on the extreme east and west of the region. These blocks exhibit SPB infestation only during very high regional epidemics. Upon removal of the "trend" most blocks become stationary, but several (those 5 blocks with orders greater than 4) are borderline cases. The high orders of blocks 1 and 9 seem to be artifacts of the removal process, but blocks 6, 16, and 17 appear important. These blocks appear to have internal conditions which enable relatively constant SPB levels to exist over long periods of time.

Besides the immediate application of the reference curve findings to survey as described above, these analyses provide a foundation for the choice of the threshold function. The implications are five-fold. Firstly, there is apparently no spatial coordination between blocks except during regional epidemics. This follows from the low order spatial series. Note that this does not rule out the possibility of coordination between groups of blocks. It does seem to rule out any frequent simultaneous outbreaks in all 24 blocks. Secondly, there are approximately four modes of possible block behavior, each of which involves differences in timing, duration, and intensity in SPB infestation occurrence. The reference curve analysis also suggests that these four modes can adequately represent the system and the forms of the curves illustrate the various differences between block behaviors. Thirdly, the system seems to be under the control of environmental factors which possibly have long term natures, such as forest growth processes. The time series analysis suggests that most blocks can be well modelled by a polynomial "trend" in time as measured from one large epidemic to another. Fourthly, a fringe versus central area difference exists as demonstrated by Fig. 5 and by Table 3. Specifically the fringe blocks appear to be low order stationary and are associated with reference curves 2, 3 and 4. Central blocks tend to be nonstationary and some are associated with reference curve 1. Fifth, the process beneath the time "trend" appears to be of order one in space and at least three in time. Such trends could likely stem from shorter term cycles (perhaps climatic in nature) superimposed on the longer trend in forest growth.

The implications of these results are quite specific in their suggestions for the function relating environmental conditions to the probability of the SPB exceeding the threshold. The basic process on each block must be one of short spatial influence and relatively long temporal influence. An active infestation in a forested area would grow in groups of highly clustered spots which would not, in general, show much spatial coordination between clusters. Most probably the occurrence of these clusters is determined by long-term host changes being acted upon by transient weather phenomena. However the shape and size of the cluster once begun is dependent mostly on the inter-spot dynamics as contained within a patchy host environment. That is, a patchwork of large, well-separated patches would have a different local history than one made up of small, well-separated patches. The theory of stochastic epidemics is probably the best approach to the study of these processes.

Once the threshold has been passed in an area however, the situation changes rather radically. The epidemic area influences its neighbors more strongly than an endemic area, with the result of coordination among separated areas. In fact, judging by the appearance of blocks following the third and fourth reference curves one can assume that some areas would never by infested without this coordination effect. Epidemics have disastrous effects upon the SPB populations that cause them because they not only utilize current susceptible host but also take out potential susceptibles. This accounts for the temporal effect of SPB infestations with some type or regeneration time being necessary for reinfestation. Note that areas which normally have rather high levels of SPB frequently should not become epidemic often and thus should be more dependent upon transient conditions than upon the "memory" of past infestational damage.

The appearance of four different types of significant block behaviors suggests that some movement of SPB infestations does occur and is partially controlled by the location and condition of past infestations. Blocks with similar associated reference curves tend to cluster geographically and curve 2 seems to dominate the entire western portion of the region. It is likely that these effects can be explained in terms of the characteristics of the blocks which exhibit them. Some cursory examination suggests that either host differences or winter temperatures might be the foundation for the distinction (MAWBY, 1980) but no concrete results have stemmed from this research yet.

Lastly the appearance of nonstationary temporal processes suggests that some long-term process is involved in the system, of such a long term that repetition does not seem to occur within the 18 available years. The most likely candidate for causative agent in this case is forest aging, a factor long associated with susceptible stands. One interesting possibility is that the occurrence of epidemics forces such a long time pattern upon itself by its depletion of large areas of host type. If this is true then control efforts might be best employed to promote little infestations every year in order to prevent the buildup necessary to cause regional epidemics.

The recommendation for a suitable threshold function should therefore have at least the following characteristics. It should be defined upon either single blocks or on groups of contiguous blocks of the same behavioral type. The function should be very short ranged in cross-block effects under low levels but should be able to exhibit rather long scale coordination during epidemic intervals. It can be expressed as a process with a time trend plus an underlying temporal autoregressive process of at least 3 years. It also must be able to retain some long-term effects of changing host type as effected by occurrence of epidemics. Lastly is should have some ability to respond to the stochastic, rather transient effects of weather and human usage.

Summary

The southern pine beetle (SPB) demonstrates a complex dynamics which necessitates a model with several levels of organization. The regional level, the entire southeastern United States, has received little or no attention in the past. In order to rectify this situation and in order to set up a background for modeling a set of representative data was collected consisting of 18 consecutive years of annual survey infromation. This basic information was then converted to a set of areal coverage values for 24 subregional areas.

The subregional data was then analyzed through two complementary statistical techniques, space-time series and reference curve analyses. The space-time series analysis attempted to determine the limits of spatial and temporal dependence in the system while the reference curve analysis tried to simplify the overall system into a more tractable one. The use of both techniques simultaneously yielded more information than if either had been used separately.

The results of the analyses suggest some interesting features of the SPB dynamics, some of immediate consequence and some of basic concern to further modeling efforts. Spatial dependence appears to be of no importance except in overall epidemics when it becomes very long-ranged. Temporal dependence is more pronounced throughout the beetle's cycle, being on the average of 2–3 years duration. There is some possibility indicated of a long range periodicity which unfortunately exceeds the duration of the data itself. The reference curve analysis indicates that 4 curves are all that is needed for 95% approximation of the system variability, with around 85% attributed to the major reference curve alone. This major reference curve follows the mean curve of infestation intensity over all subregions. In summary an adequate model of the dynamics at this level should include a 2–3 year temporal effect, a short range spatial effect, and at least 4 different classifications of sub-regional behaviors. It is also suggested that epidemic large scale behavior is fundamentally different from endemic (low-level) behavior.

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アメリカ東南部におけるキクイムシの地域的個体群動態に関する リファレンス曲線および時空的系列解析

W. D. MAWBY・H. J. GOLD

アメリカ東南部でのキクイムシの動態は，複雑であり，その動態のモデル化には，幾つかのレベル構造を組みこむことが必要である。その一つとして，本論文では，地域的レベルを考察した。本種のアメリカ東南部各州での被害面積について18年間にわたる記録が既に報告されている。このデータを基にして，アメリカ東南部を24の地域にわけ，各々の地域での被害面積を求め，それを基礎データとして解析を行なった。

地域データは，2つの相補的な統計方法，既ち，空間-時間系列とリファレンス曲線によって解析した。空間-時間系列の解析では，そのシステムの地域的，時間的な従属性の範囲を明らかにしようとした。また，リファレンス曲線解析では，全体のシステムをより扱いやすいシステムへと単純化した。2つの手法を用いることで，このシステムについて従来より多くの情報を得ることができた。

解析の結果，被害の地域的な従属性は，大発生が広い地域におよぶ時だけに見られた。一方，時間的な従属性は，このキクイムシの2～3年のサイクルを通じて顕著であった。長期間にわたっての周期性の可能性が示唆されたが，この点を確かめることはできなかった。リファレンス曲線の解析から，4曲線がシステム変異の95%近似を与え，そのうちの主要な1曲線が約85%の寄与を示した。この主要なリファレンス曲線は，全地域での平均被害の曲線を反映していた。まとめとして，地域レベルでの動態モデルは，2～3年の時間効果，近接地域効果と，4つの異なる地域集団，を含むことが好ましい。さらに，大発生時と低密度時での，動態の様相は異なっていることが示唆された。