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A MODEL FOR THE DISTRIBUTION AND ABUNDANCE OF THE
CEREAL LEAF BEETLE IN A REGIONAL CROP SYSTEM

presented by

Alan J. Sawyer

has been accepted towards fulfillment
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Dean L Haynes
Major professor

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A MODEL FOR THE DISTRIBUTION AND ABUNDANCE OF THE CEREAL LEAF BEETLE IN THE CEREAL CROP SYSTEM

By

[illegible]

A DISSERTATION

Submitted to
Michigan State University
in partial fulfillment of the requirements
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DOCTOR OF PHILOSOPHY

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ABSTRACT

A MODEL FOR THE DISTRIBUTION AND ABUNDANCE OF THE CEREAL LEAF BEETLE IN A REGIONAL CROP SYSTEM

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Previous studies on the population dynamics of the cereal leaf beetle have neglected spatial considerations despite the important role played by dispersal in the life history of this species. In this report the interaction of dispersal with regional and local factors affecting spatial and temporal variations in density are discussed.

It is hypothesized that dispersal of the cereal leaf beetle is undirected, and that the density of beetles in a field is the net result of diffusive immigration and emigration. The validity of the hypothesis is evaluated and the factors affecting the dispersal rates are examined in several analyses of existing data and new field studies.

An analysis of host crop preference and the nature of the dispersal process in the cereal leaf beetle is carried out by relating the relative abundance of beetles in winter wheat and spring oats to changes in the relative acreages of the two crops in a region.

A compartmental analysis of intercrop movement and adult mortality supports the premise that beetles may move from oats to wheat, as well as the reverse.

Multivariate spatial analyses of beetle distribution and abundance in a regional crop system reveal a complex relationship between densities in individual fields and the structural features of the surrounding environment.

Field studies are discussed which lend further support to the hypothesis of random dispersal, and suggest that beetles leave wheat in response to declining quality of the crop.

A simulation model of cereal leaf beetle spatiotemporal dynamics is developed and is used to further evaluate the hypothesis. Simulations are carried out to investigate the effects of manipulating the spatial and temporal structure of the crop system in a 16 mi^2 region on the distribution and abundance of the insect. The model emphasizes the importance of local uniqueness in producing spatial variations in density. The simulations lead to surprising results concerning the effects of resistant wheat, relative crop maturities, regional crop acreages and field size, shape and location.

To Marcia and Mariah

sine qua non

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To my fellow students, Winston Fulton, John Jackman, Dick Casagrande, Emmett Lampert, Kasumbogo Untung, Bill Ravlin and Ray Carruthers, I express my gratitude for the intellectual stimulation and camaraderie we have shared.

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"Newton ushered in the Age of Reason, during which it was the expectation of scholars that all problems would be solved by the acceptance of a few axioms worked out from careful observations of phenomena, and the skillful use of mathematics. It was not to prove to be as easy as all that."

Isaac Asimov

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INTRODUCTION

The science of population dynamics broadly deals with the distribution and abundance of organisms. Specifically, it is concerned with the processes leading to changes in these attributes for a given population. Andrewartha and Birch (1954) have pointed out that "distribution and abundance are but obverse and reverse aspects of the same problem." Several authors (Iwao 1971; Levin 1976; Watt 1962; Wiens 1976) have noted, however, that most theoretical and experimental approaches to population dynamics have ignored the spatial aspects of the problem, choosing to deal with populations as if they existed at single points in space. This has been true in the case of the cereal leaf beetle, Oulema melanopus (L.),[1] an introduced pest of small grains which has received considerable research attention in recent years. Several population models of this species have been constructed (Ruesink 1972; Gutierrez et al. 1974; Tummala et al. 1975; Lee et al. 1976; Fulton 1978), but without exception they are purely temporal models.

The efforts directed by previous workers at understanding the adult dispersal process (Ruesink 1972; Casagrande 1975) reflect their recognition of the importance of this phenomenon in the life history and population dynamics of the cereal leaf beetle. The spatiotemporal

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[1] Coleoptera: Chrysomelidae

dynamics of this species has not been systematically addressed, however, and many questions remain unresolved. For example, Fulton (1978) recently emphasized the overriding influence of the rate of movement of adults from winter grains to spring grains on the synchrony of his within-generation population model with actual field events. He noted that the lack of an understanding of this process rendered impractical the use of his model in an on-line control mode.

This thesis discusses, with reference to the cereal leaf beetle, the difficulties and deficiencies inherent in a purely temporal approach to population dynamics and suggests possible solutions to the problem. An hypothesis regarding the spatial dynamics of this species is proposed and is examined in light of existing data drawn from many years of field research. Further analyses and field observations were conducted to supply missing information. An approach to simulating the spatiotemporal dynamics of the cereal leaf beetle in a regional crop system is outlined, and the model's implementation and evaluation are described. The role of specific spatial and temporal structures of the environment in determining the distribution of beetles throughout a region and their abundance in particular fields is examined via simulation. The model's application in a pest management program and its relevance to theoretical questions in population dynamics are considered.

The word "region," as used in this thesis, refers to a geographical area of at least several square miles, encompassing many small grain fields as well as the overwintering habitats and interfield environment of the beetle. The scope of this approach is contrasted to that of single-site, or within-field, studies of population dynamics.

LITERATURE REVIEW

The cereal leaf beetle (CLB) was first discovered in Michigan in 1962 (MSU 1970) and immediately became a focus of intensive research by the USDA and several north-central states. While early research efforts were directed toward developing chemical control of this pest, it was eventually realized that a management scheme integrating both biological and chemical control was needed, and that an understanding of the dynamics of the whole agroecosystem was of central importance to this program (Haynes 1973). Numerous published papers and theses resulting from these research activities can be cited which summarize what is currently known about the CLB system, only some of which can be mentioned here. Castro (1964) and Yun (1967) described the basic biology and behavior of the CLB in the laboratory. Guppy and Harcourt (1978) reported the temperature thresholds and developmental rates of the immature stages. Helgesen and Haynes (1972) modeled the within-generation dynamics of the beetle. Ruesink and Haynes (1973), Fulton (1975), Logan (1977), and Sawyer and Haynes (1978) considered sampling problems; Gage (1972), Jackman (1976) and Sawyer (1976a) examined the interaction of the CLB with its host plants; and Gage (1974) investigated the relationship between the CLB and its principal parasite, <u>Tetrastichus</u> <u>julis</u> (Walker).[2] Ruesink

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[2] Hymenoptera: Eulophidae

(1972) and Casagrande (1975) studied the role of adult survival and behavior in the between-generation dynamics of the CLB. Several papers extending our knowledge of the CLB's basic biology have come out of S. G. Wellso's laboratory (Wellso 1972, 1973, 1974, 1976, 1978; Wellso et al. 1973, 1975; Wellso and Cress 1973; Hoxie and Wellso 1974).

As mentioned above, several population models have been developed for the cereal leaf beetle. Ruesink's (1972) model is a simple one. Although the beetle population is distributed among wheat and oat acreages having low, moderate and high densities, no spatial dynamics are involved and the model is essentially a single-site model. The models of both Ruesink (1972) and Tummala et al. (1975) are based on difference equations and are capable of simulating several generations. The models of Gutierrez et al. (1974), Lee et al. (1976), and Fulton (1978), on the other hand, are not only single-site models, but are also restricted to within-generation dynamics (Gutierrez et al. state that their model can be cycled year after year, but it was apparently not used in this way). The model of Gutierrez et al. (1974) is a discrete model with physiological time as the independent variable. It incorporates egg parasitism and a plant-submodel. Fulton's (1978) model uses chronological time as the independent variable of differential equations, and was designed to be used in an on-line mode for pest management purposes. It incorporates no parasite or host-crop components. The model of Lee et al. (1976) is a mathematical model based on partial differential equations with time and maturity as independent variables. By making simplifying assumptions and applying appropriate constraints, analytical solutions for the density of each life stage are derived.

In recent years the cereal leaf beetle has served as a prototype for the elaboration of pest management principles and systems (Fulton and Haynes 1975, 1977a, 1977b; Haynes et al. 1973; Tummala and Haynes 1977; Casagrande and Haynes 1976a).

Small scale field and laboratory studies have shown that host crop resistance, in the form of leaf pubescence in wheat, is a promising tool for the suppression and management of the CLB (Gallun et al. 1966; Schillinger and Gallun 1968; Webster et al. 1973; Casagrande and Haynes 1976b; Hoxie et al. 1975; Webster 1977; Wellso 1973). A large-scale pilot project to assess the impact of a general release of pubescent wheat on the population dynamics of the CLB is currently underway (Logan 1977; Sawyer 1976b; Sawyer 1978). An understanding of the CLB's spatiotemporal dynamics is of paramount importance in predicting the beetle's response to such a control measure.

In recent years the problem of spatiotemporal dynamics has begun to receive the attention it deserves in theoretical analyses (Bailey 1968; Birch 1971; den Boer 1968, 1971; Holling et al. 1976; Kitching 1971; Levin 1976; Watt 1968; Wiens 1976) and, more rarely, in experiments (Huffaker 1958; Iwao 1971; Pimentel et al. 1963). Many of these authors have noted that the majority of population dynamics studies in the past have neglected any spatial consideration.

Similarly, the distribution of organisms is frequently considered by way of describing, statistically, the spatial features of a population at a fixed point in time (e.g., Bliss and Fisher 1953;

Clark and Evans 1954; Lloyd 1967; Patil *et al*. 1971; Robinson 1954; Taylor 1961). Dispersal, which would logically seem to be the process linking temporal dynamics and spatial phenomena, is often dealt with as an isolated event, without reference to its role in population processes or its contribution to the spatial pattern of the population (e.g., Wolfenbarger 1975). Models of "dispersal" are even constructed which omit time as a variable (Cartwright et al. 1977; Poole 1974, p. 91-92). While these various approaches undoubtedly contribute to our understanding of the various components of spatio-temporal population dynamics, they do not elucidate the behavior of the system as a whole.

DATA SOURCES

The analyses performed in this research have utilized a huge data base accumulated over many years through the efforts of several workers.

Since 1967 detailed population studies of the cereal leaf beetle have been conducted at Michigan State University's W. K. Kellogg Biological Station near Gull Lake (Kalamazoo County), MI. These studies have been primarily concerned with the within-generation population dynamics of the beetle. Data are available (Helgesen 1969; Gage 1972, 1974; Sawyer 1976a and unpubl.; Lampert unpubl.) on basic population parameters measured during the period 1967-77 in permanent research plots generally consisting of one winter wheat field and one spring oats field each year, located near each other in section 9 of Ross Township (Kalamazoo County). Due to crop rotation practices, these plots were not located in exactly the same field each year. Data from more general surveys of adult populations in all fields in the 4 mi^2 area at Gull Lake are also available for most of these years.

A large data set has also been gathered for the resistant wheat project mentioned above (Logan 1977; Sawyer 1976b, 1978). This work was carried out in a 16 mi^2 (41.4 km^2) area in Galien Township (Berrien County), Michigan, and La Porte and St. Joseph

Counties, Indiana. Every grain field in the area (approximately 70) was intensively sampled for all life stages at frequent intervals throughout each season. Densities and rates of emergence of overwintered cereal leaf beetles were estimated for each of the major overwintering habitats. Experiments intended to evaluate the behavioral response of adult beetles to resistant wheat were also conducted and provide information on the dispersal process.

PRELIMINARY ANALYSES

At Gull Lake, the larval density in the research plots increased to a peak level in 1969, then rapidly declined and has remained very low since 1973 (Fig. 1). In this 11-year period, the density of larvae varied by factors of about 1000 in oats and 7000 in wheat. Population data for Gull Lake are summarized in Table 1. Parameters were calculated from data extracted from the following sources:

1967-69: Helgesen (1969), pp. 43, 88, 90, 93

1970-73: Gage (1972), p. 100
Gage (1974), pp. 101, 124, 127, 168-72

1974-75: Sawyer, A. J., unpublished data

1976-77: Lampert, E. P., unpublished data

The total seasonal egg and larval density estimates were made by quadrat sampling at frequent intervals, constructing a density vs cumulative degree-days curve, numerically integrating this curve and dividing the result by the mean number of degree-days that an individual insect is exposed to sampling (the developmental period) (Southwood 1966). The developmental times used were 180 and 240 degree-days > 48(F) (100 and 133°D > 8.9(C)), respectively, for eggs and larvae, as reported by Tummala _et_ _al_. 1975.[3]

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[3] Guppy and Harcourt (1978) have recently reported the developmental times to be 157 and 247°D > 48(F) (87 and 137°D > 8.9(C)).

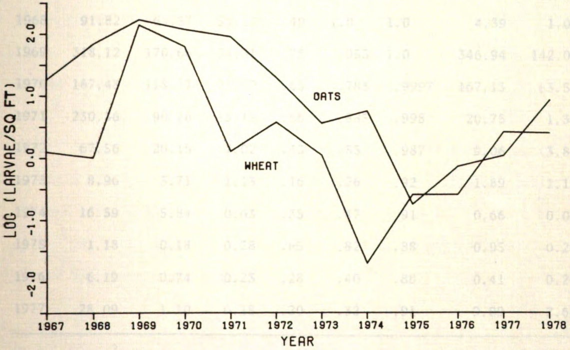

Fig. 1.--Egg and larval densities ($\log_{10}$ scale) in the Gull Lake research plots from 1967 to 1978.

Table 1.--Population parameters estimated for research plots at Gull Lake.

Year	E_o	L_o	P_o	S_P	S_{Tj}	S_I	E_w	L_w
1967	29.47	18.26	7.24	0.33	1.0	1.0	2.53	1.27
1968	91.82	69.57	51.13	.49	1.0	1.0	4.39	1.02
1969	318.12	170.66	34.31	.75	.993	1.0	346.94	142.00
1970	167.48	118.11	21.62	.65	.783	.9997	167.13	63.51
1971	230.36	90.26	13.13	.66	.885	.998	20.75	1.30
1972	67.56	20.15	7.02	.43	.55	.987	9.06	3.84
1973	8.96	3.71	1.13	.16	.26	.92	1.89	1.13
1974	16.59	5.84	0.63	.35	.47	.91	0.66	0.02
1975	1.18	0.18	0.28	.65	.82	.88	0.95	0.26
1976	6.19	0.74	0.23	.28	.40	.88	0.41	0.26
1977	28.09	1.10	0.18	.20	.32	.91	9.09	2.64

E_o = eggs/ft^2 in oats (seasonal total)

L_o = larvae/ft^2 in oats (seasonal total)

P_o = pupae/ft^2 in oats (seasonal total)

S_P = pupal survival in oats (adults emerging/pupae, from soil samples)

S_{Tj} = Survival from parasitism by *T. julis* (from soil samples)

S_I = Survival from parasitism by ichneumons (*Diaparsis* spp. and *L. curtus*) (from soil samples)

E_w = eggs/ft^2 in wheat

L_w = larvae/ft^2 in wheat

Such density estimates are intended to represent the number of individuals entering the stage. This is true, in fact, only when any mortality occurs at the end of the stage. When the mortality pattern is otherwise, the density estimates (and stage specific survival rates calculated from them) are in error. An analysis of the nature of these errors is given by Sawyer and Haynes (1979).

Of the Gull Lake data, one might well ask why the density of larvae fluctuated so dramatically during the 11-year observation period. Could knowledge of the causes lead to predictions of the direction and magnitude of population change? "Certainly there is no field of population management in which the forecast of densities is more vital than in applied entomology" (Voute 1971).

As Watt (1961) has proposed, a model for a population in a closed system may take the form:

$$N(t+1) = N(t) \cdot S_1 \cdot S_2 \cdots S_n \cdot P_f \cdot F \qquad (1)$$

where N(t+1) is the density of insects of a particular life stage in generation t+1, N(t) is the density of this same stage in generation t, the S_i are the proportions surviving through the ith of n life stages, P_f is the proportion of adults which are female, and F is the mean fecundity. A model of this form for the cereal leaf beetle is:

$$L(t+1) = L(t) \cdot S_L \cdot S_P \cdot ASF \cdot S_E \qquad (2)$$

where L(t+1) and L(t) are the larval densities in years t+1 and t, S_L, S_P and S_E are the survival rates for larvae, pupae, and eggs, and

ASF is a catch-all factor representing adult survival, sex ratio and fecundity.

The selection of the larval stage as the one on which to base the model was not fortuitous. Watt (1961) recommended the adult stage and Morris (1963) preferred the egg stage in their applications. Actually, the life stage used to calculate the index should be that which is most effectively sampled and which provides a useful result. For the cereal leaf beetle, the larval stage is relatively numerous, immobile, and visible, and is more easily, accurately, and precisely sampled than other life stages. The larval stage is also of interest as it causes most of the economically important crop damage.

Equation (2) may be rewritten as

$$L(t+1)/L(t) = S_L \cdot S_P \cdot ASF \cdot S_E \qquad (3)$$

which, in effect, decomposes the generation survival (S_G), or trend index, L(t+1)/L(t), into a product of the survival rates for each life stage. Larval survival could be broken down further into the survival rates for each of the four larval instars, but reliable age-specific data are not available for the entire 11 year period at Gull Lake. The term ASF, which covers a time span of approximately July to April, could also be partitioned into its components, but, again, the necessary data are lacking. ASF was simply calculated as a "residual" term from a knowledge of summer adult density and resultant egg density in the spring: ASF = eggs produced/adults emerging from pupation. The true significance of this factor will be examined in detail below. While pupal survival (S_P) was estimated quite directly by examining pupal cells from soil samples, egg and larval survival rates (S_E and S_L) were calculated as the ratio of density estimates for successive stages. These estimates are subject to complex errors related to the actual magnitude and timing of mortality within the stage (Sawyer and Haynes 1979).

The model (3) can be transformed into an additive one by taking the logarithm of each side of the equation:

$$\ln(S_G) = \ln(S_L) + \ln(S_P) + \ln(ASF) + \ln(S_E) \qquad (4)$$

Two approaches may now be taken to analyze the relative contribution of variations in each of the survival components to variation (and thus, prediction) of the trend index. The first comes from recognizing equation (4) as the key-factor relationship of Varley and Gradwell (1970):

$$K = k_1 + k_2 + k_3 + k_4 \qquad (5)$$

where K is the logarithm of the trend index, $k_1 = \ln(S_L)$, etc. Key factor analysis is essentially visual and subjective. Inspection of Figs. 2-7 shows that k_3, representing ASF, appears to be the key factor, and k_1, or S_L, is also of some importance. Factors k_5 (Fig. 6) and k_6 (Fig. 7) are $\ln(S_{Tj})$ and $\ln(S_I)$, where S_{Tj} is the survival (or escape) from parasitism by the larval parasite T. julis and S_I is survival from ichneumons Diaparsis spp. and Lemophagus curtus Townes.[4] These parasites kill the pre-pupa after it forms its pupal cell in

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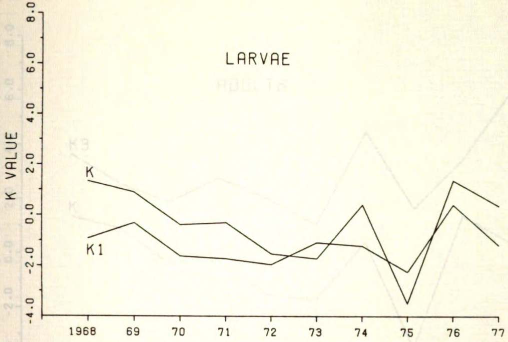
[4] Hymenoptera: Ichneumonidae



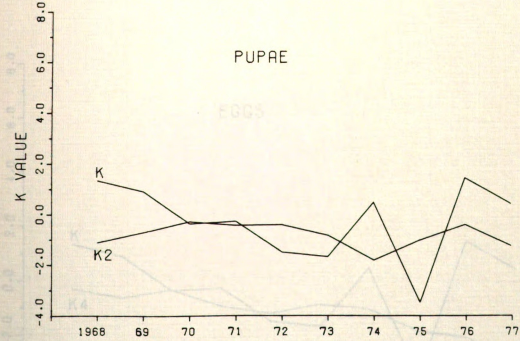
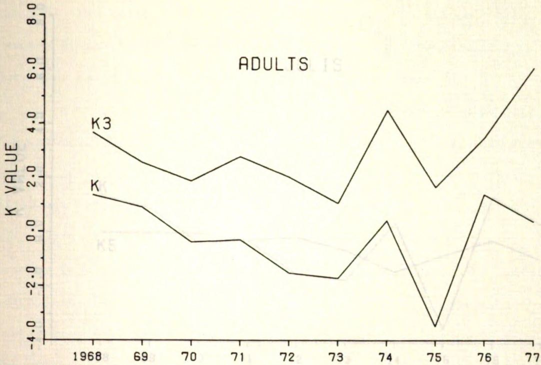


Fig. 2-7.--Key factor analysis of Gull Lake oat data ($K = S_G$, k_1 = larval survival, k_2 = pupal survival, k_3 = adult survival and fecundity, k_4 = egg survival, k_5 = survival from T. julis parasitism, k_6 = survival from ichneumon parasitism).



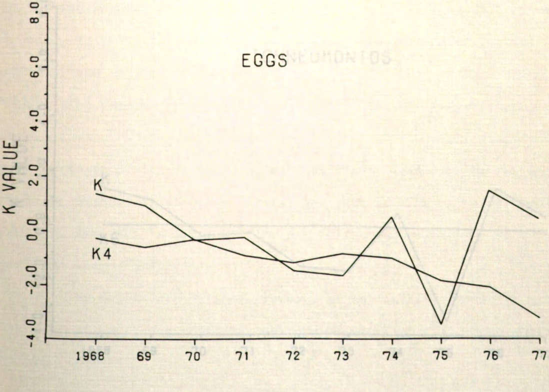


Fig. 2-7.--Continued.

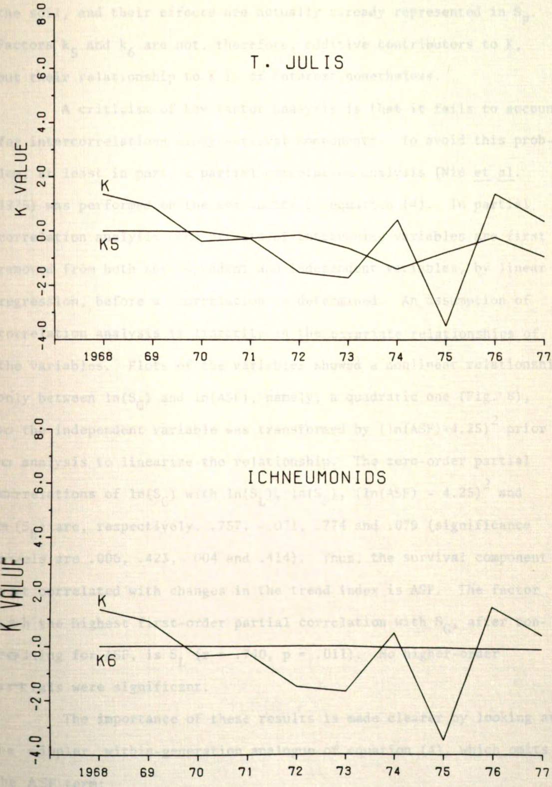


Fig. 2-7.--Continued.

the soil, and their effects are actually already represented in S_P. Factors k_5 and k_6 are not, therefore, additive contributors to K, but their relationship to K is of interest nonetheless.

A criticism of key factor analysis is that it fails to account for intercorrelations among survival components. To avoid this problem, at least in part, a partial correlation analysis (Nie _et al_. 1975) was performed on the components of equation (4). In partial correlation analysis, the effects of intervening variables are first removed from both the dependent and independent variables, by linear regression, before a correlation is determined. An assumption of correlation analysis is linearity in the bivariate relationships of the variables. Plots of the variables showed a nonlinear relationship only between $\ln(S_G)$ and ln(ASF), namely, a quadratic one (Fig. 8), so the independent variable was transformed by $(\ln(ASF)-4.25)^2$ prior to analysis to linearize the relationship. The zero-order partial correlations of $\ln(S_G)$ with $\ln(S_L)$, $\ln(S_P)$, $(\ln(ASF) - 4.25)^2$ and $\ln(S_E)$ are, respectively, .757, -.071, .774 and .079 (significance levels are .006, .423, .004 and .414). Thus, the survival component most correlated with changes in the trend index is ASF. The factor with the highest first-order partial correlation with S_G, after controlling for ASF, is S_L ($r = .740$, $p = .011$). No higher-order partials were significant.

The importance of these results is made clearer by looking at the simpler, within-generation analogue of equation (4), which omits the ASF term:

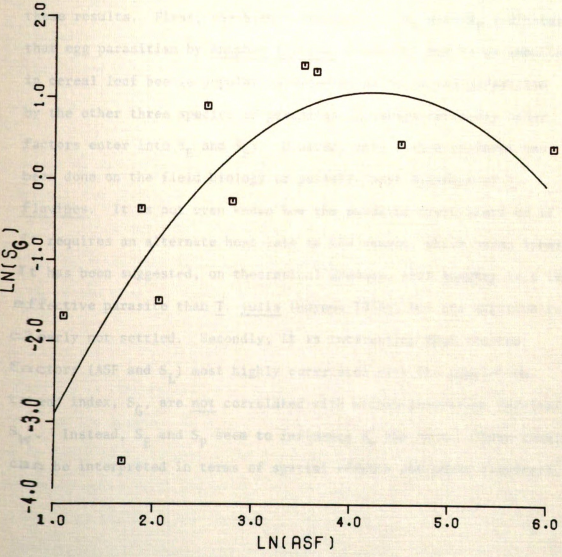


Fig. 8.--The quadratic relationship between $\ln(S_G)$ and ln(ASF) in oats at Gull Lake, 1967-77.

$$\ln(S_W) = \ln(S_E) + \ln(S_L) + \ln(S_P) \qquad (6)$$

where S_W is the within-generation survival (adults emerging from pupation/eggs laid in the same year). The simple correlations of $\ln(S_W)$ with $\ln(S_E)$, $\ln(S_L)$, and $\ln(S_P)$ are, respectively, .755, .578, and .728 (all significant at $p < .05$). Two points may be made about these results. First, the high correlation of S_W with S_E indicates that egg parasitism by Anaphes flavipes Foerster[5] may be as important in cereal leaf beetle population dynamics as is larval parasitism by the other three species of parasites (although certainly other factors enter into S_E and S_P). However, very little research has been done on the field biology or parasite/host dynamics of A. flavipes. It is not even known how the parasite overwinters or if it requires an alternate host late in the season, which seems likely. It has been suggested, on theoretical grounds, that Anaphes is a less effective parasite than T. julis (Haynes 1973), but the question is clearly not settled. Secondly, it is interesting that the two factors (ASF and S_L) most highly correlated with the population trend index, S_G, are not correlated with within-generation survival, S_W. Instead, S_E and S_P seem to influence S_W the most. These results can be interpreted in terms of spatial effects and adult dispersal.

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[5] Hymenoptera: Mymaridae.

THE ROLE OF DISPERSAL IN POPULATION DYNAMICS

Morris (1963) modified Watt's (1961) model (equation 1) by including an additional term to consider losses from or additions to the system due to dispersal of the adult stage (spruce budworm moths):

$$N_E(t+1) = N_E(t) \cdot S_E \cdot S_L \cdot S_P \cdot S_A \cdot P_f \cdot F \pm N_D \qquad (7)$$

where N_D is the density of eggs added to or subtracted from the expected $N_E(t+1)$ as a result of moth dispersal.

This model has a difficulty in that it suggests that it is the egg stage that disperses, since eggs are directly added to or subtracted from the system. A more realistic model would be:

$$N_E(t+1) = N_E(t) \cdot S_E \cdot S_L \cdot S_P \cdot S_A \cdot P_f \cdot F \cdot p + N_A' \cdot S_A' \cdot P_f' \cdot F' \qquad (8)$$

where p is the proportion of surviving adults which do not disperse out of the system, and S_A', P_f' and F' are defined as for equation (1) but apply to N_A' adults which disperse into the system. Clearly, as p becomes quite small and/or N_A' becomes quite large, the characteristics of the immigrant segment of the population take on increasing importance and those of the "resident" portion of the population lose importance in determining the trend index, $S_G = N_E(t+1)/N_E(t)$. Further complexities are introduced if the immigrants are derived from a number of sources with each group possessing very different characteristics or if some earlier life stage (or more than one life stage) disperses. In the case of the spruce budworm, three stages may disperse: 1st instar larvae in the fall, 2nd instars in the spring, and adults in the summer. Morris' (1963) approach to the problem of dispersal was to incorporate the net effect of dispersal gains and losses into the age-specific survival rates peculiar to that site. Ultimately, even the additive term N_D was dropped from the model as being inseparable from S_A. Morris, then, did not take on the complexities of a spatial approach to dispersal in which the study site is but one component in a heterogeneous spatial matrix of sources and sinks for dispersing individuals. A recent modeling effort by Holling et al. (1976) takes dispersal among 265 spatial compartments into account, but at the cost of considerable within-site detail.

Returning to the finding that ASF and S_L are important determinants of the trend index for a single-site cereal leaf beetle population model at Gull Lake, while S_E and S_P are most highly correlated with within-generation survival, we can now understand these results in terms of the life history of the species and the characteristics of its agricultural habitat. Summer adults leave the field from which they emerge from pupation, and move about in the environment--possible over a large area. Following an overwintering period in woodlots, fence rows, etc., in spring the beetles again move about before entering grain fields. Meanwhile, the grain fields themselves have "moved," because a field will not usually be planted to the same crop in two successive years. Thus, the net effect of this thorough mixing is that the entire population disperses out of a field and it may be an entirely different, heterogeneous, group of beetles which returns to the nearest field in the next year. This redistribution shows up as variations in the variable ASF.

ASF actually represents several survival and redistributional components, as well as sex ratio and fecundity:

$$ASF = S_{su} \cdot R_{su} \cdot S_{wi} \cdot S_{sp} \cdot R_{sp} \cdot P_f \cdot F \qquad (9)$$

where su, wi and sp subscripts indicate summer, winter and spring, S's are survival rates for the periods indicated, and R's are factors accounting for gains or losses due to redistribution occurring during the period indicated (this assumes that the regional population is homogeneous with respect to fecundity, sex ratio, and survivorship; heterogeneity in these components adds to the complexity). A knowledge of which of these factors are primarily responsible for observed variations in ASF is desired, but the values of these separate components are not available for the entire period 1967-77 at Gull Lake. Casagrande (1975) concluded that overwintering mortality in the soil (S_{wi}) was unrelated to cold exposure. It seems likely, then, that ASF is influenced primarily by events during the summer and spring dispersal and ovipositional periods. A multivariate analytical approach may shed some light on the identity of important factors, but an understanding of the biological processes must come from experimental studies. Deductive submodels based on assumptions about the biological processes involved may be of use in guiding research and in constructing simulation models (Eberhardt 1970; Watson 1971; Watt 1962; Varley and Gradwell 1970).

Because all of the redistributional phenomena are incorporated into ASF, it is to be expected that ASF will be highly correlated with the trend index (measured at one place) of this species in which 100% of the population disperses.

Another effect of total redistribution is to obscure, or minimize, the influence of processes operating on a field scale, such as egg and larval parasitism, on the year-to-year fluctuation in larval density in a given location. Because of spatial heterogeneity of both the parasite and cereal leaf beetle populations, parasitism may vary as much from field to field as from year to year.[6] Parasitism might, therefore, show little correlation with the change in beetle density <u>after redistribution</u>, even though it has a considerable impact on the within-generation (within-field) survival of the beetle.

Larval survival, however, is not associated with parasitism and may be affected primarily by factors operating on a regional scale, such as temperature and rainfall. This survival component, then, should affect the entire regional population similarly.

The factors, then, which determine the changes from year to year in the population density at a particular site may be visualized as falling into two categories: (1) those which are general, applying on a regional scale (such as weather) and (2) those which are local, or unique to a particular field (such as local parasite density). Factors contributing to site to site differences in density in a

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[6] In 12 oat fields in a 16 mi^2 area of Berrien County in 1976, egg parasitism ranged from 6% to 50% (Sawyer 1976b) and in 1977 ranged from 13% to 80% in 7 fields (Sawyer 1978). Similar spatial variation was found for larval parasitism.

particular year may also be classified as being either general, such as the relative acreages of winter and spring grains in a region (Casagrande 1975, p. 50; Ruesink 1972, p. 29), or unique, such as a field's planting date or its nearness to overwintering sites. Dispersal interacts with this complex of factors by tending to "homogenize the effects of local uniqueness" (Levin 1976), or, for some factors, by increasing the effects of local uniqueness. Dispersal may itself be density dependent, acting to increase or decrease density differences from field to field through intraspecific attraction or repulsion. Dispersal may initially increase a field's population with immigrants from nearby population sources, but if dispersal continues to operate, site to site differences may become homogenized. These ideas are summarized in Table 2. General factors are able to contribute to site to site differences in density only through dispersal. In the absence of dispersal, the only factors contributing to site to site differences would be those affecting year to year fluctuations in density within the isolated fields.

It is obvious that in the extreme case of total dispersal of a species inhabiting a patchy environment, such as the cereal leaf beetle, Morris' (1963) approach to studying population dynamics is particularly unproductive. No amount of on-site study of survival rates will lead to an understanding of long-term population dynamics or the ability to predict the density at that site even one generation into the future. Actually, in any situation, the appropriateness of such an approach is simply a matter of degree depending on how much an observed "survival" rate includes gains and losses to the system as a result of dispersal.

Table 2.--Examples of general (regional) and unique (local) factors affecting year-to-year (within-site) changes and site-to-site (within-year) differences in density of a population, and the direction of influence which dispersal may have on the action of these factors: (-) indicates an averaging, countering, or minimizing influence, (+) indicates an emphasizing or maximizing influence.

	General	Unique
Year-to-Year	Weather	Local parasitism and predation (-)
	Regional pest/ parasite densities	Food quality (-)
		Population Quality (-)
		Density (±)
Site-to-Site	Relative crop acreages in region	Attractiveness of site (+)
	Crop synchrony	Location with respect to population sources (±)
		Previous population level (-)

HYPOTHESES ON CROP PREFERENCE AND DISPERSAL OF THE CEREAL LEAF BEETLE

Ruesink (1972, p. 64) concluded, on the basis of surveying adult densities in all fields at Gull Lake in 1971, that

> Spring adults do not move from wheat to oats as has been assumed. It now seems clear that when beetles first emerge from overwintering, some portion of the population infests winter grains. The remainder stays in wild grasses or flies around in search of oats until the oats germinate and come up. Then the remainder infests oats. The portion in winter grains remains there, with the observed reduction in density primarily due to mortality not emigration.
>
> The portion of the population that infests winter grains is not constant from year to year. It probably also varies between geographic regions. The primary factor affecting the portion entering winter grains seems to be the size of the plant as it comes through the winter.

He incorporated this hypothesis of a fixed preference of individual beetles for one crop or the other into his simulation model of cereal leaf beetle population dynamics. The portion of the population preferring wheat immediately entered that crop upon emergence, while the remaining ("oat") beetles were held aside until oats became available, at which point they were placed in that crop. He initially fixed the proportion preferring oats at .90, but found that the regional population trend index was sensitive to variations in this parameter, and also interacted with the relative acreages of the two crops through density-dependent mortality effects.

Ruesink's (1972) assumption that there are two distinct types of beetles, those preferring oats and those preferring wheat (each type rejecting the other crop), seems an unnecessary complication (though not necessarily untrue: see discussion of host selection in Andrewartha and Birch 1954, pp. 509 and 691-3). A slightly more flexible assumption might have been that a population possesses a *probability distribution* of host preferences. For example, an average individual may *tend* to prefer oats 3 to 1 over wheat or be 3 times more *likely* to enter oats than wheat. It can readily be shown that, under this assumption, the final distribution of beetles among crops would be the same as if the population were composed of different proportions of individuals each with a fixed preference. The advantage to this probabilistic interpretation is that there is no need to hypothesize that different "kinds" of beetles exist. Each individual may possess the same set of preferences or at least have preferences drawn from a single distribution.

Fulton (1978) made a different assumption about the crop preference of beetles in his own simulation model, returning to the older picture of adults first entering winter grains and then moving to spring grains. He modeled this process by having the transfer from wheat to oats begin as soon as oats came up, and assumed that the rate of movement between crops followed a normal distribution with respect to degree-days. He found that the synchrony of observed and calculated density curves in oats was very sensitive to the parameter determining when this movement occurred.

Actually, Fulton's (1978) model is equivalent to the probabilistic form of Ruesink's (1972) model, with a beetle possessing a fixed preference for wheat for a certain portion of its life, and then shifting to a fixed preference for oats for the remainder of its life. The portion of a beetle's life spent in oats in Fulton's model is equivalent to the expectation of entering oats in the former model, with both models making probabilistic statements about the overall distribution of activity in the two crops.

The problem with both Ruesink's (1972) and Fulton's (1978) hypotheses about crop preference is that they propose a rigid relationship (within a given year) describing the expected number of adults which will be found in each crop, irrespective of the spatial patterning of the crop environment.

I propose as an alternative hypothesis that beetles not only move from wheat to oats, but may also move from oats to wheat. In general, they move continuously from field to field, most likely entering fields at random (as they chance to encounter them) and leaving them at a rate related to their attractiveness.[7] "Preference" is thus seen not as an intrinsic property of the beetle, but rather as a property of the field. The beetle may respond, through its

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[7] Fields, of course, may also be <u>entered</u> at a rate related to their attractiveness, but studies have failed to find a chemical attractant for the cereal leaf beetle derived from the host crop (Jantz 1965). In a study with blowflies, MacLeod and Donnelly (1960) observed random dispersal combined with a varying response to habitats entered by chance. An assumption of random movement greatly simplifies a simulation of the dispersal process. Even if there is some attraction to the crop, if the distance of attraction (area of discovery) is small compared to the size of a field and the spatial separation of fields, then an assumption of random dispersal should not lead to significant errors.

movements, to specific stimuli which vary from field to field, and the apparent preference for one crop over another is a function of the array of such stimuli that each crop presents. This array of stimuli, or "host quality," may vary from field to field as well as between crops (for example, planting dates of individual fields may vary). Since succulent young growth is more suitable for feeding and oviposition (Wilson and Shade 1966), spring oats will generally be a more "preferred" host than winter wheat. Beetles might then be expected to be less likely to leave oats, which would therefore act as a sink and accumulate higher densities.

This hypothesis is simple in that it assumes only random inter-field movement and fixed behavioral responses to specific environmental stimuli, but allows for the possibility of dispersal interacting with environmental heterogeneity (the unique factors of Table 2) to produce the complex spatial pattern of densities observed over a large area.

AN ANALYSIS OF HOST CROP PREFERENCE

An analysis of crop preference and beetle dispersal can be made if the regional mean egg densities in oats and wheat are known. This analysis should be able to distinguish between the random-movement hypothesis of beetle dispersal and the hypothesis of a fixed crop preference or fixed sequence of movement from wheat to oats.

The analysis deals with eggs rather than adult densities because it is much simpler to establish total egg densities than total adult densities, since it is not known how long an adult is subject to sampling. It is assumed here that egg densities are directly related to adult densities.

The total number of eggs in a region in oats and wheat are

$$T_o = E_o \times A_o \tag{10}$$

$$T_w = E_w \times A_w$$

where T_i is the total regional number of eggs, E_i is the mean regional density of eggs and A_i is the acreage of crop i in the region. T_o/T_w is the ratio of the two subpopulations. The ratio of densities in the two crops is

$$E_o/E_w = (T_o/A_o)/(T_w/A_w)$$

$$= (T_o/T_w) \times (A_w/A_o)$$

$$= (T_o/T_w) \times CR$$

where CR is the ratio of wheat acreage to oat acreage in the area. Rewriting this, we have

$$CR = (E_o/E_w)/(T_o/T_w). \qquad (11)$$

Due to changing agricultural conditions, the crop ratio may vary from year to year, but the above relationship must always hold true. It is of interest to examine which component of the right-hand-side of equation (11) covaries most directly with CR. If CR increases from one year to the next, then either E_o/E_w must increase while T_o/T_w remains relatively constant, E_o/E_w must remain constant while T_o/T_w decreases, or there may be compensating changes in both components. Which of these situations actually occurs provides information on the nature of "crop preference" in the cereal leaf beetle.

For example, if T_o/T_w remains constant despite a change in CR, it would imply that beetle distribution between the two crops is determined by some fixed preference of individual beetles for either oats or wheat (i.e., there are "oat beetles" and "wheat beetles"). This would require some mechanism of attraction of the beetles to the proper crop, or would at least require that beetles entering the "wrong" crop leave without ovipositing. Thus, an increase or decrease in oat acreage relative to wheat would not affect the total number of beetles in oats or wheat. Such an acreage change would, however, alter the density of beetles in the two crops, by concentration or dilution, so E_o/E_w would vary directly with CR.

A similar pattern would result from the situation in which all beetles first entered wheat and then moved to oats. If the crop ratio changed, the relationship between the total number in each crop would not be altered, but the relationship between densities would.

Alternatively, E_o/E_w may remain constant despite a change in CR. This would imply that beetles have no fixed preference for either crop, but rather disperse at random, entering and ovipositing in fields as they are encountered (this is not to say that the probability of leaving a field, or the oviposition rate while in the field, need be the same for both crops). As oat acreage increases relative to wheat (i.e., CR decreases), more beetles would chance to enter oat fields and T_o/T_w would increase. The relative densities in the two crops, however, would be unaffected as long as the relative suitabilities of the crops remained constant. Thus, an inverse relationship between CR and T_o/T_w would be expected, with E_o/E_w remaining constant.

While this analytical approach would seem to provide a neat way of separating some of the hypotheses, such clear-cut results are unlikely. If Ruesink's "fixed" proportion preferring oats, or Fulton's time at which beetles moved from wheat to oats, or the relative suitability of the crops varied from year to year, then a combination of varying T_o/T_w and E_o/E_w could result for any of the hypotheses. Factors contributing to variations might be the relative maturity of the two host crops and the synchrony of the insect with its hosts. Some of the "background noise" in the analysis due to these factors might be controlled, statistically, by removing the correlation of the components of equation (11) with variables thought to affect these synchronies. Such variables might include degree-day accumulations above the developmental threshold of winter grain at various points early in the year, the difference in degree-day accumulations with respect to plant and insect developmental thresholds, the amount of winter precipitation (which affects the growth of winter grains and planting date of spring grains), etc. After controlling for such effects, T_o/T_w should, theoretically, remain constant from year to year for both Ruesink's (1972) and Fulton's (1978) hypotheses. In contrast, E_o/E_w should remain constant after adjustment if intercrop distribution is random.

Two approaches may be taken in examining the components of variation in equation (11). One is to compare the relative variation in the two components T_o/T_w and E_o/E_w to determine which is more constant. Another is to compare the partial correlation of CR with T_o/T_w and E_o/E_w after controlling for the intervening environmental variables.

The limiting factor in successfully making these analyses is obtaining reliable estimates of the mean egg density for a large region for a number of years. The large-area study in Berrien County supplies such data for only three years, while the long-term data from Gull Lake are less extensive, representing just one or two fields each year. For the purposes of this analysis it was assumed that egg densities in the Gull Lake research plots at least reflected the regional mean density, but interfield variation in densities is known to be large, and inferences about regional dynamics must be made cautiously.

Gull Lake is located in the extreme northeast corner of Kalamazoo County, adjacent to both Barry and Calhoun Counties. The mean crop ratio for the three counties was used to represent the crop ratio for the Gull Lake area in any given year. These acreages were taken from various publications of the Michigan Crop Reporting Service.

At Gull Lake from 1967 to 1977, the ratio of wheat acreage to oat acreage ranged from 1.3 to 3.3. For these same years, the coefficient of variation (C.V. = $100S/\bar{x}$) for E_o/E_w was 89.6% and for T_o/T_w it was 102.0%. Thus, neither E_o/E_w nor T_o/T_w was constant. Furthermore, neither quantity was significantly correlated with CR ($r = .128$ and $r = -.255$ for E_o/E_w and T_o/T_w, respectively).[8]

To adjust for variations in relative crop maturity and beetle/host synchrony, a number of weather variables (Table 3) were considered in multiple regressions with E_o/E_w and T_o/T_w. Variables were chosen that were relevant to various aspects of crop development and beetle biology. For example, degree-days (°D) > 8.9 and 5.5 (C) represent meaningful time scales for the cereal leaf beetle and its hosts, respectively (Guppy and Harcourt 1978, Gage 1972), 55.5 and 111.1 °D > 8.9 (C) are points near the middle and end of spring adult emergence, etc. Some of the variables, such as JMAX, were recorded for other analyses, but were included here also.

Two variables were significantly related to variations in E_o/E_w: WPREC and TEMP. Together they accounted for 78% of the

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[8] All correlation analyses were accompanied by examinations of scatter plots to check for violation of the necessary assumption that the bivariate relationships are linear.

Table 3.--Weather variables considered in the analysis of crop preference at Gull Lake, 1967-77.

Variable	Description
WPREC	Total winter precipitation, Oct. - Mar. (cm)
WAVG	Mean winter temperature (Jan. - Mar.) (°C)
WMIN	Minimum winter temperature (Dec. - Mar.) (°C)
SNOW	Total days with snow on the ground $\geq$ 2.54 cm (Oct. - May)
FROST	Last day of year in spring with min. temp. $\leq$ 0°C
TEMP	Mean spring temp (April - June) (°C)
RAIN	Total spring precipitation (April - June) (cm)
JMAX	Max. temp., July of previous year (°C)
SNOWAM	Total days with snow on ground $\geq$ 2.54 cm (April - May)
AMINA	Average min. Temp., April (°C)
TEMPA	Average temperature, April (°C)
TEMPM	Average temperature, May (°C)
DDA	Cumulative degree-days > 8.9 °C on April 1
DDM	Cumulative degree-days > 8.9 °C on May 1
DDDA	°D > 5.5 °C - °D > 8.9°C on April 1
DDDM	°D > 5.5 °C - °D > 8.9°C on May 1
STR	(TEMP/RAIN)
JTR	(TEMP/RAIN)
DD55	°D > 5.5°C at 55.5 °D > 8.9°C
DD111	°D > 5.5°C at 111.1 °D > 8.9°C

variation in E_o/E_w. The standard error of estimate, given by $\sqrt{MSE}$ in the regression analysis, represents the standard deviation of the residuals of E_o/E_w after controlling for WPREC and TEMP (Nie et al. 1975, p. 331). Expressing this as a percent of the mean value of E_o/E_w yields a coefficient of variation (C.V.) for these residuals. The C.V. for E_o/E_w after controlling for the two environmental factors was 47.2%. The partial correlation of E_o/E_w with CR, after controlling for WPREC and TEMP, was .310 ($p > .05$, 7 df).

Four climatological variables were significantly related to variations in T_o/T_w: WPREC, TEMP, DDDM and DDA. Together they accounted for 95% of the variation in T_o/T_w. The C.V. for T_o/T_w after controlling for these factors was 29.5%, and the partial correlation of T_o/T_w with CR was .165 ($p > .05$, 5 df).

These results show that neither E_o/E_w nor T_o/T_w is significantly correlated with CR, but suggests that E_o/E_w is possibly more variable and more closely tied to variations in CR. These results support the idea of a fixed crop preference, but are rather inconclusive. The problems of using single field density estimates to represent the mean regional density, and of using the mean crop ratio for three counties to represent the ratio in the Gull Lake area, must be borne in mind.

The relative suitability of a field, or entire crop, may be a function of beetle density as well as crop maturity and other variables. Casagrande (1975) developed this idea into a descriptive model of beetle distribution in wheat and oats as a function of the regional population level. He noted that negative interactions between beetles (hypothesized by Helgesen in 1969) prevented the density of adults from exceeding some upper limit. In high density years these interactions would become important enough in the less preferred wheat to drive a larger portion of the population into oats. In support of this, he pointed out that over a four-year period (1971-74) the highest ratio of adult density in oats to density in wheat occurred in the year with the highest population, and the lowest ratio occurred in the year with the lowest population.

If Casagrande's (1975) model is correct, an examination of the Gull Lake data for 1967-77 might be expected to reveal a positive correlation between E_o/E_w and the total regional population, $T = T_o + T_w$. This analysis was carried out by first regressing E_o/E_w on CR, WPREC and TEMP to control for their effects on variation in the dependent variable. At this point the partial correlation of E_o/E_w with T was -.450 ($p = .264$, 6 df). The relationship, while insignificant, is opposite to that predicted by Casagrande (1975). The residuals of E_o/E_w (after fitting CR, WPREC and TEMP), are plotted in Figure 9, where it is seen that any negative correlation is due to one year (1969) in which the densities were very high. For the other years, the correlation is positive as predicted ($r = .438$) (a quadratic curve has been fitted to the data merely to emphasize these points; there is no significant regression here, either linear or quadratic). The aberrant year, 1969, might be explained as a result of the extremely high cereal leaf beetle population in that year, leading to severe defoliation of oats, early cessation of oviposition, and high egg mortality in that crop.

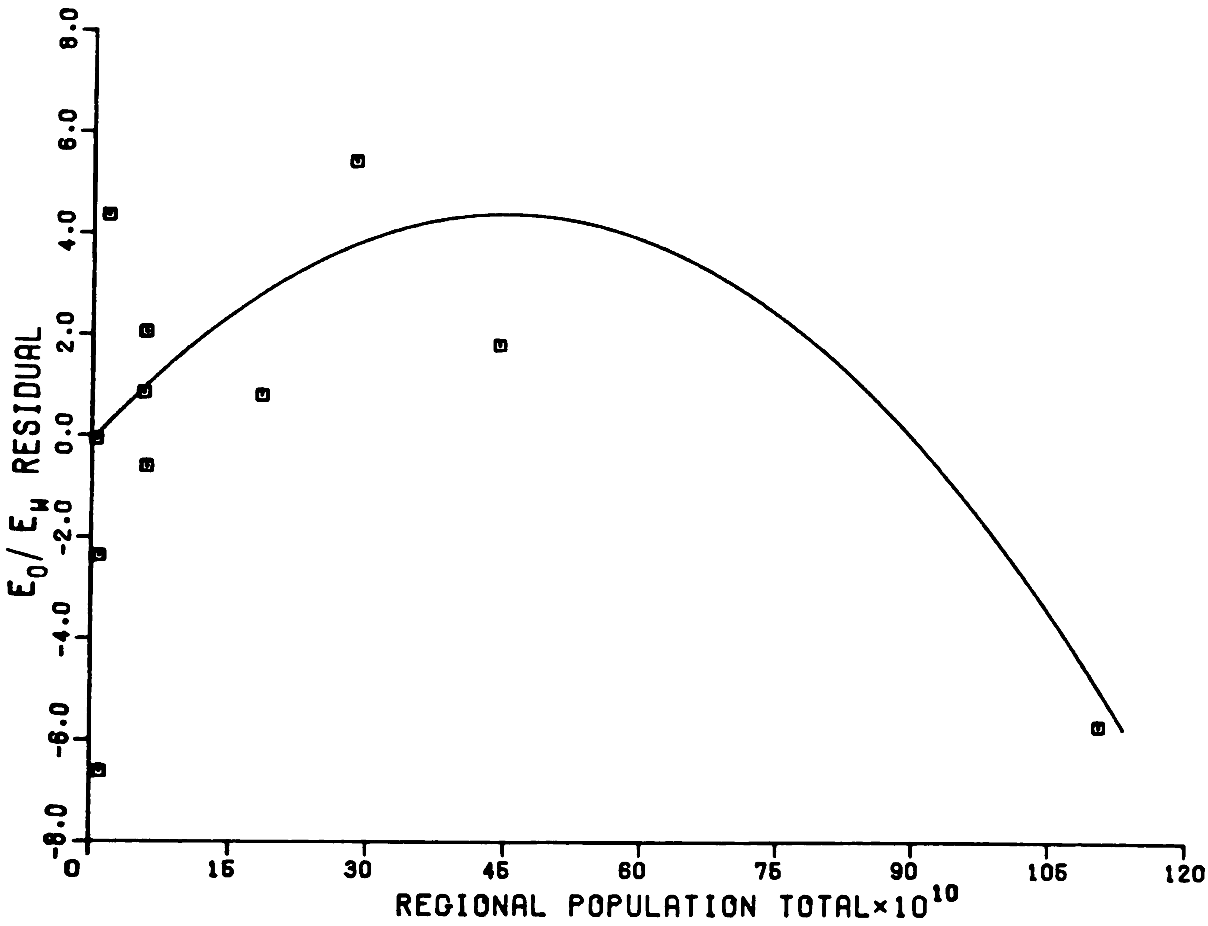

Fig. 9.--The residual of E_O/E_W, after controlling for CR, WPREC and TEMP by multiple linear regression, plotted against the total regional egg population, $T = T_O + T_W$, at Gull Lake during 1967-77.

The Galien data, while providing much better estimates of the mean regional egg density (Table 4), are from only three years (1975-77). This precludes a multivariate analysis. The situation is also complicated by the introduction of a third host crop, resistant (R) wheat. The R-wheat planted at Galien basically replaced susceptible (S) wheat acreage (the total of all wheat was 990, 1071 and 944 acres in 1975-77, but the R-wheat acreages were 0, 135 and 596 acres in these years). The R-wheat is not totally free of cereal leaf beetle adults or eggs, but densities are reduced. The expected effect of replacing some S-wheat with R-wheat, under an assumption of fixed crop preferences, would be to reduce the total number (T_s) of eggs found in S-wheat, but to increase their density (E_s). This is because part of the beetle population will be transferred from S-wheat to R-wheat but the R-wheat will sustain lower densities, with relatively more beetle remaining concentrated in the S-wheat. Thus, planting R-wheat causes the CR ratio for S-wheat and oats decline, but the effect of this is now different: both E_o/E_s and T_o/T_s would vary if the crop preference was fixed.

With random dispersal, E_o/E_s should still remain constant, since the relative density in a crop is a result of its suitability, which is unaltered by the addition of a third crop. The beetles displaced from R-wheat would end up in both S-wheat and oats in proportion to their relative attractiveness.

The coefficient of variation (C.V.) for E_o/E_s during 1975-77 at Galien was 63.7%, while the C.V. for T_o/T_s was 57.2%. Thus E_o/E_s and T_o/T_s were about equally variable. The correlation between E_o/E_s and CR was .114, and the correlation between T_o/T_s and CR was -.245.

Table 4.--Regional total and mean density of eggs in susceptible wheat and oats in the Galien study area.

	1975	1976	1977
S-Wheat			
Acres = A_s	990	936	348
Total Eggs = T_s	3.76×10^8	2.17×10^8	1.24×10^8
Eggs/Acre = E_s	3.80×10^5	2.32×10^5	3.57×10^5
Oats			
Acres = A_o	151	145	78
Total eggs = T_o	4.26×10^7	9.81×10^7	4.27×10^7
Eggs/Acre = E_o	2.82×10^5	6.76×10^5	5.47×10^5
CR = A_s/A_o	6.56	6.46	4.46
E_o/E_s	.741	2.920	1.532
T_o/T_s	.113	.452	.344
WPREC (cm)	43.48	46.43	39.01

While not significant, those are very similar to the correlations obtained for the Gull Lake data prior to adjustment for climatological variables.

WPREC was again considered as a control variable for variations in crop synchrony. In simple linear regressions, WPREC accounted for 28.4% and 4.0% of the variation in E_o/E_s and T_o/T_s, respectively. The C.V. of the residuals of E_o/E_s and T_o/T_s were then 76.2% and 79.2%. Again, the two components of CR were equally variable. There were insufficient degrees of freedom for calculating partial correlations of E_o/E_s and T_o/T_s with CR after controlling for WPREC.

In short, the limitations of both the Gull Lake and Galien data sets preclude a proper analysis of crop preference in the CLB as set forth above, and the results obtained are inconclusive. Assumptions of the method which were also undoubtedly violated were that the total regional population remained constant from year to year and that all beetles were present in one crop or the other (i.e., there is no nonhost buffer). These assumptions are necessary to ensure that any change in a crop-acreage would be followed by changes in either the total number of beetles entering the crop or their concentration.

COMPARTMENTAL ANALYSIS OF DISPERSAL AND MORTALITY

With certain assumptions, it may be possible to analyze the rates of movement of adult beetles between winter and spring grains using compartmental analysis. The outcome of such an analysis would be to establish whether movement from spring grains back to winter grains does in fact take place, what the relative rates of movement between the two crops are, and to provide estimates of the mortality rate of spring beetles.

Compartmental analysis is concerned with systems of linear first order differential equations having constant coefficients, and has been found increasingly useful in recent years in the biological sciences, particularly physiology (Wong 1978).

With reference to the cereal leaf beetle population at Galien, the analysis assumes that there are only three compartments in which all beetles are located, corresponding to S-wheat, R-wheat, and oats (Figure 10). These subpopulations are X_1, X_2, and X_3. In 1975 the R-wheat compartment did not exist and in 1976 it was so minor that winter grains were treated as a single compartment.

Other assumptions are that any beetle leaving one compartment (except by mortality) appears in one of the others; there is a pulse input of beetles into winter grain; rates of movement, α_{ij}, between crops are fixed (but not necessarily equal) proportions of the number

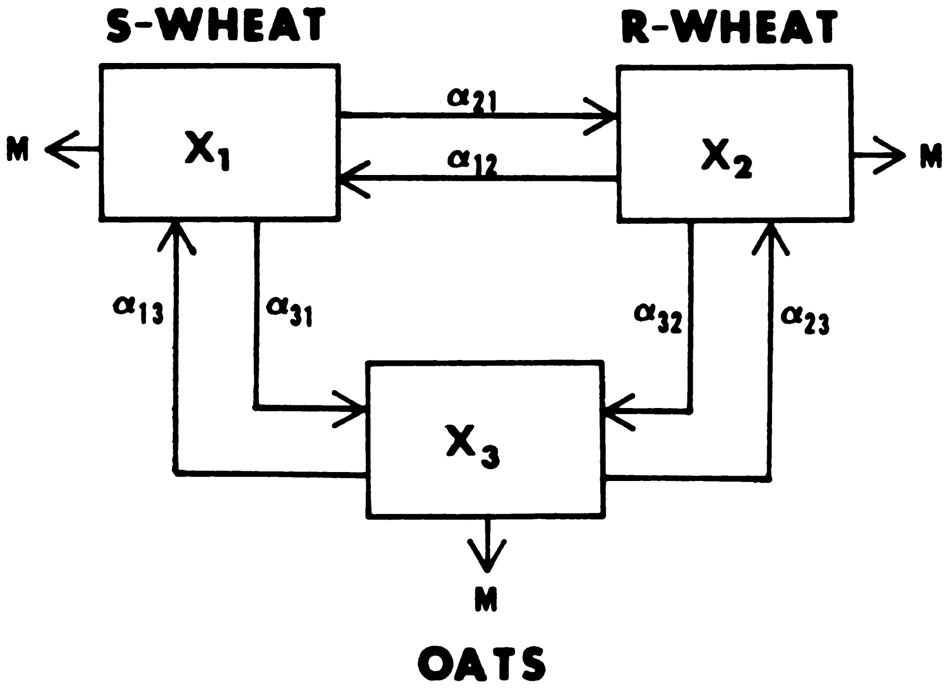

Fig. 10.--A three compartment model of intercrop movement.

in each crop during each time unit; mortality per unit time is a constant percentage of the population in each crop. For simplicity the mortality rate (m) was taken to be the same in all crops, an assumption supported by findings of Casagrande (1975). Since the oat compartment does not exist until oats germinate and emerge, this point in time was taken to be time zero, and the populations in the winter grains at this point $X_1(o)$ and $X_2(o)$ were considered to be the pulse input to the system.

A compartment need not occupy a contiguous volume of space, as long as the compartment is homogeneous and its contents are well mixed. While the fields of a given crop are discrete, their populations mix by dispersal. The movement rates being analyzed here are not this intracrop dispersal, but rather transference from one crop to another.

A potential error source is that another compartment, for which no data are available, exists. This is the nonhost cropland through which dispersing beetles must pass as they move from field to field and in which they may find wild grasses suitable for feeding and oviposition. It is assumed here that the bulk of the population is in the grain fields (particularly by the time spring oats emerge), and that beetles spend relatively little time in grasses. There is some evidence, however, presented in a later section that nonhost cropland may hold a larger number of beetles than previously thought, simply due to the time-lags involved in interfield movement.

Another possible source of error is that the parameters α_{ij} and m may change through time. In fact, this is known to occur. The data could be broken up into time series of sufficiently short duration so that this problem could be eliminated, and in fact the change in the parameters could be described. This was not done however, and the analysis will therefore provide mean values for the entire season.

The three compartment system of Figure 10 is described by three differential equations:

$$\begin{aligned} dX_1/dt &= -(m + \alpha_{31} + \alpha_{21})\ X_1 + \alpha_{12}X_2 + \alpha_{13}X_3 \\ dX_2/dt &= \alpha_{21}X_1 - (m + \alpha_{12} + \alpha_{32})\ X_2 + \alpha_{23}X_3 \qquad (12) \\ dX_3/dt &= \alpha_{31}X_1 + \alpha_{32}X_2 - (m + \alpha_{13} + \alpha_{23})\ X_3 \end{aligned}$$

Data for fitting the model were collected during 1975-77 for the pubescent wheat project near Galien, Michigan (Logan 1977; Sawyer 1976b, 1978). For every sampling date, the mean adult density in each field was multiplied by that field's acreage, and the total for all fields was obtained. If a field was not sampled on a particular day (there were too many to cover in a single day), its density for that date was estimated by interpolation from the preceding and following samples. Thus every day's total represents the population of the entire 41.4 km^2 study area. Time in (12) is expressed as cumulative °D > 48(f).

The equations were fitted to the data by supplying initial estimates of the unknown parameters, solving the system numerically by computer, and comparing the curves generated to the actual data. New parameter values were then entered and a new solution obtained.

The parameters were varied systematically over their possible range (0.0 to 1.0) until the best set of parameter values was obtained. The criterion used for specifying the best fit was a weighted sum of squares. The deviation of each observed density from that predicted by the solution to equations (12) was squared and divided (weighted) by the mean density for that crop. The optimization function, U, was thus

$$U = \sum_{i=1}^{3} \sum_{t=1}^{n} (X_i(t) - \hat{X}_i(t))^2/\bar{X}_i \qquad (13)$$

where n is the number of sample days, $X_i(t)$ is the observed density in crop i on day t, $\hat{X}_i(t)$ is the predicted density, and $\bar{X}_i = \frac{1}{n} \sum_{t=1}^{n} X_i(t)$. The parameter values were found which minimized U. Appendix A is a listing of the optimization program for 1977. For the other years (1975, 1976), the appropriate initial values ($X_i(0)$), arrays of observations ($X_i(t)$) and means ($\bar{X}_i$) were substituted. In these years the model was converted into a two compartment model by setting $\alpha_{21} = \alpha_{12} = \alpha_{32} = \alpha_{23} = 0.0$.

The resulting parameter estimates are given in Table 5, and the solutions to (12) are plotted in Figures 11-13 with the observed data. In both 1975 and 1976, the best fit to the data was obtained when α_{13} was set to 0.0, implying that no movement from oats to wheat took place. The rate of movement from wheat to oats was .15%/°D in 1975 and .19%/°D in 1976. The mortality rates were estimated to be .84% and 1.04% per °D in 1975 and 1976, respectively. With $\alpha_{13} = 0.0$, the decline of the population in wheat simply follows an exponential

Table 5.--Intercrop dispersal and mortality rates (per °D > 48(f)) estimated by compartmental analysis, and the observed initial and mean values used in the analysis.

	1975	1976	1977
α_{12}	-	-	.0003
α_{21}	-	-	.0017
α_{13}	0.0	0.0	.0023
α_{31}	.0015	.0019	.0024
α_{23}	-	-	0.0
α_{32}	-	-	.0001
m	.0084	.0104	.0048
t_o(°D > 48)	465	250	488
$X_1(o)$	5.665×10^6	8.757×10^6	4.249×10^6
$X_2(o)$	-	-	3.257×10^6
$X_3(o)$	0.0	0.0	0.032×10^6
$\bar{X}_1$	1.322×10^6	1.496×10^6	0.886×10^6
$\bar{X}_2$	-	-	1.040×10^6
$\bar{X}_3$	0.222×10^6	0.349×10^6	0.218×10^6

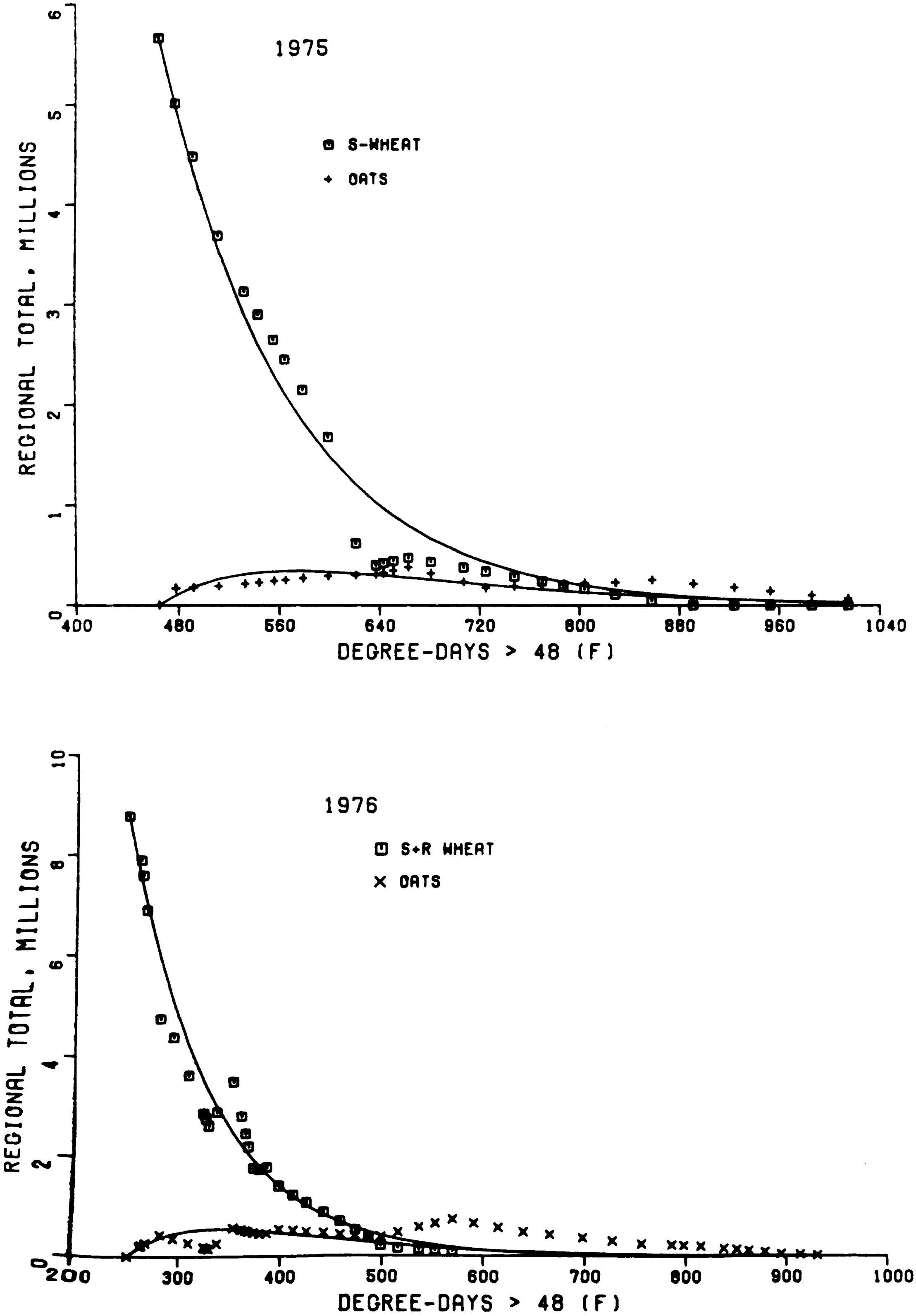

Fig. II-13.--Solutions to the compartment models of intercrop movement at Galien, 1975-77.

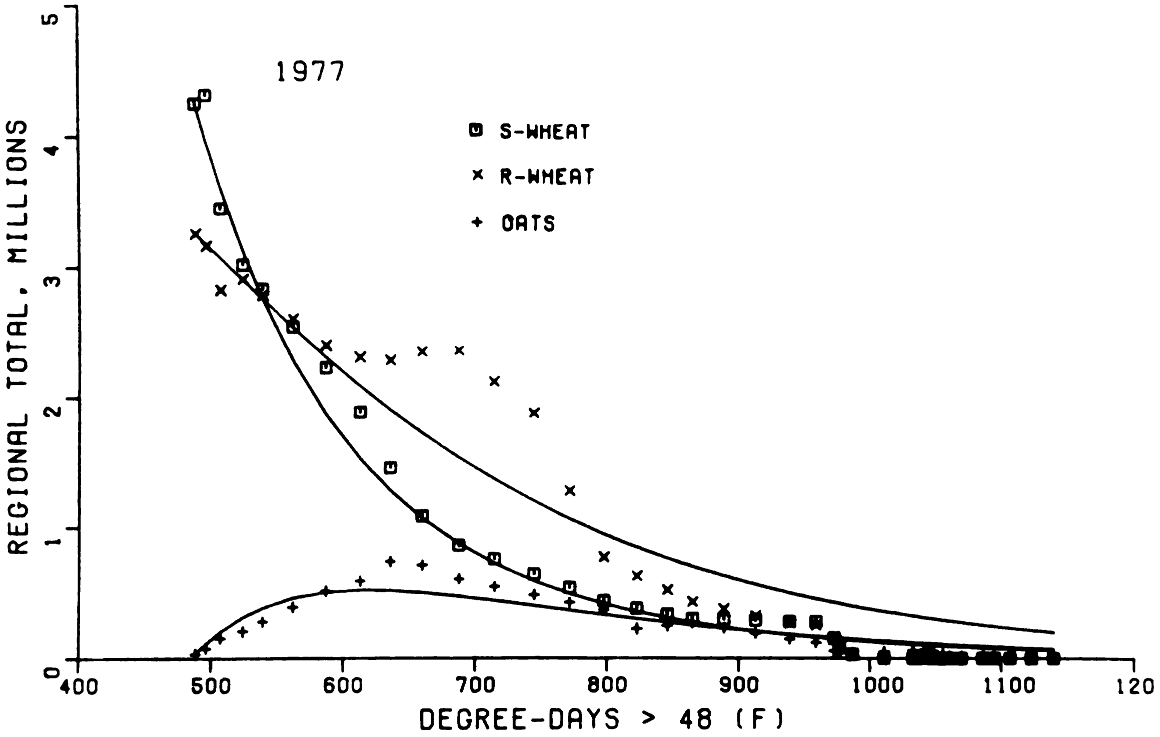

Fig. 11-13.--Continued.

decay, with $X_1(t) = X_1(0)e^{-(m + \alpha_{31})t}$. In 1977, α_{13} was as large as α_{31}, so beetles seemed as likely to move from oats to wheat as the reverse. Exchange between R-wheat and oats in either direction was minimal, as was movement from R-wheat to S-wheat, although the reverse was substantial. The mortality rate arrived at in 1977 was .48% per °D. The mortality rates obtained in the three analyses, .84%, 1.04%, and .48% per °D, agree well with those calculated by Casagrande (1975). In four years of field surveys at Gull Lake, the mortality rates, for the regional population as a whole, ranged from .368 to .710% per °D > 48. It must be remembered that a good fit of a model to the data does not ensure that the rates arrived at are correct, or that the hypothesized processes even occur. What this study shows is that the possibility of movement from oats to wheat cannot be ruled out, and that the rate of such transferral may be significant under certain conditions. These results support the dispersal and crop preference hypothesis presented earlier, and run counter to the model of beetles moving strictly from wheat to oats.

It should be noted that if Ruesink's (1972) hypothesis is correct that "oat" beetles await the emergence of spring grains and then enter these directly, then the assumption of an initial pulse input to winter grains is violated. The subsequent input of beetles to spring grain could not be distinguished from transference from winter grain. However, if Ruesink's hypothesis were true then a loss of beetles from wheat would be "primarily due to mortality not emigration"; one should not note an increased rate of loss with the appearance of spring grains. Exponential decay functions were fitted to the 1976 S-wheat data for two periods: 205-262°D > 48, representing the time from peak density in wheat to the first observation of beetles in oats, and 262-570°D > 48, representing the period after beetles entered oats. Linear regressions of the form $\ln(y) = a + bx$, where y is the regional population in S-wheat and x is degree-days, were highly significant ($p < .001$). The resulting decay rates were .48% and 1.40% per degree-day for the pre- and post-oats periods, respectively. This suggests that the beetles entering oats had come from wheat.

SPATIAL ANALYSES OF REGIONAL DISTRIBUTION AND ABUNDANCE

Defining the Uniqueness of a Field

As discussed above, site to site differences in density within a particular year are due in large part to those factors which define a site's unique characteristics. To be sure, within-site fluctuations in population can lead to such differences if the separate fields are isolated and out of synchrony, but if dispersal plays a significant role in the dynamics then such asynchronies will be minimized (Table 2). Instead, spatial and temporal features describing the uniqueness of the field will predominate and determine its density.

The densities of cereal leaf beetles in the fields of the Galien study area (41.4 km^2) vary considerably (Table 6). The objective of this analysis was to relate the seasonal total of adult activity (adult-°D) and egg density in individual fields to the principal spatial features of the environment immediately surrounding the fields, and to the relative maturity of the crop. It was hoped that this would lead to an understanding of the processes producing the observed variation in densities among the fields of a regional crop system.

The data used are from the pubescent wheat pilot project conducted near Galien, MI. Only the 1976 and 1977 data were used, as

Table 6.--The range and coefficient of variation of adult and egg densities in the fields in the Galien study area, 1975-1977. Densities are number per 60 cm of grain row (1 ft^2). Wheat is susceptible only.

	1975	1976	1977
Wheat Fields:	n = 57	n = 50	n = 25
Adult-°D[a]			
Min.	3.3	5.7	44.0
Max.	599.8	203.2	245.7
C.V.	87.3%	93.4%	55.0%
Eggs/60 cm[b]			
Min.	0.6	0.7	3.7
Max.	30.3	36.4	42.1
C.V.	89.6%	117.1%	87.3%
Oat Fields:	n = 11	n = 12	n = 8
Adult-°D			
Min.	0.6	1.0	11.3
Max.	53.5	140.1	187.5
C.V.	84.5%	81.8%	87.9%
Eggs/60 cm			
Min.	1.7	1.2	1.6
Max.	18.0	44.8	43.0
C.V.	67.4%	79.9%	116.1%

[a] Adult-degree days, the area under the density vs. degree days > 48(F) curve, a measure of total activity.

[b] Area under the curve divided by 180 °D > 48.

their analysis and summarization were more complete. Details of the data collection and analysis, the raw data and various summary statistics can be found in Sawyer (1976b, 1978). Appendix B gives the adult and egg densities in each field for the two years.

The spatial features considered in this analysis were the size, boundary length, and shape of the field, the proportion of the total acreage surrounding the field belonging to each of several habitat types, and several measures of the heterogeneity of the surrounding environment. These will all be defined below. The measure of relative crop maturity was the crop height at the time of peak regional beetle activity in the grain fields, which corresponds very closely with the completion of beetle emergence from overwintering sites.

Casagrande *et al.* (1977) described the principal overwintering habitats of the CLB. These were, in order of their importance at Galien: fence rows, woods edge, sparse woods, dense woods and cropland. A detailed inventory of the spatial distribution of these habitats was needed from the Galien area for the present analysis. To this end, high altitude color-infrared (CIR) imagery was obtained on loan from the Southwest Michigan Regional Planning Commission in St. Joseph, MI. CIR photos (1:36,000) of the study area had been taken from a NASA RB-57 aircraft on 3 June 1977. These photos were interpreted by the NASA Remote Sensing Office in the School of Urban Planning and Landscape Architecture at Michigan State University under the direction of W. R. Enslin.[9] Figure 14 is a black and white copy of one of the photos which covered all but the westernmost 1/2 mile of the area.

The 4 mi x 4 mi (6.4 km x 6.4 km) area was divided up into 1024 10-acre (4 ha) cells .125 mi (.201 km) on a side. The area is thus represented by a matrix of 32 rows (N to S) and 32 columns (W to E). Each cell was further subdivided into 25 subcells of 0.4 acres (.162 ha). The imagery was examined with a microscope and each 0.4 acre subcell was classified by its dominant land use into one of five categories: (1) buildings, (2) water, (3) sparse woods, (4) dense woods and (5) cropland. The number (1 to 25) of subcells in each category was recorded for each 10-acre cell. Also measured and recorded were the total lengths (ft) of (6) fencerows and (7) edges of woodlots in each 10-acre cell. Appendix C gives the results of the photo interpretation. The habitat definitions given by Casagrande _et al_. (1977) were slightly modified for this work. "Buildings" included roads and the yard-area around and between farm and residential structures. Sparse woods were defined as wooded areas with a canopy closure of less than 75%, and shrubby old fields and idle areas. Dense woods had 75% or more canopy closure. Cropland comprised all crops, pasture, grassy and weedy old fields, roadsides and field boundaries, and orchards. Fencerows included field boundaries and roadsides of trees or shrubs. Grassy fencerows were included with

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[9] Funds for the interpretation were supplied by Dr. R. L. Gallun (USDA, SEA and Department of Entomology, Purdue University) from monies granted for the pubescent wheat pilot project under USDA-ARS Project No. 3302-14800-001.

Fig. 14.--Aerial photograph of the research area near Galien, MI.

cropland, as these categories were difficult to distinguish on the photo and were considered to be similar habitats. An estimated mean width of 12 ft (3.7 m) was used to calculate the area occupied by fencerows; this area was subtracted from the cropland acreage. Woods edge was defined by Casagrande _et al_. (1977) as the perimeter of the woods, including 20 ft (6.1 m) into the woods. Accordingly, the area occupied by this habitat was calculated as its length x 20 ft and subtracted from the appropriate (sparse or dense) woodland. The distribution of habitat types for the entire 41.4 km^2 area is: cropland 69.6%, dense woods 14.3%, sparse woods 9.2%, woods edge 2.2%, fencerows 1.8%, water 1.7% and buildings 1.2%.

For each of the years 1976 and 1977, the location of every small grain field was coded in terms of row and column coordinates. The acreage of a field was rounded to the nearest 10 acres (anything less than 10 acres was rounded up to 10), and an appropriate number of 10-acre cells were assigned to that field, approximating as closely as possible the location and shape of the field. These assignments are given in Appendix B and are mapped in Appendix D along with the locations of the woodland habitats and water.

A computer program (Appendix E) was written to search around each field and calculate the total area occupied by each of the five overwintering habitats, S-wheat, R-wheat and oats within certain distances of the field's boundary. These distances, or radii, were .125, .250, .375 and .500 mi (.201, .402, .603 and .805 km). Acreages were tabulated separately for each of four quadrants, corresponding to the directions NW, NE, SW and SE so that directional effects, such as that of wind, could be assessed. Thus 16 acreage values (4 radii x 4 quadrants) were calculated for each of the 8 habitats for the environment surrounding a field. If a field lay too near the edge of the study area, a search around the field would partially involve areas for which no habitat information was available. In such cases, if the missing area was 50% or less of the total for the quadrant and search radius in question, it was assumed that the habitat distribution in the missing area was the same as that in the known portion. If the missing area was more than 50%, the habitat distribution for that sector was declared unknown and coded as missing.

Since the acreage within .500 mi also includes the acreage within .375 mi, and so on, these values are not independent. To correct this, the value for the next inner radius was subtracted from each value so that it represented only the area from one radius to the next. Since the area within a given distance of a field's boundary depends on the size of the field, all acreages were finally converted to proportions to characterize the distribution of habitat types.

The independent variable set at this point consisted of 128 variables defining the habitat characteristics of the environment around each field. It was soon discovered that this exceeded the computational capacity of the computer programs available for analyzing the data. The number of variables was therefore halved by combining radii .125 with .250, and .375 with .500 (mi).

To this set were added the crop height at the time of peak regional adult activity, the acreage of the field, the length of its perimeter, and an index of "edge development" describing the degree

of regularity of the field's boundary line. Edge development was defined as the ratio of the field's perimeter to the circumference of a circle having the same area as the field. That is, edge development = $p/2\sqrt{a\pi}$ where p is the perimeter and a is the area. This index is the same as the index of shore development used in lake morphometry (Welch 1948, p. 93). A circle has an edge development of 1.0 (the minimum). The higher the edge development index, the more irregular is the field's outline.

The variables calculated thus far characterize the mean habitat pattern for any quadrant-distance sector. The variance of this pattern may also be important to CLB spatial dynamics. For this reason, several additional variables were considered. Spatial patterns have many properties, such as grain, patchiness, and connectedness (Pielou 1974, p. 193). Patchiness is a measure of pattern intensity, and is readily calculated from the remote sensing data set. Pattern intensity "is high if a wide range of densities is present; conversely, it is low if the density contrasts are slight" (Pielou 1974, p. 149). By density, I mean here the proportion of a 10-acre cell that is occupied by a given habitat. If woods occupied either 100% or 0% of any cell, then the contrast between cells is high, and woods may be considered a patchy habitat. If, instead, there were small pieces of woods in every cell, the contrast is low, and woods are not as patchy. Note that patchiness is therefore intimately tied to the size of the sample unit--here, a 10-acre cell. Pattern intensity is maximum when the mean patch size is the same as the size of the sample unit. Patchiness is, however, independent of density (Pielou 1974, p. 152).

That is, woods can be just as patchy when the total acreage of woods is high as when the total acreage is low. For a given density, however, patchiness is directly related to grain; a higher degree of patchiness must be associated with coarser grain, or larger patch size.

Patchiness was defined for this study by Lloyd's index of patchiness (Pielou 1974, p. 150). It is the ratio of mean crowding ($\overset{*}{m}$) to density (m), where

$$\overset{*}{m} = \frac{\sum_{j=1}^{Q} x_j(x_j-1)}{\sum_{j=1}^{Q} x_j} \qquad (14)$$

and

$$m = \frac{\sum_{j=1}^{Q} x_j}{Q} \qquad (15).$$

Q is the number of 10-acre cells in the area under consideration and x_j is the acreage, in the jth cell, of the habitat for which patchiness is being calculated. The patchiness of sparse woods, dense woods and cropland were calculated for the areas within 0.25 mi of each field's boundary and between .25 and .50 mi. Patchiness was not defined on a directional basis, as were the habitat distributions, since this would have generated a prohibitively large number of variables. Furthermore, it was felt that measures of habitat variation, like patchiness, were not as likely to interact with wind or other directional effects as were the mean amounts of various habitats, and the interpretation would be more difficult.

Some examples of the consequences of habitat patchiness are in order. Sparse woods is an important overwintering habitat, but makes up only 9.2% of the land area at Galien. If the distribution of this habitat was very patchy, then the probability of beetles finding sparse woods in which to overwinter might be reduced. For the more abundant dense woods and cropland habitats, a high degree of patchiness reflects uniformity within the 10-acre cells. For maximum patchiness of cropland, for example, each cell is either pure cropland or it has none, creating a more homogeneous environment within the cells. Cropland, in such cases, will have fewer overwintering sites nearby. Woodlots are likely to be larger, denser, and have relatively less edge, therefore being less suitable for overwintering.

Another measure of the spatial variability of the environment near a field is the habitat diversity. An appropriate measure of diversity in this situation is the Brillouin index (Pielou 1974, p. 304),

$$H = \frac{1}{NT} \log_2 \frac{NT!}{N_1!N_2!N_3!N_4!N_5!} \qquad (16)$$

where N_i is the acreage (to the nearest integer) of the ith habitat and $NT = \sum_{j=1}^{5} N_i$. The five habitats included were the usual woods edge, sparse woods, fencerows, cropland, and dense woods. The Brillouin index is used because the sum of acreages within a given distance of a field is finite, and this "collection" of acres is fully censused (Pielou 1974, p. 304). H was calculated for the areas within 0.25 mi and between .25 and .50 mi of each field's boundary, as was Lloyd's index of patchiness. A high value of H would imply that the environment surrounding the field is more heterogeneous.

A final measure of the spatial variability of the habitats around a field was the degree of "woods edge development" (WED) within the same two annuli defined above. This was calculated in the same manner as edge development for the field itself. Thus, $WED = L/2\sqrt{w\pi}$, where L is the total length of woods edge within the search area, and w is the total area occupied by woodlots, both sparse and dense. A high value for this index indicates that the woodlots are irregular in outline or are divided into small pieces. In either case, there is relatively more edge for a given acreage of woods.

With these spatial variables in hand, two types of analyses were considered: multiple regression and cluster analysis.

Regression Analyses

The regression analyses were done first, before the data set had reached its final state. At this point the indices of patchiness, habitat diversity and woods edge development had not been added. The four radii had not been consolidated into 2, and the acreages had not been converted to proportions of the total area in each sector. Because there were too many variables (132) to consider all at once, different subsets of the variable set were dropped from the analysis, depending on the crop under consideration. The decision on which variables to drop was based on preliminary runs with one of the radii excluded and which indicated that certain variables were unlikely to be important. When analyzing densities in S-wheat fields, the acreages of cropland and oats near the fields were omitted as independent variables. When analyzing densities in R-wheat fields, cropland and dense woods were omitted. Note that for R-wheat only adult densities were analyzed since egg densities are strongly influenced by the degree of resistance the wheat in a particular field exhibits, which was observed to vary. Adult densities are less reduced by pubescence (Sawyer 1976b). When analyzing densities in oat fields, acreages of S-wheat and oats were omitted. The former was omitted because there was only one oat field within .5 mi of an S-wheat field in 1977.

The objective of the multiple regression analysis was to find a small set of variables which accounted for the observed variation in adult and egg densities among the fields, and could be used to predict the density in particular fields. The regression analyses were done using the 1977 data to obtain the best fitting models, which then were tested with the 1976 data. Stepwise forward regressions were performed using the Statistical Package for the Social Sciences (SPSS) (Nie _et_ _al_. 1975). A maximum of five variables were admitted for the analysis of wheat fields, and two for oat fields, to prevent saturation of the model, which occurs when too few degrees of freedom remain in the residual term.

The results of the multiple regression analyses varied considerably depending on the dependent variable under consideration, and might best be described in general terms. In all cases it was possible to define a set of five or fewer independent variables which accounted for 80% or more of the variation in densities among the fields. All distances, from .125 to .500 mi, contributed significant independent variables. All directions contributed significant variables, although the southwest was most often selected (Table 7). Wind velocity was recorded in 1977 when each sample was collected. Based on calculations of mean velocity x frequency of occurrence, the winds during April and May were mostly from the southwest, west, south, and southeast, in order of predomination. These general results suggest that beetles may move considerable distances to arrive at the host crop, and wind may possibly be a factor of influence.

More specifically, for S-wheat fields, sparse woods lying to the southwest contributed positively to both adult and egg densities (Table 7). Fence row acreage was also related to adult densities. Dense woods and woods edge nearby had a negative influence on egg densities, while if farther away they had a positive influence on both adult and egg densities. These results are at first confusing, but make sense in light of simulations described later. In these simulations, woods surrounding a field at some distance act as barriers to emigration, keeping beetles in the field later into the season. However, if too close to the field they may eliminate more important overwintering habitats from the area immediately around the field and thereby reduce early population levels. For R-wheat fields, the most important variables were acreages of S-wheat and oats. These may serve as sources of immigrants, partially countering the higher loss rate from the resistant host. Similarly, for oats, the most important variable was the acreage of R-wheat, a likely source of immigrants as the oats emerge (remember there were no S-wheat fields near oats).

Table 7.--Variables found to be significantly related ($p < .05$) to adult and egg densities in a multiple regression spatial analysis of the 1977 Galien data.

Dependent Variable	Independent Variable[a]	Distance (mi)	Direction	Influence[b]
S-wheat adults	1 Sparse woods	.375-.500	SW	+
	2 Fence row	.375-.500	SE	+
	3 Sparse woods	.250-.375	SW	+
	4 Sparse woods	0-.125	NW	+
	5 Dense woods	.375-.500	NE	+
S-wheat eggs	1 Sparse woods	.375-.500	SW	+
	2 Dense woods	0-.125	SW	-
	3 Woods edge	.125-.250	NW	-
	4 Woods edge	.250-.375	SW	+
	5 Dense woods	.250-.375	SW	-
R-wheat adults	1 S-wheat	.250-.375	NE	+
	2 Oats	.375-.500	SW	+
	3 Woods edge	.375-.500	NW	+
	4 Crop height	-	-	+
	5 Fence row	.375-.500	NW	-
Oats adults	1 R-wheat	0-.125	SW	+
	2 Cropland	.375-.500	NE	-
Oats eggs	1 R-wheat	.125-.250	NW	+
	2 Woods edge	.125-.250	SW	-

[a] Ranked in order of partial F to remove.

[b] Sign of regression coefficient.

The regression equations obtained with the 1977 data were tested for validity with the 1976 data. Since the regional mean population level may change from year to year, the criterion used for successful prediction was the correlation between predicted and observed densities, rather than a matching of the absolute levels. Of interest was the ability to predict relative densities within a year; i.e., to identify fields likely to have a high density, etc. The values of the required independent variables were obtained for every field in 1976 and were entered into the appropriate equation.

For 44 S-wheat fields in 1976, the correlation between observed and predicted adult densities was $r = .152$ ($p = .16$); for eggs in 45 fields it was $r = -.001$ ($p = .50$). For adult densities in 8 R-wheat fields, $r = .346$ ($p = .20$). For adult densities in 10 oat fields $r = .325$ ($p = .18$); for eggs in 12 fields it was $r = .325$ ($p = .15$).

There are many possible reasons for the failure of the regression models to predict the relative densities in 1976. Violations of the assumptions underlying the use of multiple linear regression must be considered first. These assumptions are that the samples (densities) were drawn at random and independently of each other, that they are identically and normally distributed for fixed values of the independent variables, that the independent variables are not highly intercorrelated (multicollinear), and that the relationship between density and each of the independent variables is linear.

Since the use of the analysis was not inferential, but, rather, was descriptive and predictive, the assumption of normality need not be met (Searle 1971, Ch. 3).

The densities were estimated from every field in the region and all during the same year, so they are not independent random samples drawn from the population of all possible responses. This is perhaps the most likely reason for the failure. If, for example, wind patterns or crop synchronies differed in the two years, then the models would almost certainly fail in their predictions.

Multicollinearity is unlikely to be a serious problem since correlations on the order of 0.8 must be present to cause computational problems with inversion of the correlation matrix of the independent variables (Nie _et al_. 1975, p. 340). Such high correlations are not expected due to the heterogeneity of the environment surrounding fields and the nature of the variables and their computation. A possible exception might be found within the smallest radius, since for a 10-acre field only 27.5 acres of habitat lie within .125 mi in one quadrant. In this small area, the acreage of cropland might be negatively correlated with the acreage of dense woods.

The remaining assumption is that of linearity. This was assumed, but not carefully evaluated, as a first-order approximation. The large number of variables prevented a thorough investigation of this. If the work were pursued, clearly this assumption should be more closely examined, at least by analyzing the residuals.

The fact that field densities were not closely related to any particular environmental condition which was measured could also be due to biological causes. For example, if beetles are quite active and disperse widely, or if they move around considerably (among wild grasses, say) between emergence and entry into the fields, then the densities will become homogenized and the effect of a field's local features will be obscured. But in this case, between-field variation would not be expected to be as great as that observed (Table 6). This will be discussed more fully in relation to simulation results in a later section.

The independent variables chosen may have been too specific and numerous. Thus, by chance alone, a subset was found which "explained" the 1977 data but was of no use with a different set of data. I attempted to prevent this by purposely limiting the number of independent variables included in the final model to a small fraction of the number of observations.

Cluster Analyses

Cluster analysis is a broadly descriptive term covering a number of multivariate statistical techniques (Anderberg 1973). The general goal of cluster analysis is to discover and describe the structure of a complex data set. Anderberg (1973, p. 3) defines the problem in cluster analysis as one of "finding the 'natural groups'" in the data. That is, "to sort the observations into groups such that the degree of 'natural association' is high among members of the same group and low between members of different groups." When the goal is exploration rather than rigorous analysis, few assumptions need to be made about the data for many of the techniques.

In the context of the current problem, the data units are fields. The observations on these units were the 76 spatial and temporal features: 64 variables describing the distribution of eight habitats in four quadrants and two distance ranges (.00 - .25 mi and .25 - .50 mi); ten variables characterizing patchiness of sparse woods, dense woods and cropland, habitat diversity and woods edge development in the two annuli; field size, and crop height at the time of regional peak densities. Oat fields were not included in these analyses because there were so few of them.

Two approaches were taken in analyzing these data by cluster analysis. First, the fields were organized into natural groups as determined by their environmental features, and the groups, or clusters, were compared with respect to their mean CLB density. Where differences were found, the principal factors responsible for the grouping were identified. In the second approach, fields were first organized into classes based on their insect density. Then an effort was made to identify those environmental features which were best able to discriminate between the classes. In both cases the data were standardized prior to analysis by subtracting from each variable the overall mean of that variable and dividing by its standard deviation. This placed all variables on the same scale with a mean of 0.0 and standard deviation of 1.0, eliminating the artifact of measurement scale (Anderberg 1973, p. 102).

An agglomerative hierarchical clustering procedure (Anderberg 1973, Ch. 6) was used to organize the fields into natural groupings. Starting with each data unit (field) as a cluster, clusters were merged sequentially based on their similarity until there was one cluster containing all data units. The criterion of similarity used was Euclidean distance in the 76-dimensional feature space. The complete linkage method was used to define the distance from a newly formed cluster to any other cluster. This distance is defined as that separating the most distant members of the two clusters. Complete linkage tends to produce globular clusters with assurances that if two data units lie within the same cluster then they are at most a known distance apart. The outcome of hierarchical clustering, known as a dendrogram, can be depicted graphically as a tree (Figure 15). By visually examining the tree a number of fairly distinct groups can usually be defined. For example, in Figure 15, at an intragroup distance of slightly more than 18 standardized units a well-defined group of seven fields (numbers 1228 to 413) joined all the rest of the fields. In the step before that, a cluster of three fields (348, 346 and 141) merged with a larger group to form a new cluster 16 units in diameter. The experience of the analyst and his knowledge of the problem at hand play a role in deciding how many clusters the final clustering will have. In difficult cases more objective methods can be devised to determine what constitutes a "good" or "natural" clustering.

The final cluster memberships for the fields of each crop in 1976 and 1977 are given in Appendix B. Table 8 gives the final number of fields per cluster, and the mean and standard error for the densities within each cluster. Analyses of variance tested for significant differences between the clusters with regard to adult and

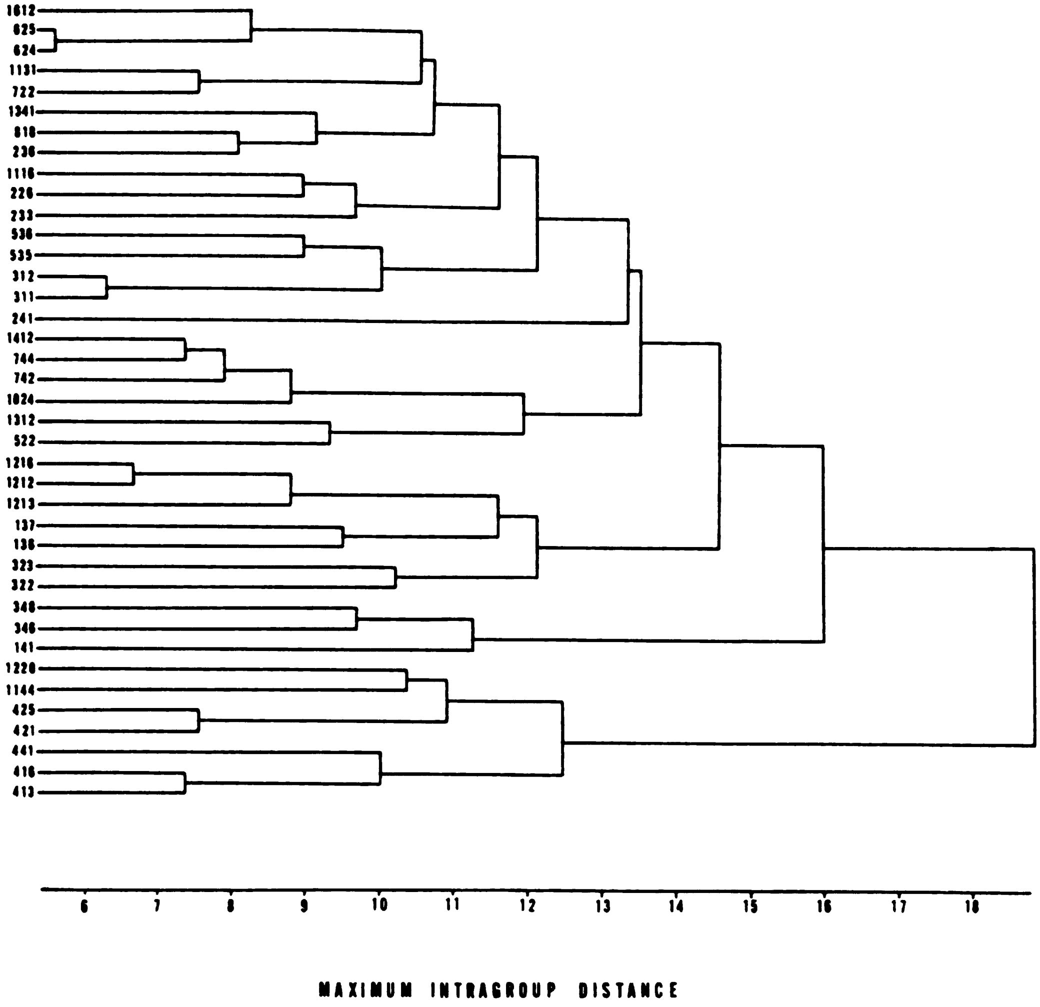


Fig. 15.--Complete linkage hierarchical tree for the R-wheat fields at Galien in 1977, based on 76 environmental features.

Table 8.--Final clustering of Galien-area fields based on their environmental features using hierarchical cluster analysis, and mean CLB densities within the clusters. Cluster memberships are given in Appendix B.

Year	Crop	Cluster	Fields[a]	Adult density[b]		Egg density[c]	
				$\bar{x}$	SE	$\bar{x}$	SE
1976	S-wheat	1	2	9.80	26.80	5.84	4.58
		2	11	49.61	11.43	5.62	1.95
		3	6	88.16	15.47	13.36	2.64
		4	14	24.45	10.13	2.80	1.73
		5	17	47.00	9.19	6.06	1.57
1976	R-wheat	1	3	52.20	9.99	4.26	0.49
		2	5	36.33	7.74	2.66	0.38
1977	S-wheat	1	2	50.60	35.24	4.67	6.11
		2	4	112.20	24.92	9.58	4.32
		3	10	86.67	15.76	7.56	2.73
		4	8	94.10	17.62	14.85	3.05
1977	R-wheat	1	7	37.13	8.64	1.76	0.85
		2	3	62.47	13.19	3.72	1.29
		3	7	47.67	8.64	3.74	0.85
		4	20	54.97	5.11	3.95	0.50

[a] Number of fields for which density estimates were available.

[b] Adult - °D > 48(F) for season.

[c] Eggs/60 cm, seasonal input.

egg densities. Where shown to be necessary by Bartlett's test, a logarithmic transformation was used to stabilize the variances (Sokal and Rohlf 1969, pp. 370, 382).

Where significant differences in density were found among the clusters, discriminant analysis was used to identify features contributing to separation of the clusters. Discriminant analysis (Nie et al. 1975, Ch. 23) is a procedure which weights and linearly combines the features into discriminant functions in such a way that the predefined groups are as distinct as possible in their scores on these functions. The maximum number of discriminant functions derivable is one less than the number of groups, but satisfactory separation of the groups may be possible with fewer than this number of functions. The functions are ranked in order of their contribution to discrimination between groups. The relative importance of each variable to a discriminant function is given by the absolute value of its standardized weighting coefficient. The theoretical significance, if any, of the derived discriminant functions may thereby be assessed. All variables need not be included in each discriminant function. For the present work, the ten most significant features were selected for each function by a stepwise procedure which maximized Wilk's lamda statistic, a measure of group discrimination (Nie et al. 1975, p. 447). The result of a discriminant analysis can be viewed as a projection of the data from a high, say 76, dimensional space to a space whose (lower) dimensionality is equal to the number of discriminant functions. Each function represents a dimension, or axis in this reduced space.

For S-wheat in 1976 there were significant differences (p = .02) in adult density among the five clusters. Specifically, cluster 1 had a lower density than all other clusters except cluster 4, and cluster 4 had a lower density than cluster 3. The discriminant analysis showed that cluster 4 was distinguished from cluster 3 by having a higher index of patchiness of sparse woods within .25 mi, greater acreage of S-wheat within .25 mi, and lower habitat diversity within .25 mi. By examining the aerial photo (Figure 14), it was seen that 13 of the 14 fields of this cluster all fell into two sets of neighboring fields located in areas of very few woodlots or tree lines. Unfortunately, the fields of cluster 1 all had missing data (habitat features found to be important discriminators) due to their location near the edge of the study area, and were not included in the discriminant analysis. However, cluster 1 was placed most closely to clusters 2 and 3 by the hierarchical clustering. It might be expected that its fields shared little in common with those of cluster 4, and that more than one set of conditions leads to low density. Indeed, by examining the aerial photo, it was seen that these fields were bordered by large areas of dense woods.

There were no significant differences in egg density among the S-wheat fields in 1976 after transforming the data to stabilize the variances.

Among the S-wheat fields in 1977 there was no clear definition of habitat groups. Four rough clusters were delimited, but analyses of variance of adult and egg densities showed no significant differences between these groups.

The eight R-wheat fields in 1976 were separated by hierarchical clustering into two clusters. An analysis of variance showed that the mean egg density in group 2 was lower (p = .04). Because of the low number of fields, a discriminant analysis was not done, but inspection of the aerial photo showed that the fields of cluster 2 were near very few woodlots and fencerows.

The R-wheat fields in 1977 were grouped into four fairly distinct clusters (Figure 15), but no significant differences among the clusters were evident for either adult or egg densities.

The second approach to a cluster analysis of CLB densities and the spatial structure of the environment began with a classification of the fields into groups based separately on their adult and egg densities. This was done by plotting every field's density on a number line, and then breaking the line up into segments at points that gave a total of three to five groups and divided the line at naturally occurring gaps in the distribution of densities. It was possible to select breakpoints meeting these criteria and which also had the same value in both years. For adult densities (adult-°D/60 cm) the breakpoints were 62, 120 and 160 for S-wheat and 40, 55, 65 and 95 for R-wheat. Thus there were four density classes for S-wheat and five for R-wheat. As an example, an S-wheat field with a total seasonal adult activity of 70 adult-°D/60 cm would fall into density class 2 for that crop. For egg densities (eggs/60 cm) the breakpoints were located at 10 and 20 for S-wheat and 4.5 and 7 for R-wheat; there were thus three egg density classes in each crop. In this manner the fields were divided up into groups based on their relative density, ranging from low through moderate to high.

Discriminant analysis was then employed to determine if these density classes could be distinguished by any combinations of the spatial features describing a field's environment. To test the validity of any discriminant functions found, the analyses were first performed using one year's data to define the functions, then the other year's data set was "classified" using these results. Classification is the other, perhaps major, role of discriminant analysis, besides defining the relative importance of discriminating variables. Discriminant analysis provides classification functions which are used to calculate the probability of membership in each group for a new, unknown data unit. The procedure is commonly used in numerical taxonomy (Sneath and Sokal 1973). The success or failure of the analysis in defining meaningful functions was judged by the percentage of correct classifications of the "unknown" fields from the other year.

In all cases, the validation procedure indicated a failure to identify a significant percentage of the unknown fields with their correct density class using the classification functions derived from the other year. This was true for both S-wheat and R-wheat fields, for both adult and egg density classes, and regardless of which year was used to construct the classification functions. Furthermore, the same variables were not given as those most important to discrimination in the two years (Table 9).

Table 9.--Principal environmental variables contributing to the discrimination of the highest density class from all other classes.

Year	Crop	Variable	Distance (mi)	Direction	% Contribution[a]	Sign[b]
		Adult density				
1976	S-wheat	Fencerows	.00 - .25	NW	17	-
		Cropland	.25 - .50	NE	14	+
	(1)[c]	Patchiness of cropland	.25 - .50	--	11	+
		R-wheat	.25 - .50	SW	11	-
		Fencerows	.25 - .50	SW	11	+
					64%	
1977	S-wheat	Sparse woods	.25 - .50	SW	27	+
		R-wheat	.00 - .25	NW	17	+
	(2)	Crop height	---	--	11	-
		R-wheat	.00 - .25	NE	9	-
		Fencerows	.25 - .50	SW	9	-
					73%	
1977	R-wheat	Woods edge	.00 - .25	NW	16	+
		S-wheat	.25 - .50	NE	13	+
	(2)	Fencerows	.00 - .25	NW	11	+
		Woods edge	.25 - .50	NW	10	+
		Woods edge	.00 - .50	SW	10	-
					60%	
		Egg density				
1976	S-wheat	Fencerows	.00 - .25	NW	19	-
		Dense woods	.25 - .50	NE	14	+
	(1)	Cropland	.25 - .50	SW	13	+
		S-wheat	.00 - .25	NW	13	+
		Crop height	---	--	9	-
					68%	

Table 9.--Continued.

Year	Crop	Variable	Distance (mi)	Direction	% Contribution[a]	Sign[b]
1977	S-wheat	Sparse woods	.25 - .50	SW	23	+
		Woods edge	.25 - .50	SE	16	+
	(3)	Sparse woods	.00 - .25	NE	13	+
		Oats	.25 - .50	NE	13	-
		Cropland	.00 - .25	NE	11	+
					76%	
1977	R-wheat	Dense woods	.25 - .50	SE	23	-
		Cropland	.25 - .50	SE	19	-
	(3)	R-wheat	.00 - .25	SW	15	-
		Crop height	---	--	13	+
		S-wheat	.25 - .50	SW	8	+
					78%	

[a] Of 10 variables included in the primary discriminant function, percent contribution by this variable to separation of groups along the axis represented by the function.

[b] (+) means high score on variable moves classification toward highest density class along principal discriminant axis; (-) means high score moves classification away from highest density class.

[c] Number of fields in highest density class.

A major problem with the analysis was that the highest density class generally contained only one to three fields. This class was usually widely separated from the other classes along one of the discriminant axes (Figure 16). Discriminant analysis seeks, statistically, to minimize the ratio of within-group scatter to total scatter. A set of variables was probably found which, combined, uniquely described the few fields of the high density class. The group was then placed far from the others along the axis defined by a discriminant function made up of these variables, thereby greatly increasing the total scatter. In this way the fields in the highest density class dominated the analysis. The principal discriminant function, and the variables defining it, merely indicated how these few fields were different from all others. Apparently the factors responsible for creating unusually high densities in a couple of fields are not often the same.

The principal features contributing to separation of the high density classes are given in Table 9. As in the regression analysis, all distances and directions contributed to discrimination of the high density fields, and the significant environmental features varied between crops and years. Again, a likely explanation is that the determinants of high density are many and are complexly interrelated, so that more than one set of environmental conditions leads to high densities. As Anderberg (1973, p. 192) notes, heterogeneity within a group (such as "high density fields") can lead to failure of a discriminant analysis. Conditions associated with high density are likely to vary from one year to the next because of differences in

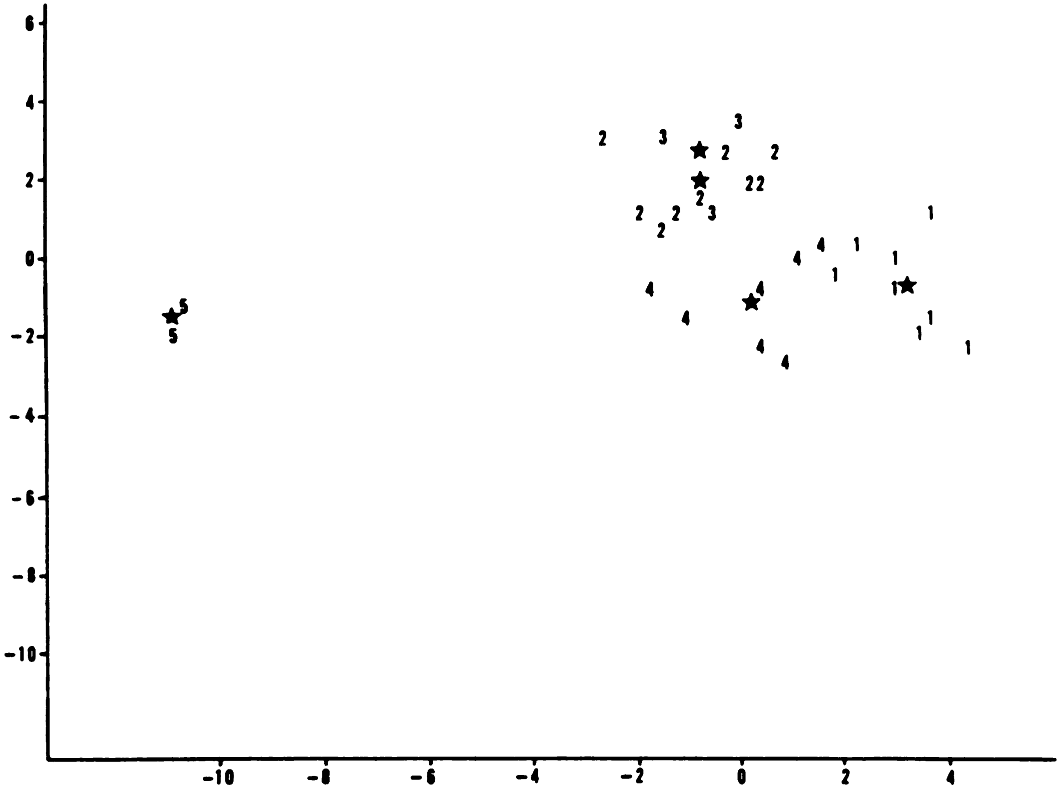


Fig. 16.--Ordination of the 1977 R-wheat fields on the two principal discriminant axes. Numbers refer to adult density classes (5 is highest). Stars indicate cluster centroids.

weather, planting times and other factors affecting CLB/host crop synchronies, wind patterns, and the spatial arrangement of the fields. There is little hope of unraveling these between-year relationships with data from only two years. In effect, all of the observations of a single year are reduced to a single point representing a set of conditions and a population response.

To avoid the problem of having so few fields in the highest density class, the fields might better have been divided into just two groups, corresponding to above median and below median density. This however, may just aggravate the situation of intragroup heterogeneity, if that is the problem.

Autocorrelations

If specific structural features of the environment are associated with high CLB densities, then it might be expected that certain locations would continue to exhibit a tendency to have high densities year after year. It was noticed, in fact, that certain fields did seem to have unusually high densities in successive years. Correlation analysis of 21 fields which were planted with the same crop in both 1975 and 1976 at Galien, and 14 fields planted with the same crop in both 1976 and 1977 showed that densities at the same site were indeed highly correlated in successive years. In a few cases the site in one year was not exactly the same as in the other, but was immediately adjacent and the surrounding habitat did not appear to be different in any way. Where heteroscedasticity resulted from the variance increasing with mean density, a logarithmic transformation was applied to the densities prior to analysis. The correlation between adult densities (log transformed) in 21 fields in 1975 and 1976 was $r = .43$ ($p = .05$). For egg densities (no transform) in these years $r = .68$ ($p < .01$). For the 14 fields in 1976 and 1977, the logarithms of density were also significantly correlated: $r = .63$ ($p < .05$) and $r = .74$ ($p < .01$) for adults and eggs, respectively.

Autocorrelation of densities could also account for the observed relationship between two successive years, rather than the nature of the site being responsible. That is, a high density at a site in one year may be followed by a similar density in the next year, just because the former provides the starting point from which the population level changes. The nature of autocorrelation is such, however, that its effect decreases as time progresses, and densities measured two years apart should be less correlated than those measured just one year apart. Unfortunately, not a single field was planted with the same grain in <u>all</u> <u>three</u> years at Galien. A few fields were planted to S-wheat in both 1975 and 1977, with something else planted in the intervening year. Such a disruption of crop continuity would effectively eliminate any effect of autocorrelations, but would perhaps have little or no effect on a process in which a field's beetle density was determined by the surrounding environment of the field. Permanent habitats, such as woodlots, fencerows, etc., would be the same in both years. For eight fields for which adult densities were available, and nine for egg densities, no significant correlations in densities two years apart were evident.

Egg and larval densities in the wheat and oat research plots at Gull Lake over a 12-year period (1967-78) give similar results.

Here the sites were essentially the same each year. Twelve density estimates provide 11 pairs separated by one year, 10 pairs separated by two years, and 9 separated by three years. For both egg and larval densities, in both the wheat and oat plots, the correlation between pairs of estimates declined with each additional year of separation.

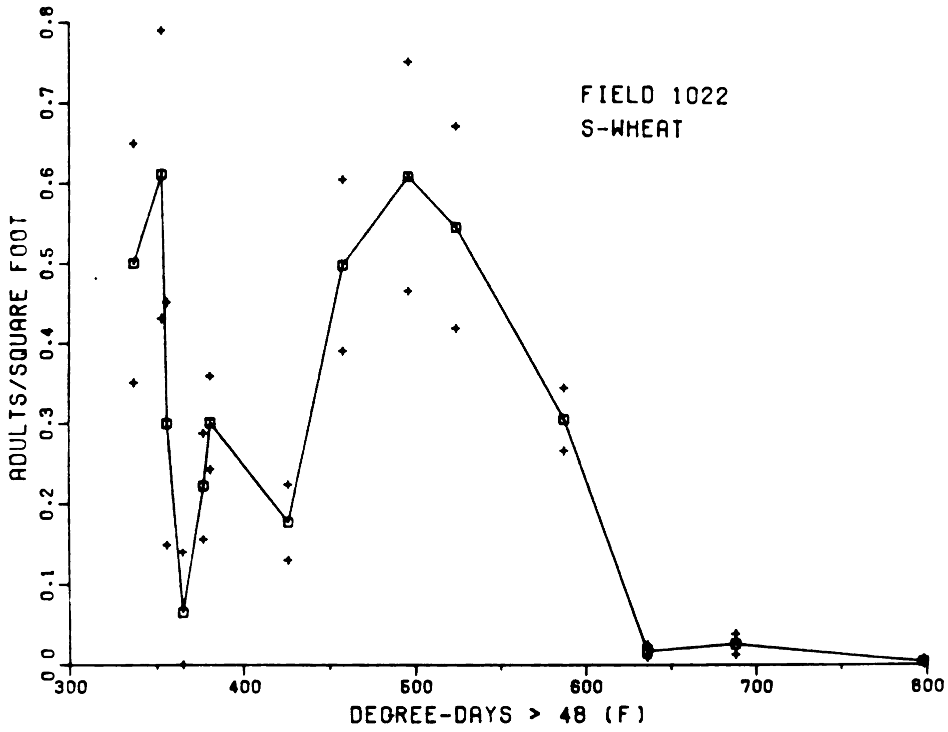
These results suggest that the observed similarity in a field's density in two successive years is merely the result of autocorrelation and not necessarily because that site is consistently a favorable or poor one. This does not help to explain why a field's density is high or low to begin with.

FIELD STUDIES OF DISPERSAL

Fluctuations in Density

The density of adult cereal leaf beetles in a field can change rapidly. Figures 17-19 show the mean and 95% confidence interval of density at frequent intervals in three fields that were intensively sampled at Galien in 1977. Except in very short grain, samples consisted of 20 randomly taken sets of 25 sweeps with a 15 in (38 cm) diameter sweepnet. Sweepnet counts were converted to density estimates using the model of Ruesink and Haynes (1973). When the crop height was less than 10 in (25 cm), samples consisted of 20 random visual counts along 10 ft (3 m) of two adjacent grain rows. The precision of these estimates is high enough to show that the density may be significantly different on successive sampling days. What is interesting about this is that on occasion the density dropped one day and rose the next, showing rapid fluctuations rather than gradual changes.

On 26 April 1977, (365°D > 48F) a low point was observed in the densities in fields 1022 and 1024. It had rained .25 in the day before, and the fields were still damp. The previous three days had been very cool, with only 1°D > 48 accumulating. The night before the minimum temperature had been 29°F (-1.7°C). At sampling time it was sunny, windless, and near noon. The maximum temperature that day



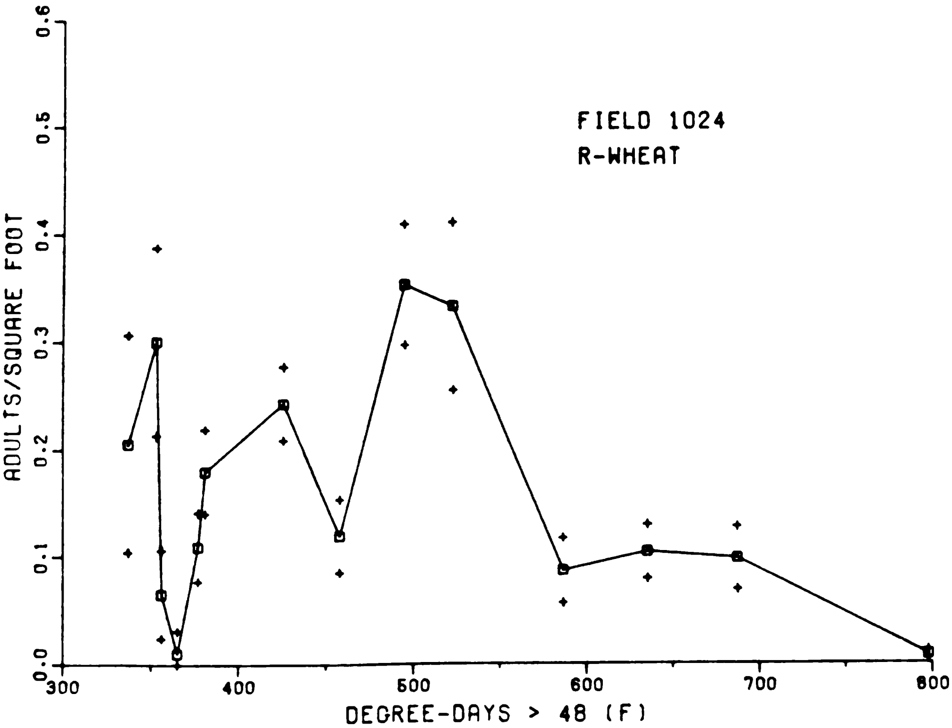


Fig. 17-19.--Mean adult density at frequent intervals in three intensively sampled fields at Galien in 1977. Ninety-five percent confidence intervals are indicated by (+).

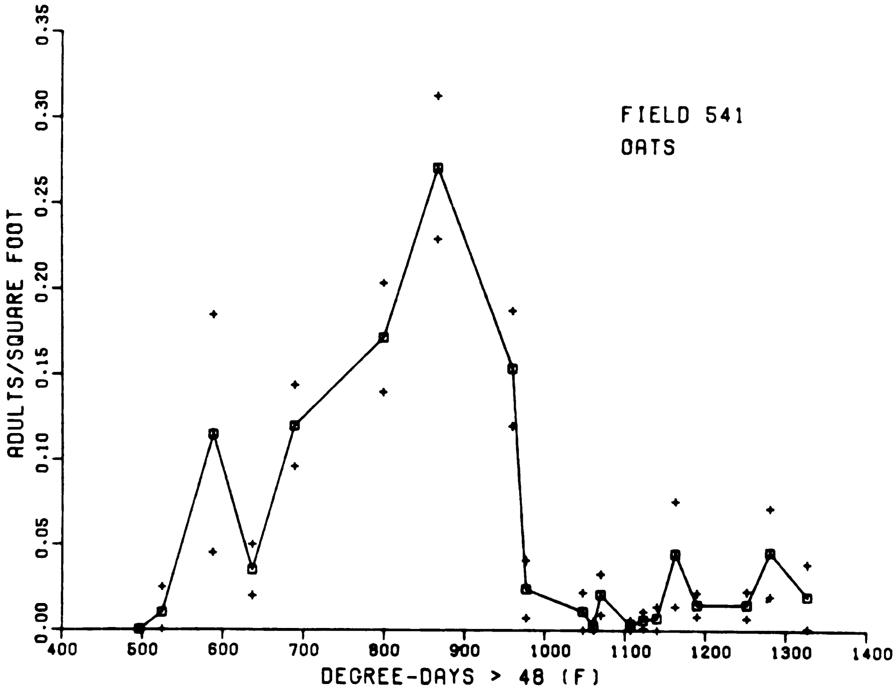


Fig. 17-19.--Continued.

was 58°F (14.4°C). Neither the minimum temperature the night before nor cool weather earlier nor the rain adequately account for the low density, since on 29 April (381°D) the minimum was 26°F (-3.3°C), only 4°D had accumulated the previous two days, and .2 in of rain had fallen the day before. The density on 29 April, however, had just increased. It is difficult to account for the low population on 26 April.

Similarly, on 3 May the population in field 1022 was again significantly lower than on either the previous or the following sampling day. It had been cloudy and had rained .25 in the day before but at the time of sampling it was sunny and near noon, the field was dry, and there was only a 6 mph wind (from the Northeast). The maximum temperature that day was 70°F and the minimum the night before had been 49°F. Again, it is difficult to account for the drop in density in field 1022. Note that on this same day the density in adjacent field 1024 increased. On 5 May (458°D) the reverse occurred, with field 1024's population declining significantly while 1022's increased. In each case the two fields were sampled at the same time. The wind at the time of sampling on 5 May was from the West. Field 1024 was located directly west of 1022. Thus, wind might have carried beetles from 1022 to 1024 on 3 May, when winds were from the Northeast, and from 1024 to 1022 on 5 May. Problems with this interpretation are that there was a very dense tree row between the two fields, approximately 15 ft (4.6 m) thick, the wind at the time of sampling may not reflect the total wind pattern during the days when dispersal must have occurred, and on 26 April, when winds were very light, the entire regional population exhibited the same sort of decline that the two study fields showed. Some other explanation must be sought for the fluctuations, at least on 26 April.

I have no such explanation, but offered this example to make certain points. First, field densities in all crops fluctuate frequently and significantly. This shows that beetles do not stay in the field that they happen to enter, but instead are highly vagile and may move in or out of any crop at any time. I say the density fluctuations represent movement into and out of the fields rather than changes in sampling efficiency under different weather conditions for several reasons. The sweepnet model (Ruesink and Haynes 1973) makes some allowance for the influence of temperature, wind, and solar radiation on sampling efficiency, and the direct visual counts are little affected by these factors. The conditions *at the time of sampling* were never particularly adverse anyway. The populations in the two adjacent fields changed in opposite directions on both 3 May and 5 May although sampling conditions were identical in the two fields. A second point demonstrated by the example is that while the rates of movement are undoubtedly affected by weather, these relationships are not obvious and are probably complex. Dispersal activity may be great even in cool, cloudy weather.

The series of contour plots presented in Appendix F provides many examples of fluctuating densities in fields. The plots were drawn by computer, using the Surface II graphics package (Sampson 1975) and a Calcomp plotter. These maps represent the entire 41.4 km^a study area of the pubescent wheat project in 1977. Each set of concentric contours represents a field, or group of neighboring fields. The concentration of contour lines reflects the density of adult cereal leaf beetles in that field. Fields are located in terms of the same 10-acre cells used in the habitat analysis, above. Specific fields can be identified on the contour plots with the aid of the digital and traditional maps in Appendix D, and the cell assignments given in Appendix B. Plotted values are the estimated densities in every field at daily intervals, generated by interpolating from actual samples collected approximately twice weekly. It is not difficult to find examples among these plots of densities rapidly falling or rising, of some fields increasing while others decrease, and of apparent transfers of beetles from one field to a neighboring field.

An interesting example of the latter is given by the sequence of events in fields 722, 236 (both R-wheat) and 235 (Oats) beginning on 10 May (plot No. 25). An enlargement of this group of fields (marked by an arrow in plot No. 25) is given in Figure 20. Oat field 235 is located between the two R-wheat fields. On 13 May the density in oats began to increase while those of the neighboring R-wheat fields declined, the latter apparently serving as a source for the beetles entering the oats. This continued until on 23 May the densities in the R-wheat fields were almost zero. On 24 May, however, the densities in R-wheat began to increase again with oat field 235 the apparent source. Here, then, is an example which seems to show beetles transferring from oats back to wheat. The evidence is circumstantial, of course, and only direct observation of the movement, say by marking individuals, could confirm the statement, but the suggestion is strong.

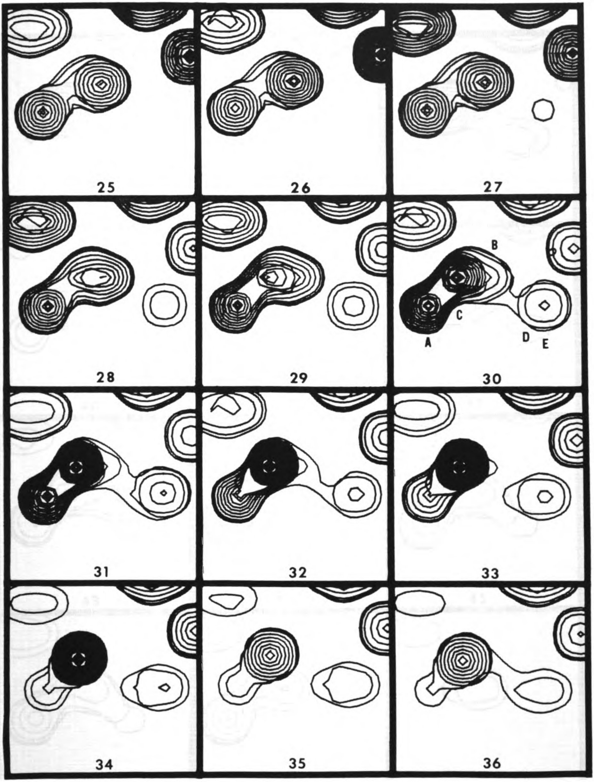


Fig. 20.--Contour plots of adult density in R-wheat fields 722 and 236 and oat fields 235, 613 and 612 (A-E, respectively) at Galien in 1977. Plotted daily beginning 10 May.

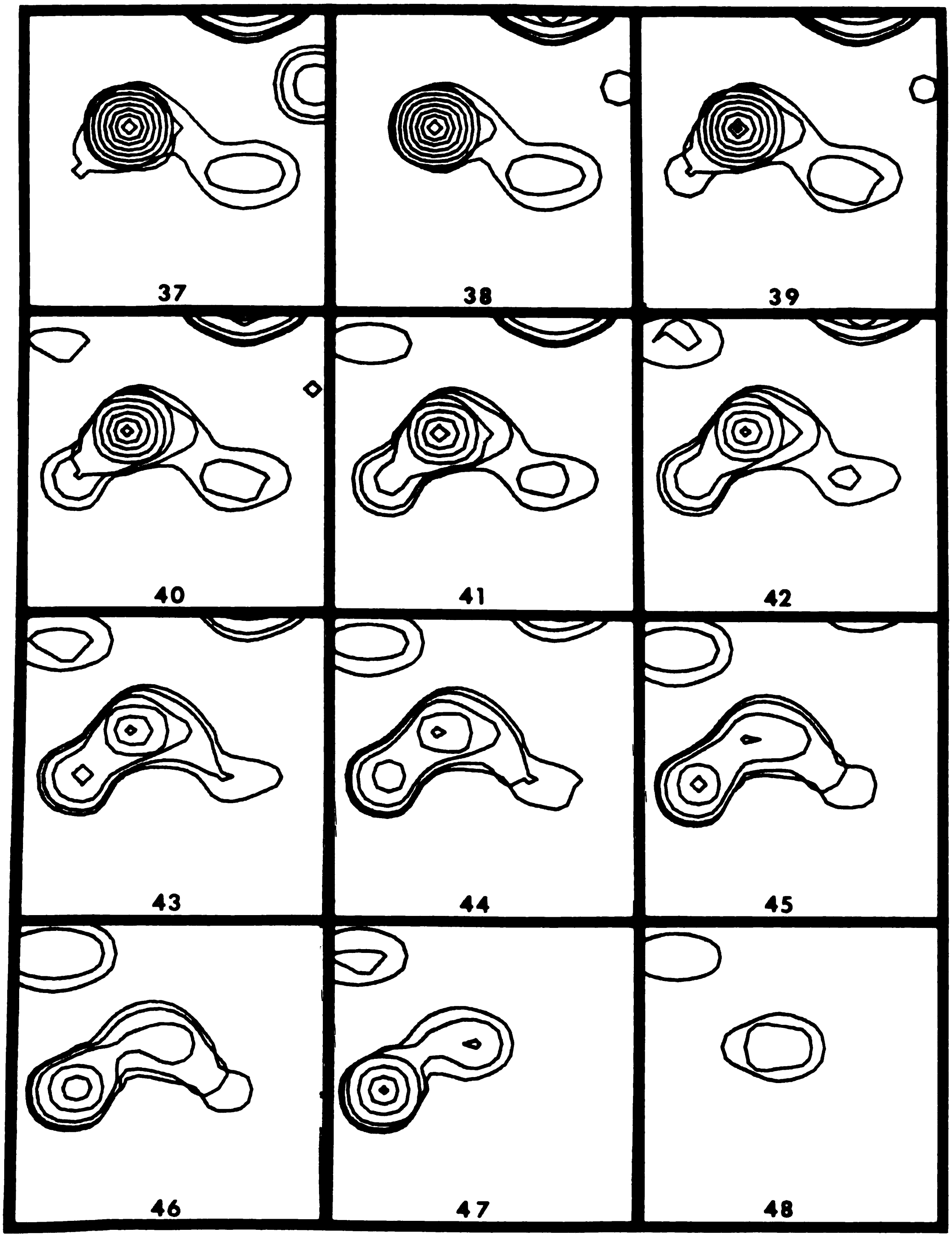


Fig. 20.--Continued.

The number of spring adults in a field at any time t is given by N(t), the integrated difference of dispersal rates into and out of the field and losses due to mortality:

$$N(t) = \int_{o}^{t} (IN - OUT - M)d\tau \qquad (17)$$

Quantification of these rates was sought in terms of environmental and biotic variables through three types of field studies: (1) field emptying rate studies, (2) sticky board trapping, and (3) the measurement of within field diffusion rates.

Field Emptying Rates

This experiment was directed toward defining a functional relationship between the rate of movement out of a field and such factors as crop species (wheat or oats), crop maturity and beetle density. While the experiment did not work out, I report the approach here to guide future work.

Movement out of a field might be considered in two parts: movement within the field and movement across the field boundary, and these may take place at different rates. What lies outside the boundary may influence the rate of crossing, but this complication was eliminated here by plowing and discing a clear buffer space around the plots.

It is not known what constitutes a "boundary" for the cereal leaf beetle--that is, the distance into the field at which the effect of the edge is no longer significant. Therefore, plots of various sizes in a geometric series were considered, ranging in size from

.25 ft^2 to 10,000 ft^2 (.023 m^2 to 929 m^2) (Table 10). It was hoped that the use of this series would give information on the effective width of a boundary so that further experiments could be restricted to the largest plot which could be considered "all boundary."

Table 10.--The number of beetles that were to be released in plots of various sizes to attain various densities. (For the smallest plots the number of beetles released is followed by the resulting densities.)

Side (ft)	Area		Adult Beetles/ft^2				
	ft^2	Acres	.03	.1	.3	1.0	3.0
.5	.25	.000006	1(4)	2(8)	3(12)	4(16)	5(20)
1.5	2.25	.00005	1(.44)	2(.9)	3(1.3)	5(2.2)	7(3.1)
5.0	25	.0006	1(.04)	2	7	25	75
15.0	225	.005	7	22	68	225	675
50.0	2500	.06	75	250	750	2500	-
100.0	10,000	.23	300	1000	3000	-	-

Plots were prepared by subdividing an existing winter wheat field at the Collins Road entomology research area in East Lansing, Michigan by plowing it on 23 May, 1976.

Starting densities of adult CLBs were also to be in a geometric series ranging from .03/ft^2 to 3.0/ft^2 (Table 10). Of course, in the smaller plots the lowest densities were not possible and in the larger plots the number of beetles required was prohibitive at high densities. A reasonable set of combinations required about 9000 beetles. Beetles were obtained by vacuuming a high-density wheat field at Galien, Michigan on May 5, 1976 and later dates, but it proved impossible to collect more than about 6000 due to poor weather and declining densities. The beetles were transported to Collins Road and stored in a 13 x 19 ft field cage in wheat. By the time the plots were prepared the stock of beetles had dwindled due to mortality. Because they required fewer beetles, the smallest plots were used first. It was assumed that in these plots the number of beetles leaving per unit time could be measured directly by observing individual flights. This assumption proved to be overly optimistic. For the larger plots the emptying rate was to have been inferred from the number remaining in the plot, estimated by sampling.

The experiment failed for two reasons. First, the beetles were very inactive. They would sit in one place, crawl very slowly, or fall to the ground and either crawl into crevasses or away from the plot. Some beetles mated. Second, due to the inactivity of the beetles, very long observation times were required. It was impossible to be attentive enough to keep track of as few as four or five beetles in even the smallest plot (6 in x 6 in) and be sure one had not flown away.

The difficulties may have been related to the lateness of the season when the experiment was begun (beetles were old, crop was tall) or to the artificially of such small plots affecting beetle behavior.

Sticky Board Trapping

During 1977 an attempt was made to quantitatively measure the rates of movement of adult cereal leaf beetles into and out of six grain fields in Berrien County, Michigan using sticky board traps. A total of 120 sticky board traps were distributed around and within two susceptible and two resistant wheat, and two oat fields. The traps were 122 cm (4 ft) tall by 15.24 cm (6 in) wide, constructed of two pieces of .32 cm (1/8 in) thick tempered pegboard bolted to a 183 cm (6 ft) long stake and painted with "crescent yellow" exterior enamel latex paint (Silver Lead Co.). Unpublished data (Jantz 1965) showed that "canary yellow," a similar color, was the most attractive to adult CLBs of several colors tested, and it was desirable in this experiment to catch a large number of beetles on which to base an analysis (since it was not known what color of trap would be totally neutral, I decided that catching as many beetles as possible would be the next best situation). Four traps were placed, vertically, along each border of each field, and four in the interior of each field (20 traps per field) by pounding the stakes into the ground until the bottom of the trap was about 20 cm (8 in) above the ground. The border traps were placed so that one surface (labeled "B") faced the interior of the field and one surface (labeled "A") faced away from the field. These were assumed to monitor outgoing and incoming flight, respectively. The traps were coated with "Tacktrap," a sticky substance which entangles any insects flying into it, and were recoated as necessary. The traps were divided, vertically, into four sections of equal area to determine the vertical distribution of dispersal flight. Traps were examined twice a week.

To relate trap catch to the actual number of beetles entering and leaving a field, accurate estimates of the change in density of adults in the field over the trapping interval were needed. Changes in density must be due to the differential effects of mortality and beetles entering and leaving the field (in the absence of new beetles emerging from pupation). For a finite time interval this can be expressed as

$$N_2 = N_1 - \text{mortality} + \text{immigration} - \text{emigration}$$

or $$(N_2 - N_1) + \text{mortality} = \text{immigration} - \text{emigration} \qquad (16)$$

or $$\Delta N + M = IN - OUT.$$

The change in the field's total population was estimated by sampling adults at frequent intervals, as described earlier.

To estimate mortality rates, screened cages (30.5 cm high by 7.6 cm diam) (Casagrande _et_ _al_. 1977) were used to hold adult CLBs on the host crop for a several-day period. Ten beetles, captured with a sweepnet in the same crop, were placed in each of five cages in one resistant and one susceptible wheat and one oat field. After several days the number which had died was recorded as well as the time elapsed. Many beetles escaped from the cages (between the foam plug and cage), so the number of remaining live beetles was also recorded. Mortality was calculated as the number dying divided by the sum of those dying and those live beetles which had not escaped. This method probably overestimated mortality since it assumes that escape is independent of mortality, while in fact dead beetles can not escape but live ones can. The mortality over n days (M_n) was converted to the rate of mortality per day (M_d) by the equation

$$M_d = 1 - (1 - M_n)^{1/n}. \tag{17}$$

This rate was assigned to the midpoint of the test period and used to calculate the total number dying in a field over a sampling interval. At the end of the test period the beetles were discarded and the cages were moved and restocked with freshly caught beetles. On the average, two tests per week were conducted.

Ultimately I wanted to relate the quantified rates of movement into and out of the field to such factors as beetle density, crop height, crop moisture, crop type (susceptible or resistant wheat, or oats), time and weather conditions. As a measure of crop moisture, four random samples of plant material were taken from fields 1022 (S-wheat) and 1024 (R-wheat) each week from 9 May to 27 June. The samples consisted of the above-ground portion of the crop plants in about 60 cm of row. The plants were put in tared paper bags and immediately weighed in the field on a portable balance. After oven drying (24 hr at 100°C) the samples and the empty bags were reweighed. Plant moisture was then calculated as percent, by weight, of fresh weight, and is shown in Figure 21.

From equation (16), the quantity IN-OUT is equal to $\Delta N+M$, which was measured in the field over each sampling interval, but the separate rates IN and OUT are unknown. These were thought to be estimated by sticky board trap catches on sides A and B, respectively, and related by some functions F_1 and F_2:

$$\begin{aligned} IN &= F_1(\widehat{IN}) \\ OUT &= F_2(\widehat{OUT}) \end{aligned} \tag{18}$$

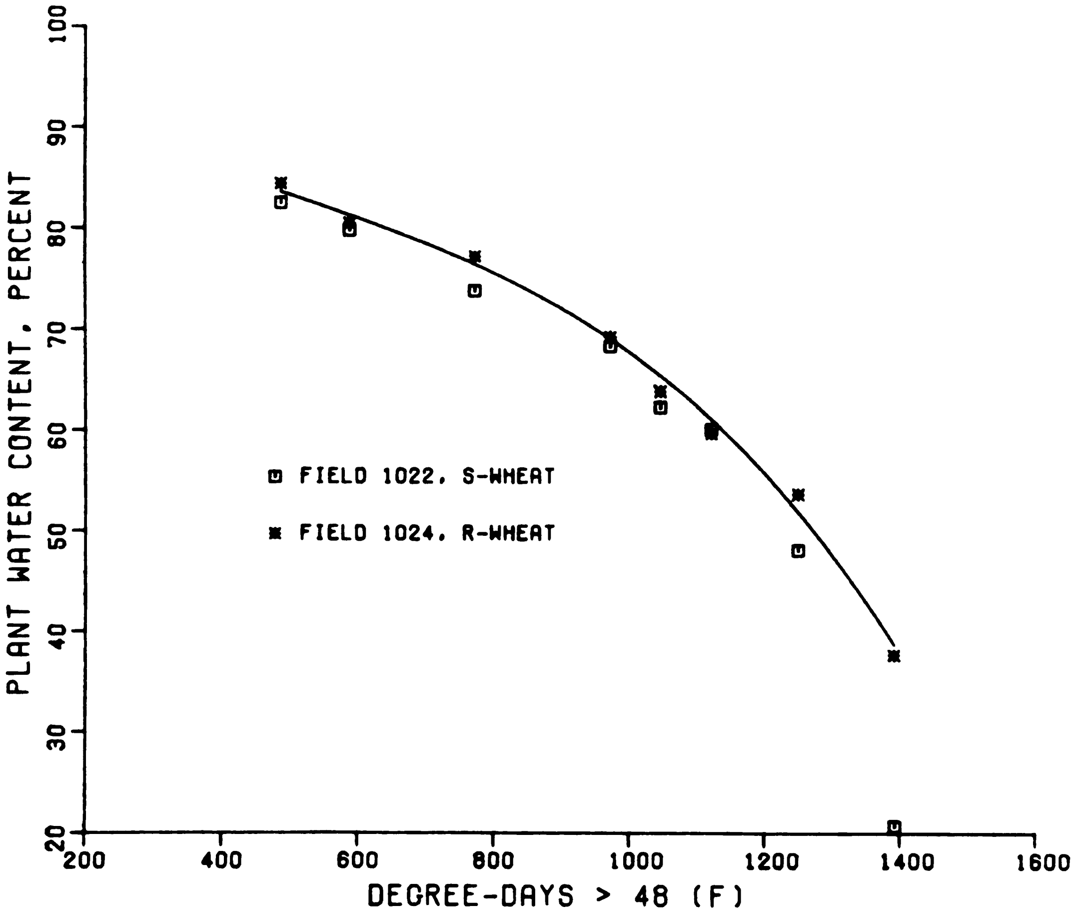


Fig. 21.--Crop moisture in two of the fields used in the sticky board trap study.

By assuming that the same function applies to trapping incoming and outgoing beetles, we have IN-OUT = $F(\widehat{IN}) - F(\widehat{OUT}) = F(\widehat{IN}-\widehat{OUT})$ for a linear function, F, where $F = F_1 = F_2$. A regression of $\Delta N + M$ on $\widehat{IN} - \widehat{OUT}$ should provide the function F, and from this the separate dispersal rates IN and OUT can be obtained.

$\widehat{IN}$ and $\widehat{OUT}$ were determined from trap catches by using the stratified sampling estimator of a population total (Cochran 1963, Ch. 5):

$$\hat{Y} = \sum_{h=1}^{4} N_h \bar{y}_h \qquad (19)$$

where $\bar{y}_h$ is the mean trap catch (on the appropriate side of the trap) along border h, and N_h is the length of the border in terms of trap units (border length/trap width). There were four traps along each of four borders in each field. The trap catches along the four borders of a field were usually quite different, often with a large number of beetles "entering" across one border and "leaving" across another border.

A summary of the sticky board trap catches for the border traps of fields 1022 and 1024 is given in Table 11. The counts are the total number of CLBs caught on the entire "A" side (IN) and "B" side (OUT) of the 16 border traps in each field since the previous observation. The traps in these two fields caught a majority of the beetles (6870 out of the 8177 beetles caught in all six fields), so only these data are presented here for illustrative purposes. The raw data for these and the other four fields are given

Table 11.--Total daily catch of incoming and outgoing CLBs on sticky board traps in field 1022 S-wheat and 1024 R-wheat (16 traps per field).

Date	Field 1022		Field 1024	
	In	Out	In	Out
4/19	traps established			
4/20	0	0	1	2
4/21	11	9	0	0
4/22	3	9	0	0
4/26	2	1	0	2
4/27	2	1	0	0
4/29	0	0	1	1
5/3	2	1	5	2
5/5	1	4	0	3
5/9	15	18	7	2
5/12	19	42	14	15
5/18	294	218	449	243
5/20	59	152	373	406
5/24	55	75	179	289
5/27	16	8	36	55
6/1	16	9	19	42
Spring total	495	547	1084	1062
6/8	9	14	7	16
6/13	9	8	0	2
6/14	0	5	1	3
6/16	127	454	13	16
6/21	373	670	28	42
6/24	411	696	83	98
7/1	119	177	152	149
Summer total	1048	2024	284	326
Grand Total	1543	2571	1368	1388

in Appendix G. The data are separated at June 1 into spring adult activity and summer adult activity. The trap catch follows, in general, the buildup and decline of field densities and clearly shows a lull in activity between the spring and summer generations. This indicates that sticky board catch is, in some manner, related to beetle activity.

The vertical distribution of trap catch for all six fields is given in Table 12. These data show that flight activity (as measured by sticky board trap catch in the air-space 1.4 M or less above the ground) declined above 1.0 M, with only 15% or so of the beetles being caught on the top section of the traps. Furthermore, the vertical pattern of activity is very similar for incoming and outgoing beetles (except in one oat field). There appeared to be a difference in vertical activity in the susceptible and resistant wheats, with a greater portion of the beetles in resistant wheat being caught closer to the ground. The reason for this is unknown.

Table 13 gives the results of the mortality cage studies. The mortality rates arrived at here are quite different from those reported by Casagrande *et al*. (1977) for four years of research at Gull Lake, Michigan, particularly in the rapid increase to very high mortality rates at the end of May. However, the current data may reflect the particular conditions existing in the study fields during the trapping period, and were therefore the estimates used. Mortality over the period from 21 April to 20 May, for susceptible wheat, and 24 April to 20 May, for resistant wheat, was rather low and constant. Average rates of 1.0%/day and 0.5%/day were used for these periods in the two

Table 12.--Vertical distribution of sticky board trap catch (proportion of total (n) caught on that side of trap) for both spring and summer beetles.

Crop	Field	Side A (In)				n	Side B (Out)				n
		Height (m)[a]					Height (m)				
		.35	.66	.96	1.27		.35	.66	.96	1.27	
S-Wheat	1022	.310	.297	.237	.155	1543	.311	.303	.243	.142	2571
	322	.179	.321	.333	.167	84	.184	.279	.324	.213	136
R-Wheat	1024	.509	.230	.147	.114	1368	.401	.308	.186	.106	1388
	323	.432	.250	.227	.091	44	.463	.179	.284	.075	67
Oats	541	.568	.242	.129	.060	433	.547	.231	.141	.081	320
	613	.290	.290	.280	.140	93	.469	.238	.185	.108	130

[a] Height above ground to middle of trap section.

Table 13.--Calculated mortality rates of adult CLBs in each crop.

Date[a]	No. beetles[b]	No. dying	No. days	Mortality %/day[c]
		Susceptible Wheat		
4/21	16	0	2	0.00
5/1	43	1	5	0.47
5/8	40	4	6	1.74
5/13	39	3	5	1.59
5/18	45	1	4	0.56
5/21	41	33	3	42.00
5/24	48	38	1	79.17
5/28	86	85	3	77.34
5/30	48	46	1	95.83
		Resistant Wheat		
4/21	16	8	2	29.29
4/24	15	3	4	5.43
4/28	85	0	2	0.00
5/1	44	0	5	0.00
5/8	20	0	6	0.00
5/13	37	0	5	0.00
5/18	30	2	4	1.71
5/21	44	32	3	35.15
5/24	50	48	1	96.00
5/30	46	42	1	91.30
		Oats		
5/24	33	8	1	24.24
5/25	31	11	3	13.59
5/27	28	13	6	9.88
5/28	32	31	3	68.50
5/30	38	36	1	94.74

[a] Midpoint of the test period.

[b] Alive + dead at end of test (excludes escapes).

[c] $1-(1-d/n)^{1/t}$ where d is the number dying out of n beetles (alive + dead) not escaping after t days.

crops. From 24 May to 1 June the mortality was again rather constant, but very high. Average rates of 83%/day and 94%/day were used for this period in the two crops. Over the short interval from 20 May to 24 May, mortality rates increased rapidly. Appropriate rates for each day were obtained from a line drawn through a plot of the mortality rates for this period. A similar approach produced estimates for the period from 21 April to 24 April in resistant wheat, over which mortality declined. Mortality in oats started out quite high on 24 May, declined, and then became very high by 30 May. As will be seen, the modeling effort for the wheat fields was not very successful, so the analysis was not carried out with the less complete oat data, and these mortality rates were not used.

Table 14 presents the calculated values of ΔN, M, $\hat{IN}$ and $\hat{OUT}$ for field 1022 (S-wheat), required for the quantification of trap catch. Similar calculations were done for the other three susceptible and resistant wheat fields, but are not presented here. For each sampling day, the density (no./60 cm) of adults is given, taken from Sawyer (1978, Table S1). These values were next converted to the total field population by considering the acreage of the field. The change, ΔN, in the population since the last sample was then obtained by subtraction. Total mortality was estimated by applying the appropriate rate, in %/day, to the population. If more than one day elapsed between sampling dates, the mortality for intervening days was obtained by estimating, by linear interpolation, what the total population was on these days. This method was only used when the mortality rate was low (before 20 May) or if the population increased. At high rates of

Table 14.--Adult density, change in total field population (ΔN), total mortality (M) and total immigrants ($\hat{I}N$) and emigrants ($O\hat{U}T$), estimated from sticky board trap catches, for frequent intervals in field 1022 S-wheat. Also given are ΔN + M and $\hat{I}N$ - $O\hat{U}T$.

Date	Adults/60 cm	ΔN	M	$\hat{I}N$	$O\hat{U}T$	ΔN + M	$\hat{I}N$ - $O\hat{U}T$
4/20	.500			0	0		
4/21	.610	62,520	2,842	4,147	3,393	65,362	754
4/22	.300	-176,190	3,467	1,131	3,393	-172,723	-2,262
4/26	.065	-133,575	4,819	754	377	-128,756	377
4/27	.222	108,110	370	754	377	108,480	377
4/29	.301	51,619	3,162	0	0	54,781	0
5/3	.177	-81,022	4,469	817	377	-76,553	440
5/5	.497	209,088	3,358	377	1,697	212,446	-1,320
5/9	.571	48,351	13,721	6,348	7,038	62,072	-690
5/12	.134	-285,535	11,558	7,352	16,338	-273,977	-8,986
5/18	.017	-76,446	13,055	114,996	85,462	-63,391	29,534
5/20	.026	5,881	255	23,440	59,881	6,136	-36,441
5/24	.004	-14,374	10,749	22,562	30,795	-3,625	-8,233
5/27	.009	3,267	9,220	6,095	3,016	12,487	3,079
6/1	0.000	-5,881	18,981	6,221	3,393	13,100	2,828

mortality linear interpolation would lead to an overestimate of the population level and hence, mortality. This is because the population will decline rapidly in an exponential fashion when subjected to a daily loss (mortality) rate of, say, 83%. For these situations, the population (and numbers dying, M) were estimated by applying an exponential interpolation from one known density to the later, lower, density. The sum of the estimated numbers of adults dying over the sample interval is given in Table 14 as the value M.

Ideally, if the sticky board trap catches were truly unbiased random samples of the number of beetles entering and leaving the field, and if the estimates of ΔN and M are also unbiased, then the equation $\Delta N + M = \widehat{IN} - \widehat{OUT}$ should hold and a plot of these estimates should produce points scattered about a line of slope 1.0. Of course, it is not expected that all beetles fly below 1.4 M, nor that the traps neither attract nor repel beetles. As discussed above, some functional relationship is expected, then, by which trap catches are related to actual dispersal rates. This was to be determined by regression analysis.

Table 14 gives the calculated values of $\Delta N + M$ and $\widehat{IN} - \widehat{OUT}$ for each trapping period in field 1022. Similar calculations for the other three wheat fields provided a total of 49 data points. From a plot of $\Delta N + M$ vs $\widehat{IN} - \widehat{OUT}$, it was obvious that no functional relationship between the two variables existed.

There are several possible reasons for the failure of the sticky board trap model, falling into two broad categories: (1) some or all of the model components (ΔN, M, $\widehat{IN}$, $\widehat{OUT}$) were not measured accurately, precisely, or frequently enough, and (2) some or all of the components did not measure, or represent, what they were assumed to be measuring. Examples of (1) might include an insufficient sampling frequency, so that the field population fluctuated greatly between density estimates but this went undetected. This would cause trap catch to be apparently unrelated to population change. In light of an earlier discussion, this is a likely possibility. Beetles may have avoided, been attracted to or repelled by, or failed to stick to the traps, or air currents may have carried flying beetles around the traps. These would make the traps an inaccurate (biased) sampling device. If such biases were variable or dependent on specific conditions, then again, the trap catch would be unrelated to actual dispersal rates by any single function. Sample sizes may have been too small, thereby producing estimates lacking precision.

Examples of (2) might include the possibility that most dispersal across field boundaries occurred above the level of the traps, so that trap catch did not really reflect this activity. The apparent changes in density may not have been due to actual changes in the number of beetles present in the field, but rather to varying susceptibility of the beetles to observation by the sampling method. For example, in the case of sweeping with a net, the model used to convert sweepnet catch to absolute density may have failed to adjust for the effect of weather on the proportion of beetles in the path of the net or the probability of capture once in the net's path (Ruesink and Haynes 1973). This possibility was discussed above, and was not considered to be a serious problem. The mortality rates of caged beetles may not have been representative of field mortality. The assumption that the two sides of the traps monitored dispersal in two opposite directions may have been false; beetle dispersal may not take place in straight lines of flight, but instead, may be very erratic. This last suggestion is a very real possibility, as will be seen in the next section.

Diffusion Rates

According to Pielou (1977, p. 166), "the movements of animal populations are of two types: migration and diffusion. Diffusion consists in the apparently aimless, undirected movements of animals that seem to be wholly random." Many ecologists use the words diffusion and dispersal synonymously, as I will here. I hypothesized, above, that cereal leaf beetle movements between fields are random, or diffusive, and that the probability of leaving a field once entered is related to the suitability of the crop in that field. Diffusion could account for the emigration process, too, if the diffusion rate varies, depending on conditions in the field. The mathematics of this process will be developed in a later section. Here, field studies are described which were intended to support the idea that within-field activity is diffusive, and to estimate the diffusion rate.

The rate of spread of a diffusing substance (or population) across a plane surface is related to the two-dimensional diffusion coefficient (Pielou 1977, p. 170):

$$D = \frac{(\Delta l)^2}{4\Delta t} \tag{20}$$

where Δl is the distance a beetle moves over the time period Δt. Casagrande and Haynes (1976a) used the concept of diffusion in a simulation of strip spraying for the cereal leaf beetle, and calculated D from data collected at Gull Lake in oats. Proper calculation of a mean diffusion coefficient requires paired observations of Δl and Δt. Casagrande and Haynes (1976a) failed to make paired observations, and attempted to correct for this by calculating D from the product of the mean values of $(\Delta l)^2$ and $1/\Delta t$. This is correct <u>only</u> when the two components, $(\Delta l)^2$ and $1/\Delta t$, are independent. Casagrande and Haynes (1976a) cited an <u>observed</u> independence of the two parameters. The only way such an independence could be observed would be to make paired observations, which, if they were in hand, would have permitted the correct calculation to be made. Furthermore, a low <u>correlation</u>, between the two (which is probably what was "observed") is insufficient to assure independence. This is because the expected value of the product of two random variables, say x and y, is $E(x) \cdot E(y) + COV(x,y)$. The covariance of x and y is given by $COV(x,y) = \sigma_x \sigma_y \rho_{x,y}$. That is, the product of the standard deviations and the correlation between the two variables. For data collected in the present study, $r_{x,y}$ was indeed low (-0.092 for 86 paired observations of $(\Delta l)^2$ and $1/\Delta t$), supporting Casagrande and Haynes' (1976a) impression of "independence." However, S_x and S_y were so large (3146.6 and 5.065 for $(\Delta l)^2$ and $1/\Delta t$, respectively) that the resulting covariance was a very substantial figure (-1466) to be added to $E(x) \cdot E(y) = 3157$. The resulting estimate of D was 423, rather than 789 as Casagrande and Haynes' (1976a) method would have yielded. Calculating the mean value of D directly from the individual observations of $(\Delta l)^2/4\Delta t$ yielded the same figure, 423. These results also illustrate the variability of the rate of diffusion among individual beetles.

Since Casagrande and Haynes (1976a) estimated D only for oats, additional studies in S-wheat and R-wheat, as well as in oats, were made. Supplementary estimates of D were also calculated from data gathered by E. P. Lampert (unpubl.) in wild grasses, grain stubble, wheat and oats at Gull Lake in 1976.

At Galien in 1977, paired observations of Δl and Δt were obtained by the following method. A beetle at rest on a host plant was located well inside the field boundaries. The observer watched the beetle from a distance until the beetle took flight. A white-tipped bamboo stick was stuck in the ground where the beetle had been resting, and the beetle was followed. When the beetle landed again, a stopwatch was started to time the interflight resting period associated with the previous movement (flight time was considered to be negligible). When the beetle took flight again, the stopwatch was stopped and another stick was placed at the second resting spot. The distance between the two sticks (the flight distance) was measured. Notes about the flight, resting behavior and interactions with other beetles were recorded. Similar observations were also made of beetles resting near the field border (within a M) to determine if dispersal behavior is different near the edge than it is in the interior of the field.

Figure 22 shows the path of one beetle whose movements over 21 minutes were recorded by E. P. Lampert (unpubl.) at Gull Lake in

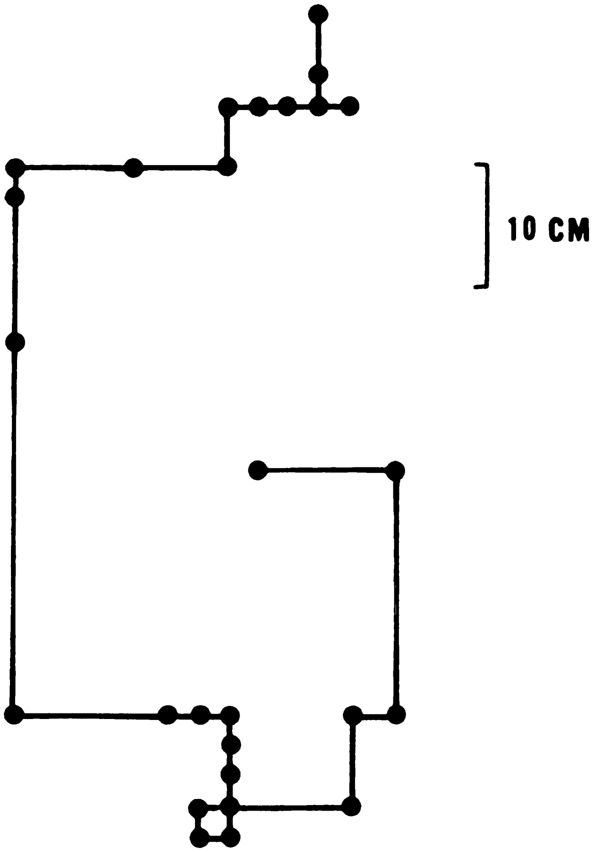


Fig. 22.--The path taken by a dispersing beetle in grass (1976 Gull Lake data from E. P. Lampert).

wild grasses (5/19/76, plot 5-50, beetle no. 16). Such a movement pattern, typical of many observed, would seem to justify an assumption of undirected, random movement.

Thirty-nine observations on beetles in R-wheat yielded a mean value for D of 304.4 in^2.min. For 47 beetles in S-wheat, mean D was 525.9. After a logarithmic transformation to stabilize the variances, there was no significant difference between the two crops. The overall mean D was 425.5 in^2/min, with a standard error of 143.3. In oats, 112 observations yielded a mean value for D of 669.8 in^2/min with a S.E. of 198.8. There was no difference in the diffusion rates observed for beetles near the border and for beetles in the interior of the field for any crop.

Casagrande and Haynes (1976a) observed a decline in D through the season in oats. They found no relationship between the diffusion rate and time of day, temperature, or solar radiation. Sufficient observations were collected by neither myself nor Lampert (unpubl.) to add any to an understanding of the relationship between diffusion and these weather factors. A likely cause of the decline in D with the progress of the season is an increase in crop height. It could also be due to changing physiological condition of the beetles, or to other changing qualities of the host crop. It would be impossible to separate these without detailed behavioral and physiological studies. For purposes of the simulation described below, I wanted simply to relate D to some monotonic variable in such a way that D declines with the season.

A nonlinear regression of D on crop height showed this variable to be a fairly good predictor of D. All available data, including that of Casagrande (1975), that collected by Lampert at Gull Lake in 1976, and that collected at Galien in 1977, were pooled for this analysis. A total of 709 observations on crop height and D, combining data from all small grain crops, were used. Figure 23 shows the best fitting equation, $D = 4230/Ht - 148.3$, where D is given as in^2/min and Ht is in inches. This gave an R^2 of .45 ($p = .002$, 16 df).

From Lampert's (unpubl.) Gull Lake data, the mean values for D in grasses and stubble fields were 762 and 16 in^2/min, respectively. Combining these gives an estimated mean diffusion rate in nonhost habitats of 584.2 in^2/min, based on 63 observations.

Since the dispersal observations in 1977 included the direction of movement, these movements could be examined in relation to wind direction and orientation toward the field boundary. Vectors representing the movement of individual beetles were plotted on maps representing each field, and the wind direction at the time of observation was also drawn in. Visual inspection of 198 observations showed no consistent relationship between wind and direction of movement for any crop, either near the border or in the interior of the field. On one or two occasions the majority of observed movements were in the direction of the wind, but these amounted to only 12 observations, and on other days with an equally strong wind (8-10 mph = 13-16 km/hr) no such orientation was seen.

There was no significant movement either toward or away from the border by those 81 beetles observed near (within 1.0 m of) the

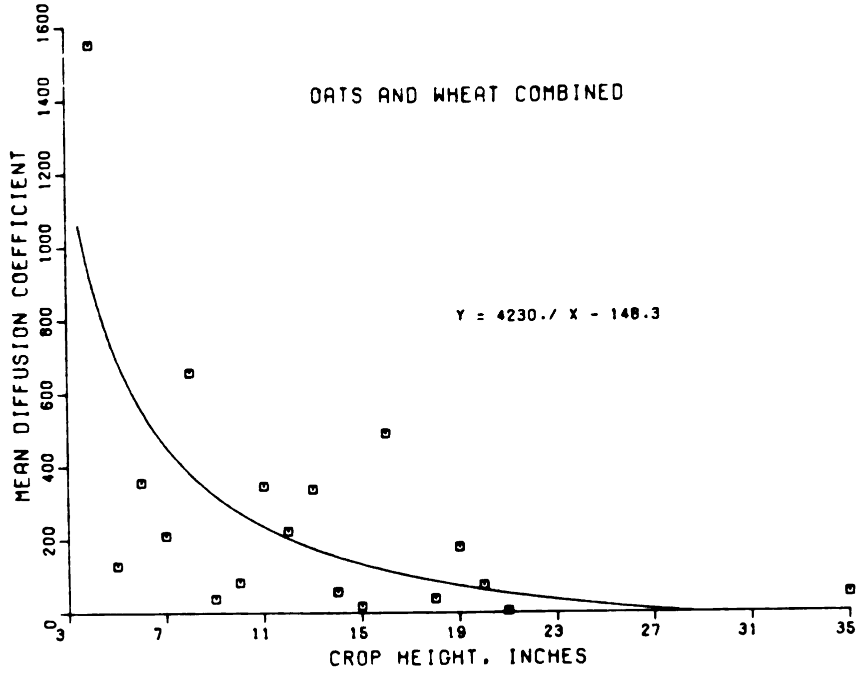


Fig. 23.--Diffusion rate (in^2/min) in grains as a function of crop height.

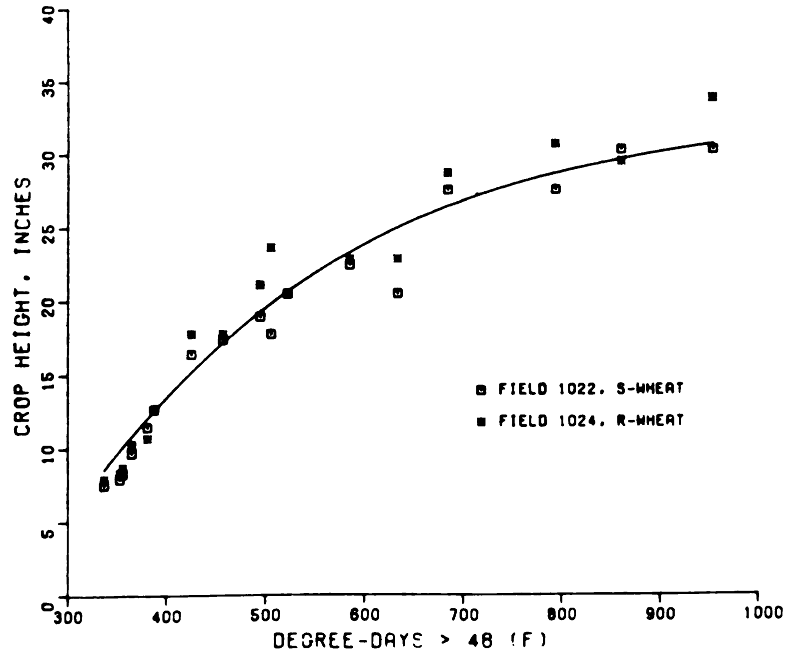


Fig. 24.--Crop height in two of the fields used in the sticky board trap study.

border, as tested against the binomial distribution with a probability of 0.5 for moving in either direction. Thus, movement near the border seemed unaffected by proximity to the border. However, no beetle was ever observed to actually cross the border and leave a field in these studies.

Exodus from Wheat

The adult populations in fields 1022 (S-wheat) and 1024 (R-wheat) rapidly declined over the period 11 May to 19 May 1977 (500 to 650°D > 48) (Figures 17 and 18). The possibility that this was caused by some changing condition of the crops was examined, by looking at plant water content and height.

The crop moisture is shown in Figure 21. Over the period of concern, water content of the above-ground plant material declined from about 83% to 79%. Water normally constitutes 80-90% of the fresh weight of most herbaceous plant parts (Kramer 1969, p. 5). It seems likely, then, that although the decline in water content was very slight and gradual, this point represented the beginning of dessication in wheat.

The physiological processes involved in heading may render the crop unsuitable to the cereal leaf beetle. A sudden increase in crop height may accompany heading, but Figure 24 gives no indication of this event occurring until perhaps 700°D, after the exodus was complete. During the interval from 500 to 650°D > 48, crop height increased gradually from 19 to 25 in. Unfortunately, the actual event of heading was not recorded.

Mortality rates at this time were quite low (Table 12), and did not begin their rapid increase until two days after the exodus was complete (21 May). Furthermore, the great increase in sticky board trap catch (Table 11) on 18 May in these fields support the idea that it was emigration, not mortality, which caused the decline in the population. It is interesting that almost as many beetles were caught on the outer faces of the traps as on the inner, indicating that the movement which "emptied" the fields may still have been diffusive rather than directed, although at a greatly increased rate.

A process which may account for both the exodus from 11 May to 19 May and the rise in mortality two days later is crop senescence. There are many physiological changes associated with the initiation of plant senescence (Salisbury and Ross 1969, p. 648). It may be that such changes (perhaps a decline in leaf water content below some threshold) signaled the beginning of crop maturation to the beetle, and emigration then began before the quality of the crop became so low as to be lethal. By 21 May any beetles confined to the crop in cages succumbed to starvation or other stresses associated with the low host quality. The weather both before and after 21 May was sunny, dry, and warm. The temperatures on 20 and 21 May were the warmest (92°F) yet recorded that year, but seem inadequate to account for the rapid increase in mortality following that date. That the kind of mortality observed at Galien in 1977 was not reported by Casagrande (1975) for four years at Gull Lake may be due to the extremely early maturation of crops at Galien in 1977. Wheat combining actually began in late June due to an early spring and a warm, dry season.

The hypothesis developed here to explain the observed exodus from wheat should be investigated further with specific behavioral and physiological experiments. Gutierrez _et al_. (1974) also observed a mass emigration of adults from oats and thought it was related to competition with large larvae. This is unlikely to have been responsible for the exodus from wheat observed in 1977, since densities and feeding damage were low.

To summarize the field studies on dispersal, it was found that densities within and between fields are dynamic. Beetles enter and leave both wheat and oat fields throughout the season. These rates of movement are probably affected by weather conditions, but not in any simple way. Dispersal within a field and near its border appear to be similar in rate and lack of orientation. Diffusion rates in both wheat and oats are loosely related to crop height, and after adjusting for this influence, are probably not different. Beetles probably begin to leave wheat by an increase in their diffusion rate when it becomes unsuitable as a host. In 1977 this occurred when the wheat reached a height of approximately 20 in (51 cm).

A SIMULATION MODEL

Overview

The need to consider a spatial approach to population dynamics leads to a familiar methodological dichotomy--namely, that of small plot, intensive studies versus large scale, extensive studies. The kind of research needed to gain a detailed understanding of age-specific survival rates generally requires intensive work done on small plots, including frequent and precise determinations of density, age distribution, parasitism rates, etc. Varley and Gradwell (1970) considered this type of study to be of prime importance.

However, the type of research needed to understand the redistribution process of an insect like the cereal leaf beetle requires extensive work done in a number of fields over a large area. The time and labor involved in each approach preclude combining them into a single effort except in unusually well-funded, short-lived projects. Even so, the resulting data are bound to be unwieldy.

Experiments designed to test hypotheses about a large and complex system's behavior under specific conditions or to evaluate alternative control measures and system designs may not be feasible in the real world. They may be too costly, time consuming, or even physically impossible to perform (Watt 1966). What, for example, would be the effect of doubling the wheat acreage in an entire region on the mean density of beetles in wheat? Properly controlled and replicated experiments on this scale are difficult to achieve in the field.

A logical solution to these problems is to use simulation techniques, where the results of separate studies which have taken different approaches are synthesized into a model whose behavior hopefully compares well with that of the whole system. Some general comments on the use of systems analysis in ecology are given by Arnold and deWitt (1976), Levin (1975), Patten (1972) and Watt (1966). The role of computer modeling is aptly described by Watt (1968): "A . . . difficulty in the description and analysis of dispersal phenomena is the sheer complexity of the bookkeeping because of the number of variables involved, the number of different points in space involved, and the number of different times at which we must record the variate values for the several variables at each point in space. We are led inexorably to computers."

Levin (1976) reviewed the topic of population dynamics models for heterogeneous environments, illustrating the construction of models for two situations: a patchy environment of discrete habitats, and an environment continuously varying in space. Examples of models of the former type are given by Kitching (1971) and Levin and Paine (1974). Population models in which space is treated continuously include those of Bailey (1968), Richardson (1970) and Scotter _et al._ (1971).

A combination of discrete and continuous spatial approaches must be taken in simulating cereal leaf beetle spatial dynamics in order to capture the essential features of dispersal for this species.

The habitat of the cereal leaf beetle is inherently discontinuous, or patchy (see maps, Appendix D). It may be assumed that some biological processes, such as feeding and oviposition, occur primarily in grain fields. However, if dispersal between fields is random, as hypothesized, then dispersing beetles may not be treated as if they move directly from patch to patch; a continuous model of dispersal, such as Bailey's (1968), is needed. Furthermore, the inter-patch, noncrop environment plays a vital role in processes such as mortality and in imposing varying time delays on dispersal between the discrete sites.

The spatiotemporal spruce budworm model of Holling et al. (1975) suffers from a lack of detail and realism in the within-site submodel. The reason for this is given by the authors themselves (Holling et al. 1976, p. 31): "Even though the previous steps of bounding may seem to have led to a highly simplified representation, the number of state variables generated is still enormous. The 79 variables (of which only one represents the insect population) in each site are replicated 265 times to give a total of 20,935 state variables. Thus even this drastic simplification . . . leads to a system that is enormously complex." Due to the limitations that the complexities of an ecosystem impose on a simulation model, the intended use of the model must govern the structure that it will have, and the resolution with which the system is simulated (Arnold and DeWitt 1976).

Models describing the within-field dynamics of the cereal leaf beetle have already been constructed (Gutierrez et al. 1974; Fulton

1978; Lee et al. 1976; Tummala et al. 1975). Since it is only the adult which disperses, a spatiotemporal model need only include this stage, and can be linked to the detailed single-site models of the other authors by a single variable: the egg input to specific fields. Fulton's (1978) model, for example, required this information for initialization.

To deal adequately with the spatial complexity of the system, then, and because within-generation population models of the cereal leaf beetle already exist, the spatiotemporal model developed here is limited in temporal scope to the period from spring emergence of overwintered adult beetles to oviposition in the host crop. It has a high degree of temporal resolution to capture the dynamics of dispersal. Its spatial scope is a region of 16 mi^2, with a spatial resolution of ten acres.

An overall block diagram for a spatiotemporal model of the cereal leaf beetle in a regional crop system is given in Figure 25. As mentioned, the within-generation dynamics component was not incorporated into the model developed here, and the host crop component is very simply represented by the height and relative suitability of each crop. The components within the box drawn with a dashed line represent the aggregate of regional processes; the solid arrows represent vectors of flow rates between sites. The components outside the dashed line represent within-site processes--namely, the integration of net dispersal and mortality rates to arrive at adult density, oviposition within the field, and the process by which the probability of leaving the site is determined. The letters S, T and

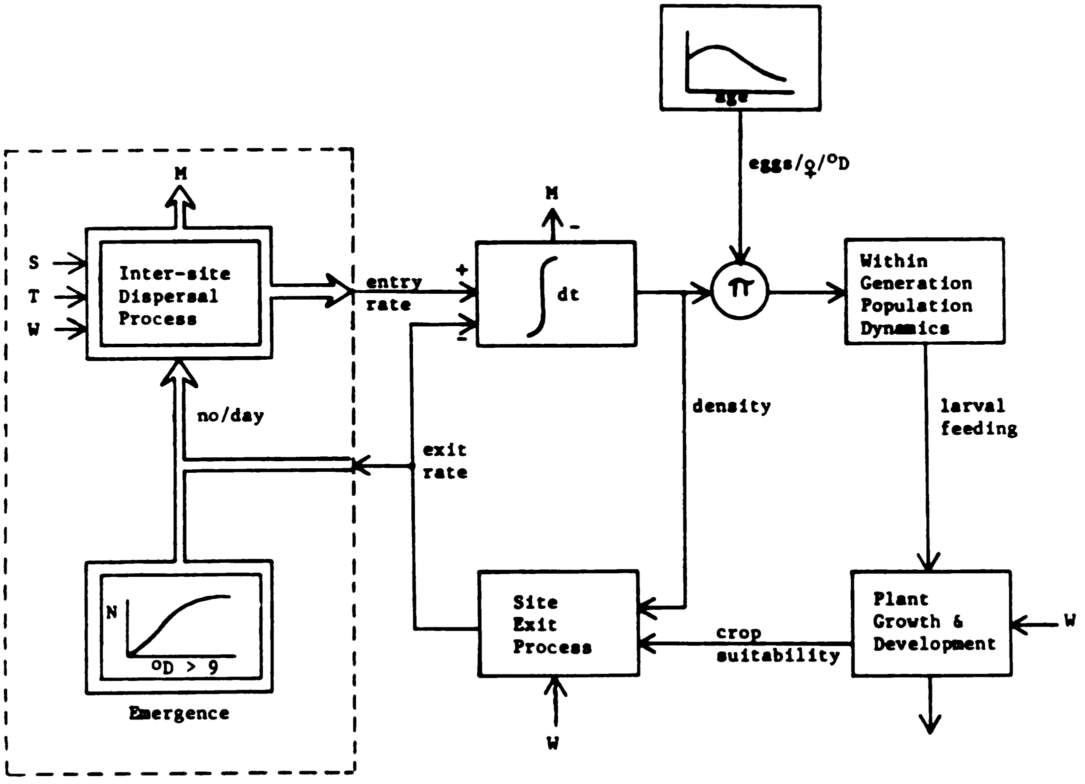


Fig. 25.--Block diagram of a model for the distribution and abundance of the cereal leaf beetle.

W stand for spatial, temporal, and weather factors which affect these processes, and M denotes mortality.

In the simulation model, the 16 mi^2 area is represented by a 32 x 32 grid of 10-acre cells. The simulated area can be patterned after the pubescent wheat study area near Galien by using the habitat data from the remote sensing work to assign a dominant habitat to each cell. These habitats are (1) S-wheat, (2) R-wheat, (3) oats, (4) nonhost cropland, (5) sparse woods, (6) dense woods and (7) water. To determine the initial locations of overwintering adults, the distributions of woods edge and fencerows are also utilized, but in the model these small habitats occupy no space and have no effect on dispersal rates. Prior to oat emergence, oat fields are treated as nonhost cropland.

State variables which are kept track of by the model include the number of adults and eggs in every cell, the cumulative total of emerged beetles and of sexually mature beetles, the height of each host crop, the time, in days, since 1 April, and the degree-day accumulations above 42°F (5.5°C) and 48°F (8.9°C).

Input variables include the daily degree-days above both bases, the mean daily temperature, and the size of the overwintering population.

Fixed design parameters are the numerical distribution of overwintering adults among the different overwintering habitats, the emergence rate of adults as a function of $°D > 48$, the maturation delay for female adults as a function of temperature, the adult mortality rate as a function of temperature, the oviposition rate in each crop as a function of beetle age, the diffusion coefficient in the host crops as a function of crop height, and the maximum height of each host crop and its rate of growth as a function of °D > 42.

Tunable design parameters, or those which can be varied to evaluate alternate system designs, are the spatial pattern of nonhost habitats, the crop pattern for the year, in terms of the size, shape, location and variety of each small grain field, the degree of resistance for the pubescent wheat, the relative synchrony of the beetle with its host crops, the synchrony of winter and spring grains, the diffusion rate in each nonhost habitat, the degree to which each habitat acts as a barrier to diffusion or is attractive to dispersing beetles, the height at which wheat becomes unsuitable as a host and the degree of this unsuitability.

A listing of the FORTRAN computer program for the simulation model is given in Appendix H.

Mathematical Approach to Diffusion

The probability of a diffusing particle being outside of a bounded area after a fixed length of time, given that it started out within the area, is related to the diffusion coefficient. Two dimensional diffusion without drift is described by the partial differential equation

$$\frac{\partial\phi}{\partial t} = D \; \frac{\partial^2\phi}{\partial x^2} + \frac{\partial^2\phi}{\partial y^2} \tag{21}$$

where $\phi(x,y,t)$ gives the probability that at time t the particle will be at position (x,y) and D is the 2-dimensional diffusion coefficient introduced earlier (Pielou 1977, p. 170). The solution to this equation can be shown to be the bivariate normal distribution,

$$\phi(x,y,t) = \frac{1}{2\pi\sigma^2} e^{-[(x - x_o)^2 + (y - y_o)^2]/2\sigma^2} \tag{22}$$

where (x_o, y_o) is the initial position and $\sigma^2 = \text{var}(x) = \text{var}(y) = 2Dt$.

For the simulation model we need to know the probability that a diffusing beetle will be outside of (has left) a 10-acre cell at time t. For a fixed time span and cell size, this probability depends only on the values of D and (x_o, y_o). By assuming that the population is uniformly distributed within the cell, we can find the mean probability of leaving[10] the cell for the population as a whole. This will depend only on D. To do this the probability density function (22) must be integrated over the range of x and y coordinates representing the field, as we let (x_o, y_o) range uniformly over the entire cell. This integral gives the probability of being <u>inside</u> the cell, so its value subtracted from 1.0 gives the desired quantity. Thus, the probability of leaving the cell is

$$P = 1.0 - \frac{1}{16a^2\pi Dt} \int_{-a}^{a}\int_{-a}^{a}\int_{-a}^{a}\int_{-a}^{a} e^{-\frac{1}{4Dt}[(x-\mu)^2 + (y-\nu)^2]} dx\,dy\,d\mu\,d\nu \tag{23}$$

---

[10] Actually, the probability of leaving the cell is not the same as the probability of <u>being outside</u> after some interval, since the beetle may return. The probability wanted for the model is the latter, and its derivation is given, although for convenience I may refer to this as the probability of leaving the cell.

where (o,o) is the center of the cell which is 2a x 2a in size and (μ,ν) gives the initial location of an individual in the cell.

Figure 26 shows the probable location of a beetle starting out in the center of a 10-acre cell after t minutes given a mean diffusion rate D such that $2Dt = 2 \times 10^6$ in^2. For example, if D = 500 in^2/min, then t = 2000 min, or 33 hr. The volume under the bell-shaped surface is the probability of being inside the field, in this case .74. Thus the probability of being outside is .26. Figure 27 shows the probability density function for a beetle starting out half way from the center toward each edge of the cell, with the same value for 2Dt. Clearly, there is a higher probability of being outside of the cell. Equation (23) gives the mean probability for all possible starting locations. Figure 28 shows the same density function as in Figure 27 but with 2Dt twice as large. That is, after twice as long a time or with twice the diffusion rate. The probable locations are obviously spread farther in all directions.

Although P in equation (23) depends only on 2Dt for a fixed cell size, there is no closed solution to the equation; it must be solved by numerical integration. This was done for a 10-acre cell, and the resulting solution is shown in Figure 29. The equation,

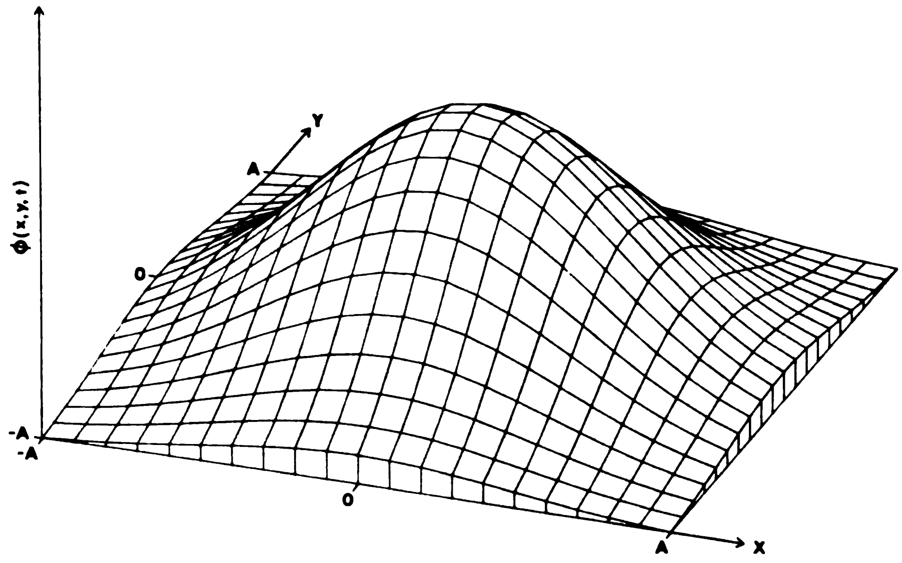
$$\mathrm{LOG}_{10}(Y) = -3.688 + 0.4958\ \mathrm{LOG}_{10}(X), \tag{24}$$

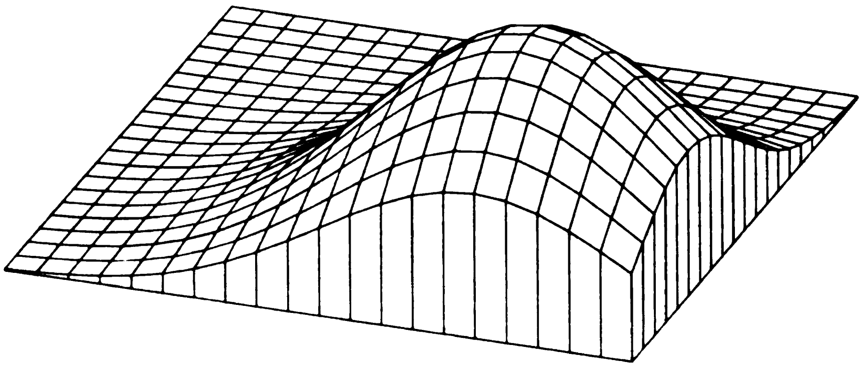
where Y is the probability of being outside of the field (averaged over all possible starting locations) and X = 2Dt, fits the calculated points extremely well except for very high values of 2Dt. This is because equation (23) is asymptotic at 1.0, but equation (24) goes to

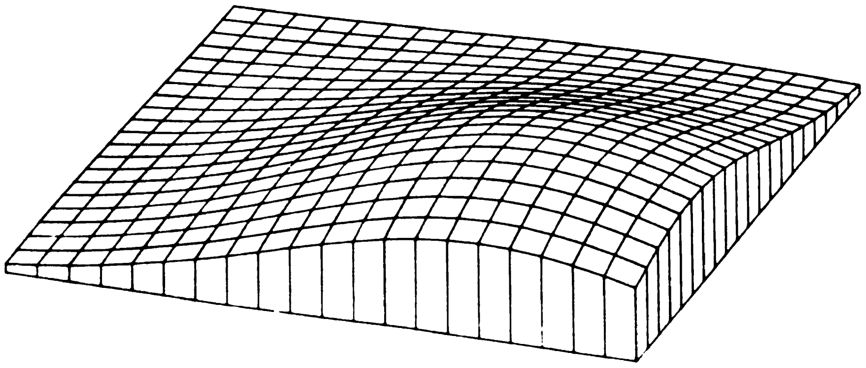
Fig. 26.--Probability density for the location after t minutes of a beetle starting out in the center of a 10-acre field given a diffusion rate D such that $2Dt = 2 \times 10^6$ in^2.

Fig. 27.--Probability density for the location after t minutes of a beetle starting out half way toward each edge from the center of a 10-acre field given a diffusion rate D such that $2Dt = 2 \times 10^6$ in^2.

Fig. 28.--Probability density for the location after t minutes of a beetle starting out half way toward each edge from the center of a 10-acre field given a diffusion rate D such that $2Dt = 4 \times 10^6$ in^2.


φ(x,y,t)
Y
A
0
-A
-A
0
A
X





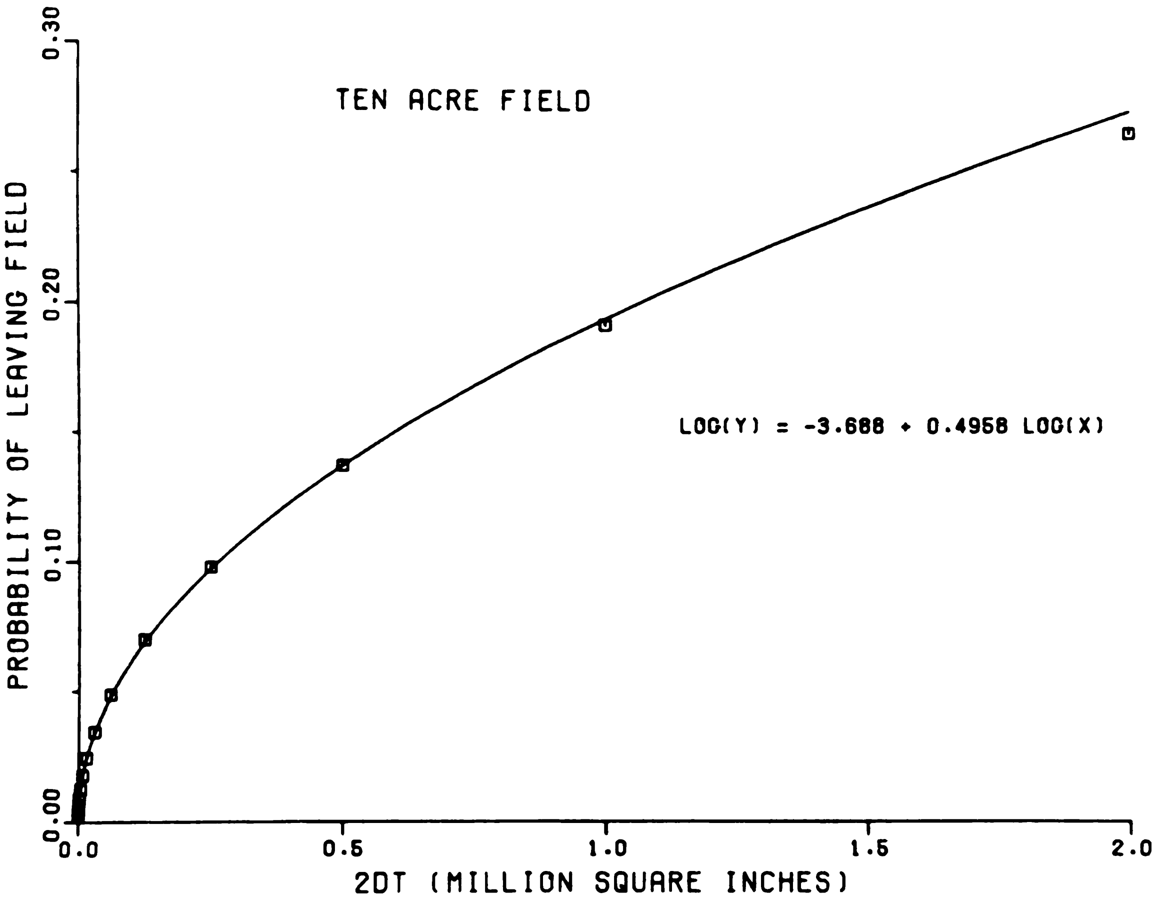


Fig. 29.--Mean probability of being outside of a 10-acre cell as a function of time (t) and the diffusion rate (D).

infinity. The maximum point plotted, however, represents a fairly high diffusion rate or long time interval, say D = 1000 in^2/min and t = 1000 min = 16.7 hr. The simulation model requires daily rates (15 hr day), so the maximum point plotted represents one day of diffusion at a continuous rate higher than normally observed (Figure 20).

Bailey (1968) has developed equations to express the change in the size of a spatially distributed population with stochastic birth, death, and migration processes. The simplifying assumptions are made that the birth, death, and migration rates, λ, μ and ν are constant through both time and space. Bailey hypothesizes a population existing at the nodes of a square lattice, and permits migration to lattice point (i,j) only from its four nearest neighbors (i+1, j), (i-1, j), (i, j+1) and (i, j-1). He gives the rate of change in the mean value, m_{ij}, of the random variable $X_{ij}(t)$, the colony size at (i,j) at time t, as

$$\frac{dm_{ij}}{dt} = (\lambda - \mu - \nu)m_{ij} + \nu/4\ (m_{i,j+1} + m_{i,j-1} + m_{i+1,j} + m_{i-1,j}). \tag{25}$$

Bailey (1968) then develops equations for the explicit solution to (25). For the present simulation model, the explicit solution is of little use, since the parameters λ, μ and ν are not constants, but vary in time and space (in different habitats). These complexities are easily handled in a computer simulation by solving an equation such as (25), with variable parameters, numerically.

Bailey's (1968) differential equation (25) was modified to incorporate the possibility of nonrandom exchange between neighboring cells. This was done to evaluate alternative assumptions about the nature of the dispersal process. These assumptions are, in order of stringency: (1) neutrality (random exchange), (2) repulsion (habitats may act as barriers to dispersal) and (3) attraction. These variations were incorporated by introducing an absorptivity constant, A, associated with each habitat type. An absorptivity of $A = 0.0$ signifies a perfect barrier: no dispersing beetles enter such a habitat. This was used for the boundary surrounding the simulated region, for water, and for dense woods. A nonabsorptive habitat may be regarded as a perfect reflector, also. Beetles that might have entered that habitat are, in effect, turned back. By placing a perfectly reflecting barrier along the boundary of the region, mirror-image symmetry is accomplished: losses from within the region are exactly balanced by gains from outside. An absorptivity of $A = 1.0$ gives a neutral model, such as Bailey's (1968). When $0 < A < 1$, partially reflective barriers are created, where the probability of exchange between the two sites is A times the probability for a neutral model. When A is greater than 1, a habitat is attractive, and the probability of an individual entering the site from a neighboring cell is also A times the random probability. Repulsion is considered to be a less-demanding assumption because it does not necessarily involve action at a distance. It simply states that a portion of those beetles which would otherwise have crossed the boundary are turned back. For attraction to be operative, beetles which would not have approached the boundary must be drawn to and across it. Comparison of the model's behavior under the various assumptions permits their validity to be evaluated. In general, the simplest hypothesis which explains the observed behavior should be made.

The rate of change of a cell's population of adults is thus given by the following modification of equation (25):

$$\frac{dm_{ij}}{dt} = E_{ij} - (\mu + \nu_{ij}NB_{ij})m_{ij} + A_{ij}/4\,(m_{i,\,j+1}\,\nu_{i,\,j+1} + m_{i,\,j-1}\,\nu_{i,\,j-1} + m_{i+1,\,j}\,\nu_{i+1,\,j} + m_{i-1,\,j}\,\nu_{i-1,\,j}). \tag{26}$$

All rates are expressed on a per-day basis. E_{ij} is the rate of emergence from overwintering sites within the cell, μ is the daily mortality rate of adults, ν_{ij} is the probability of leaving the cell in one day by random diffusion (from equation 24), NB_{ij} is the non-barrier portion of the cell's boundary, and is given by the mean absorptivity of its four neighboring cells. For example, if all absorptivities are 1.0, then emigration is the same as for random diffusion. If dense woods, a perfect barrier, borders the cell on two sides, then $NB_{ij} = (1 + 1 + 0 + 0)/4 = .5$, and the loss rate from the cell is reduced by half. If one neighboring cell is attractive, say with $A = 2.0$, then $NB_{ij} = (1 + 1 + 1 + 2) = 1.25$, and the rate of loss from the cell is increased. If the cell in question is, itself, reflective ($A_{ij} < 1.0$), then immigration from neighboring cells is reduced accordingly.

The model outlined here is essentially the same as Bailey's (1968), except the population is located in cells which cover the region rather than at the nodes of a grid. Furthermore, by allowing parameters to differ in the various habitats, the heterogeneity of the cereal leaf beetle's environment is taken into account. Bailey's explicit solution involved a probability of exchange between each site and all others, however distant. This poses computational difficulties. By solving (26) numerically and considering rates of change in sufficiently small time steps, only exchange between neighboring cells need be considered. This is, in effect, a random-walk approximation to diffusion (Karlin and Taylor 1975).

The standard values used initially in the model were A = 1.0 for host crops and nonhost cropland, A = 0.5 for sparse woods, and A = 0.0 for dense woods, water and the boundary of the region.

The standard diffusion coefficients, which determine the probability of leaving a cell by random dispersal, were D = 584 for nonhost cropland, grain fields prior to emergence of the seedlings, and water. This was the mean value in grasses and stubble fields at Gull Lake in 1976. Cells dominated by water, although perfect barriers, require an associated diffusion rate because they may contain minor acreages of other habitats. Overwintered beetles emerging from these habitats must be permitted to disperse out of the cell. For lack of any information, the diffusion rate in sparse and dense woods was arbitrarily set to 500. In the host crops, the diffusion coefficient was calculated as D = 4230/HT - 148.3, where HT is the crop height in inches (Figure 23). To simulate the exodus of beetles from maturing wheat, a critical height can be specified at which point the diffusion rate and/or absorptivity of wheat may be altered.

In the standard simulation, this height was 20 inches (the height at which the exodus in 1977 was observed to begin), and the diffusion rate at this point was changed to that of nonhost cropland. The absorptivity remained unaltered at 1.0.

Other Components

Timing of Events

The model simulates events over the period 1 April to 15 July. All rates are calculated on a daily basis, but may be functions of degree-days or mean daily temperature. Rates of plant growth are related to °D > 42(F) (5.5°C), while those affecting the CLB are in terms of °D > 48(F) (8.9°C). Degree-day accumulations by date are given in the model by the 30-year mean accumulations at Eau Claire, Michigan (Berrien County) over the period 1931-60 (Figure 30). These were obtained, by interpolation, from accumulations reported by Van Den Brink *et al*. (1971) for the bases 40, 45 and 50°F. Van Den Brink calculated °D > 42 as (Max + Min)/2 - 42, where (Max + Min)/2 is a good approximation to mean daily temperature.

Mean daily temperature (°F) was therefore back-calculated in the model as TEMP = DD42 + 42. This overestimates the temperature slightly early in the season, since Van Den Brink set °D > 42 to zero when the mean daily temperature was less than 42. Degree-day accumulations were stored as arrays and a table look-up function retrieved the current accumulation.

It would be an easy matter to input actual field temperatures to calculate degree-day accumulations and mean temperatures, if

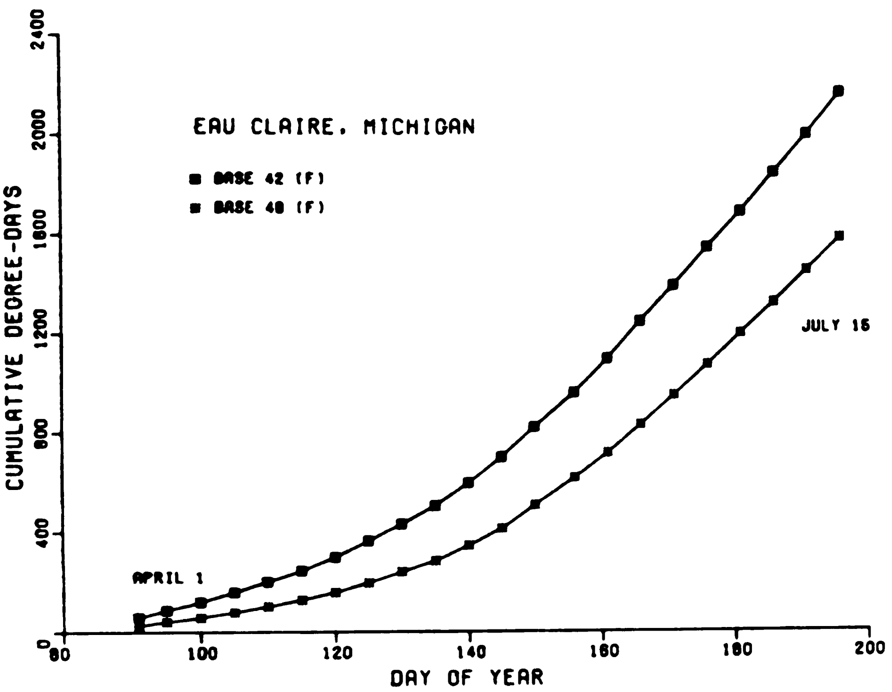


Fig. 30.--Mean degree-day accumulations at Eau Claire, MI for the period 1931-60.

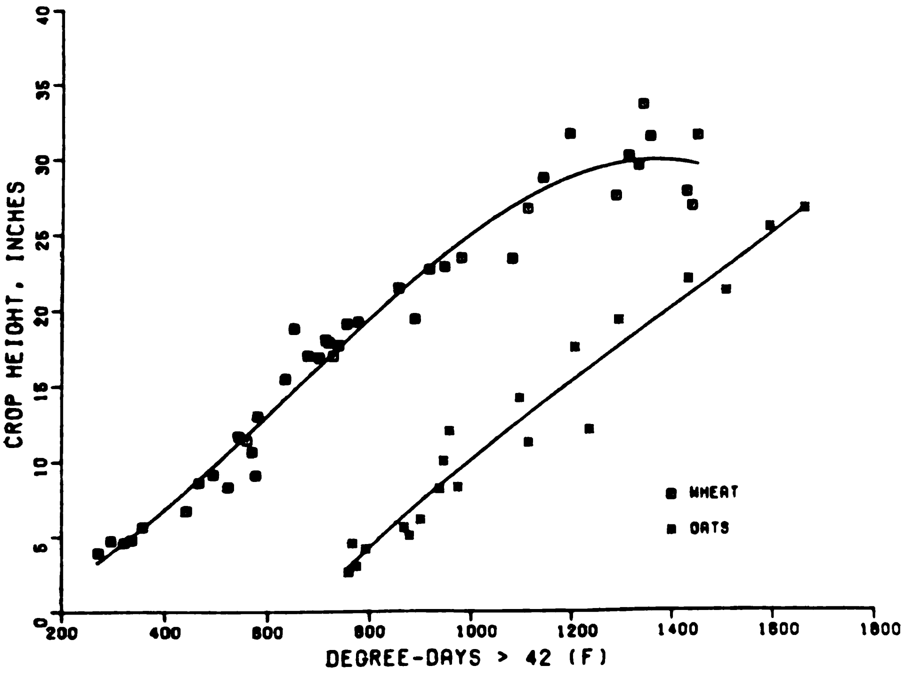


Fig. 31.--Crop growth curves for the standard simulation.

desired. The goals of the simulation work were general, however, and such detail was unnecessary. The model was used to evaluate the influence of general spatial and temporal patterns on beetle distribution and abundance, and for this purpose average temperature conditions were an appropriate simplification.

Crop Growth

Crop growth was simulated by defining functional relationships between crop height and accumulated °D > 42 (DD42). No variation in height between fields was incorporated, again because of the general goals of the current work. The mean height of wheat on each sampling date in 1977 at Galien is shown in Figure 31. A cubic regression was fitted to the data to describe the relationship:

$$\begin{aligned} HTW = &-1.55 + 9.57 \times 10^{-3}\ DD42 + 3.58 \times 10^{-5}\ (DD42)^2 \\ &-1.89 \times 10^{-8}\ (DD42)^3 \end{aligned} \qquad (27)$$

where HTW is the mean wheat height, in inches.

The 1977 data were used to develop the wheat equation because, due to the early season, a fairly complete growth was observed. Only eight oat fields provided data for 1977, however, and they were planted over a wide range of dates. A plot of mean oat height for this year was therefore very atypical. For this reason, the 1976 mean oat height data were used. These are shown in Figure 31, translated 200°D > 42 later to give the wheat and oat growth curves a temporal relationship which seemed typical of other years. The cubic regression for oat height is:

$$HTO = -21.2 + .0563\ X - 2.82 \times 10^{-5}\ X^2 + 8.18 \times 10^{-9}\ X^3 \qquad (28)$$

where HTO is the mean oat height in inches and X = DD42 - 200. Oats were permitted to reach a maximum height of 30 in, the maximum attained by wheat.

To evaluate the effect of varying the synchrony between the beetle and its hosts, or between winter and spring grains, the two crop growth curves can be independently shifted earlier or later by any °D > 42 value using the parameters DWX and DOX.

Wheat Resistance

There are three means of simulating resistance in wheat in the model. Adult densities can be reduced by increasing the diffusion rate (and hence, emigration rate) in R-wheat by multiplying the D value for S-wheat by a factor, DINCR. Adult densities can also be reduced by setting the absorptivity, A, to less than 1.0 to make R-wheat a partially repulsive crop. Neither of these options was used in the standard run. There is no evidence for the latter phenomenon. The mean diffusion rate measured in R-wheat at Galien in 1977 was not significantly different from that in S-wheat. In 1977 the mean density of adults was lower in R-wheat, but in 1976 it was not (Sawyer 1976b, 1978). Thus, in the standard run, DINCR = 1.0 and A for R-wheat = 1.0.

The other way to incorporate resistance is by reducing the oviposition rate per female by a factor, OVRED. There is ample evidence for this phenomenon (Sawyer 1976b, 1978; Gallun *et al*. 1966;

Schillinger and Gallun 1968; Hoxie et al. 1975; Casagrande and Haynes 1976b). For the standard run, OVRED = 0.68, the observed reduction in eggs laid per adult-°D at Galien in 1977.

Spring Adult Emergence

Casagrande et al. (1977) reported the relative density of cereal leaf beetles in the five overwintering habitats at Galien, based on two years' (1974-75) trapping data. Data from 1976 and 1977 (Sawyer 1976b, 1978) were added to the earlier information, and updated distributions (Table 15) were calculated by the method described by Casagrande et al. (1977). Let T be the sum of the mean densities/yd^2 of emerging beetles in the five habitats. Then the last row of Table 15 gives the expected density in each habitat as a percent of T. The actual acreage of each habitat in each cell at Galien was available from the remote sensing data. T was entered as an input variable. For each cell (i,j), the total number of adults emerging was calculated as:

$$AE_{ij} = 48{,}400 \sum_{h=1}^{5} A_{hij} \, d_h T \qquad (29)$$

where A_{hij} is the relative area occupied by habitat h in cell (i,j), $d_h T$ is the mean regional density of emerging beetles in habitat h, and 48,400 is the number of yd^2 in 10 acres.

The daily rate of emergence was related to °D > 48 using data and the approach given by Casagrande (1975, pp. 20-22). Regressions of the probit of cumulative proportion emerged on the logarithm of °D > 48 were calculated separately for Casagrande's 1971, 1973 and

Table 15.--Relative density of cereal leaf beetles in each of five overwintering habitats at Galien, 1974-77 (modified from Casagrande *et al.* 1977).

	Habitat					
	Crop Land	Dense Woods	Sparse Woods	Woods Edge	Fence Rows	Total
1974						
Traps	3	5	7	6	8	29
Density/yd^2	.333	.800	1.429	1.500	5.125	8.854
% of Total	3.761	9.035	16.140	16.941	57.883	
1975						
Traps	0	12	12	12	12	48
Density/yd^2	-	1.917	6.417	6.583	4.833	19.750
% of Total	-	9.706	32.491	33.331	24.470	
1976						
Traps	26	18	30	30	23	127
Density/yd^2	1.346	0.111	0.667	2.067	3.565	7.756
% of Total	17.354	1.431	8.600	25.650	45.964	
1977						
Traps	20	30	20	16	14	100
Density/yd^2	1.050	0.200	1.800	2.063	1.500	6.613
% of Total	15.879	3.025	27.221	31.198	22.684	
Weighted $\bar{X}$	15.920	4.279	18.917	28.129	37.394	104.639
Adjusted $\bar{X}$	15.214	4.089	18.078	26.882	35.736	100

1974 data. The average slope and intercept, weighted for each year's number of data points, gave the following equation:

$$\text{PROBIT (Proportion)} = -7.772 + 6.098 \text{ LDD48} \qquad (30)$$

where LDD48 is the common logarithm of °D > 48. This equation is equivalent to a log-normal probability density function (pdf) with mean μ = (5-intercept)/slope = 2.094 and standard deviation σ = 1/slope = 0.164 (Finney 1971, p. 24). The point of 50% emergence is given by $10^{\mu} = 124.3$°D > 48. The cumulative proportion emerged is found by integrating the density function over time (log °D scale).

Figure 32 shows the emergence of overwintered adults where the log-normal pdf has been integrated in increments of one °D > 48.

In the model the emergence curve can be shifted earlier or later by any specified °D > 48 using the parameter DEM.

Sexual Maturation

Once beetles have emerged they begin to disperse through the environment, but do not begin to oviposit until they have undergone a temperature-dependent maturation process. A slight modification of Fulton's (1978) approach to modeling the process was used here. Maturation is represented by a time varying distributed delay (Manetsch and Park 1977, as modified by Fulton 1978), the length of which is a decreasing function of temperature (Yun 1967). The relationship between maturation time and temperature, and the properties of the delay process, are exactly as in Fulton (1978, p. 16). The input to the delay is the emergence rate. The output is the

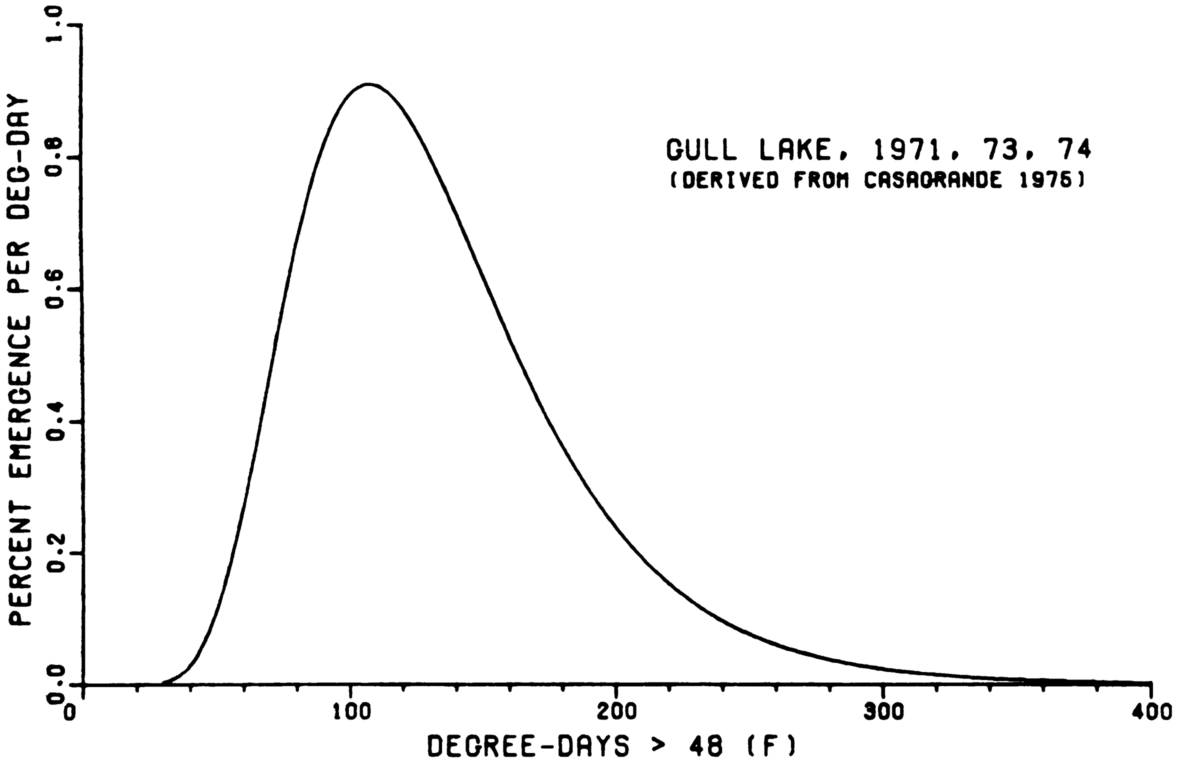


Fig. 32.--Emergence of overwintered cereal leaf beetles as a function of °D > 48(F).

rate of maturation. These two rates are integrated through time, and the ratio of cumulative maturation to cumulative emergence gives the proportion of emerged adults which are sexually mature. Using this factor it is an easy matter to calculate the number of sexually mature, hence ovipositing, females present in each cell. A sex ratio of 50:50 was assumed.

Oviposition

Unpublished data of S. G. Wellso were used to relate the oviposition rate of females to their age in terms of °D > 9(C) since the first eggs are laid in the crop. For wheat, the "zero-age" was taken to be when 5% of the emerged females had sexually matured. For oats, the starting point was when oats emerged. These points were assumed because in Wellso's (1976) experiment beetles were confined in a field cage until the first eggs appeared, then observations on the oviposition rate were begun. Twenty-two beetles were used in wheat, so one mature beetle is about 5%. For oats, I assumed beetles are already mature and begin ovipositing as soon as they enter the crop, which is as soon as it emerges.

Probit regressions were fitted to Wellso's data on cumulative eggs/female vs °D > 9(C). The best fitting equations gave the normal curves shown in Figures 33 and 34, generated at intervals of 1°D > 9. The normal equations have parameters $\mu = 144$, $\sigma^2 = 27{,}321$ for wheat and $\mu = 146$, $\sigma^2 = 48{,}968$ for oats. Daily oviposition rates are calculated in the model by integrating the probability functions over one-day intervals.

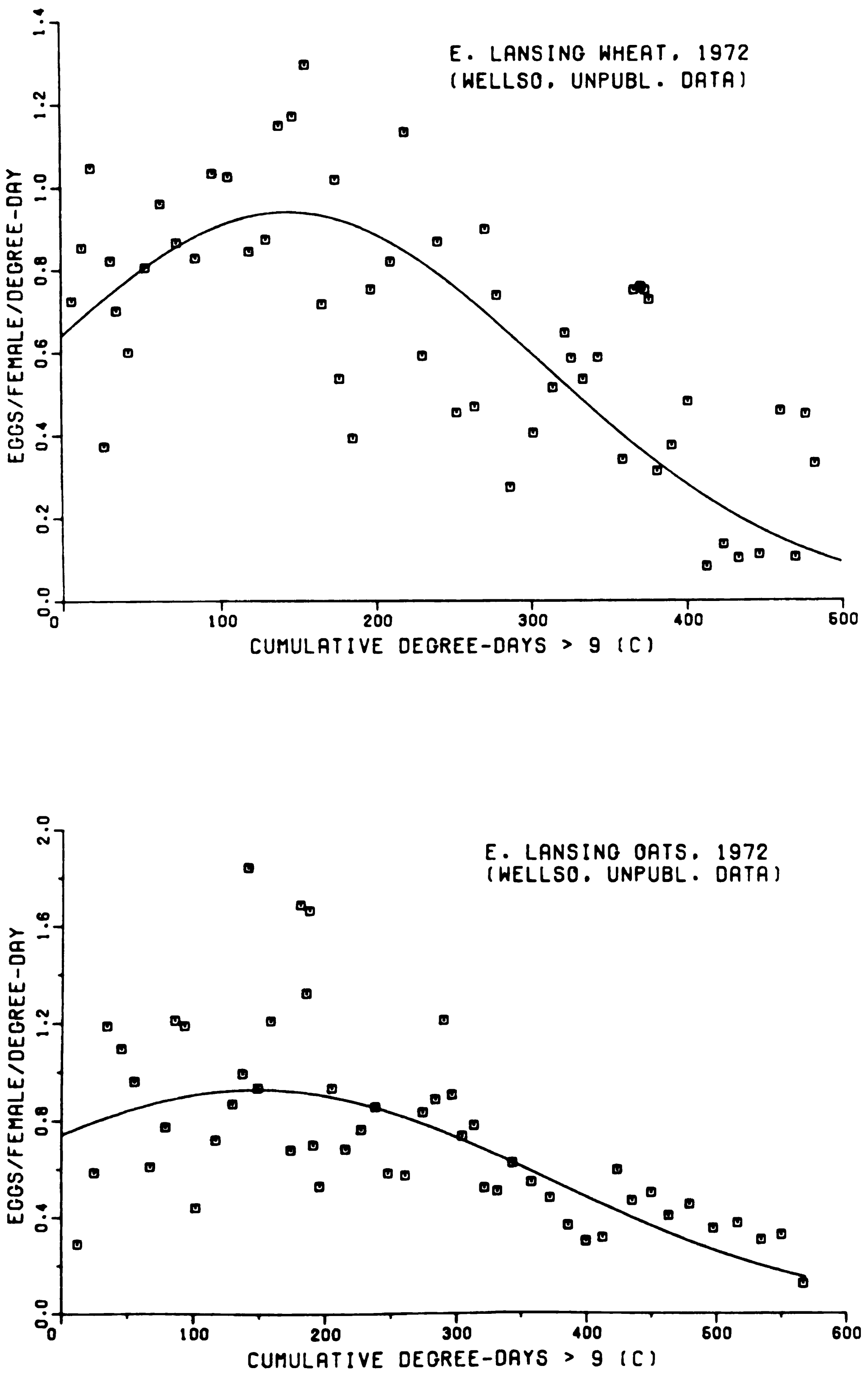


Fig. 33-34.--Oviposition rates in wheat and oats as a function of °D > 9(C) since first egg.

Adult Mortality

Adult mortality in the model is a function of temperature. The approach taken by Fulton (1978) was used here. Upon consulting his data source (Casagrande 1975, p. 28), however, it was discovered that several points were apparently calculated erroneously by Fulton (1978, Figure 6), so the original data were reworked here. Figure 35 shows the regression of instantaneous survival (per day) on temperature (°C), which differs only slightly from Fulton's (1978) equation. The equation is:

$$a = .00194 - .00206\ (\mathrm{TEMP}) \qquad (31)$$

where a is the instantaneous survival rate and TEMP is the mean temperature (°C) over the period for which the mortality applies. The daily mortality rate is given by 1-exp(a) in the model since exp(a) is the proportion surviving through one day (Fulton 1978).

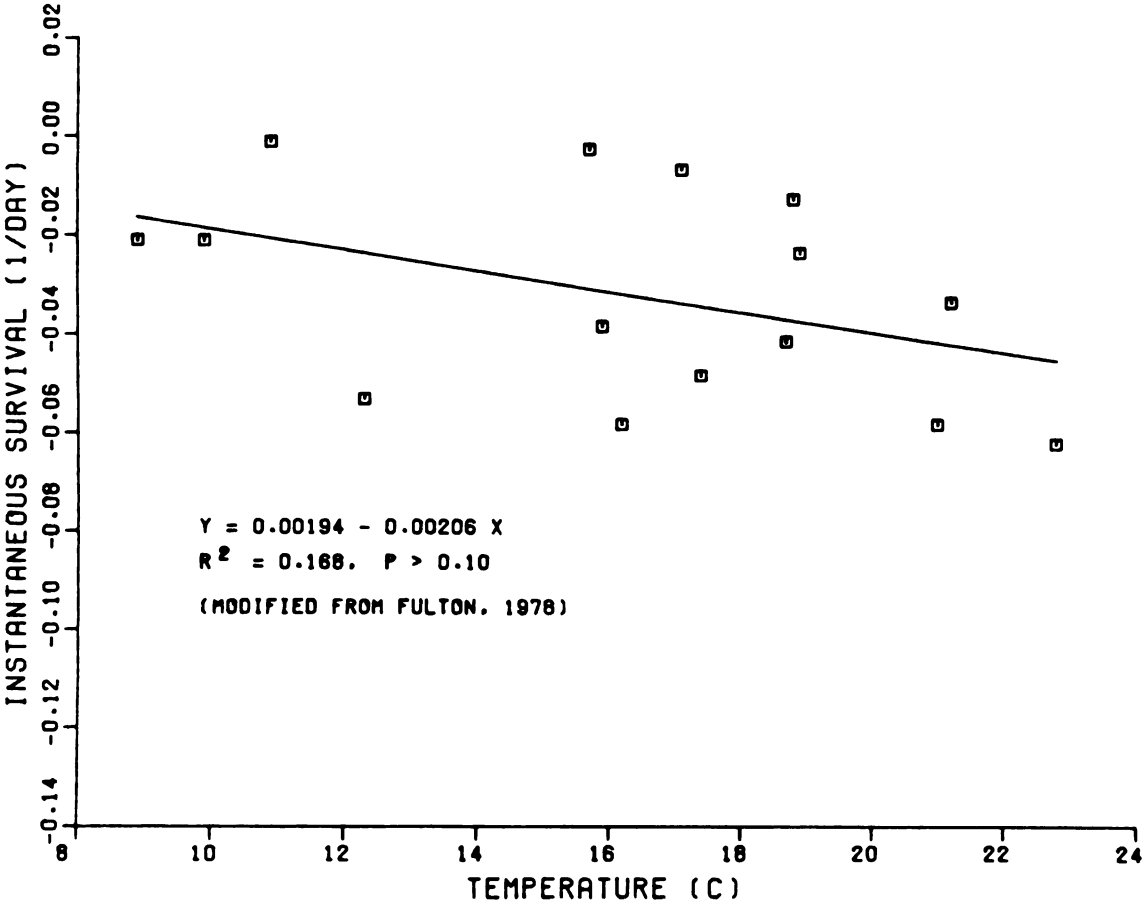


Fig. 35.--Instantaneous survival rate of adults as a function of temperature.

MODEL VALIDATION

Time Increment

Before evaluating the model it was necessary to check the stability of the output as the time increment, dt, was varied. A small dt produces smaller integration errors and avoids instability in the delays and feedback loops, but increases the cost of executing the program. The output from the standard run was examined as dt was given the values .025, .05, .1, .2, .25, .5 and 1.0 day. Instability resulted at dt = 1.0 (that is, the output changed dramatically as dt was changed from 0.5 to 1.0), and the cost of execution increased rapidly for $dt < 0.2$. A value of 0.25 day was used in all subsequent simulations. One run of the program takes 75 seconds of central processor time on the CDC 6500 computer, and costs $2.50 (excluding printing) at the lowest priority rate.

Evaluation Criteria

The model's output was compared to observations made at Galien in 1976 and 1977. The model was essentially constructed independently of these observations, but certain initializing parameters had to be set. These included, obviously, the spatial configuration of land use for each year and the regional mean overwintering density. Also, needed, however, were parameters adjusting the timing of beetle emergence and crop growth, because these events vary somewhat in their occurrence even on the appropriate degree-day scale. For example, the height of winter wheat early in the year may be related to the amount of winter precipitation, the planting date of oats depends on field conditions and the farmers' work schedules, and the emergence of cereal leaf beetles may be either early, as in 1972 at Gull Lake (Casagrande 1975) or late, as in 1977 at Galien (Sawyer 1978) on a °D > 48 scale if the spring is unusually cool or warm. Until these phenomena are better understood and can be modeled, initial observations must be made to establish the timing of events. In the simulations, the values of DWX, DOX and DEM were adjusted so that the simulated rates of wheat growth, oat growth and spring adult emergence, respectively, were in agreement with the timing of these events as observed in the field. These constants were added to or subtracted from the °D > 42 and °D > 48 accumulations serving as the independent variables in equations describing the growth and emergence curves, thus "shifting" the curves earlier or later. The degree of resistance shown by R-wheat varies, too, depending on the variety used, etc., so OVRED was set from its observed value.

The criteria used to judge the success of the model in predicting actual events in 1977 included the total adult degree-days and egg input for the year in each crop (total number and density per acre), the peak adult population in small grains and the time of its occurrence, the total adult activity and egg densities in each field, and the general correspondence between model and observation in the pattern of population trends through time in each crop (a graphical evaluation). For 1976 only the graphical output was evaluated.

Standard Parameters

For the standard 1977 simulation, the absorptivities, critical wheat height (signaling maturation of the crop), degree of R-wheat resistance, and timing of growth curves for wheat and oats were all set as discussed above. The point of 50% emergence of overwintered adults was shifted 100°D > 48 later, since in this year with a warm, early spring the median emergence point was not until about 224°D > 48.

The peak regional populations estimated by the model with these parameter values were too low, and, contrary to observation, the peak regional population was greater in R-wheat than in S-wheat. Apparently, dispersing beetles were spending too much time in nonhost habitats compared to small grains, and since R-wheat and S-wheat were identical except for the oviposition rate, the larger number of beetles in R-wheat simply reflected a greater acreage of this crop.

Since the diffusion rates in nonhost crops have not been studied (except for a small number of observations by Lampert), these values had been set rather arbitrarily in the model. They were row adjusted upward until the peak population in S-wheat was near the observed value. To reduce the population in R-wheat, DINCR was increased until the peak population in that crop was also near its observed value. The values arrived at were D = 8000 in^2/min for all nonhost habitats and for wheat taller than the critical height, and DINCR = 10.0.

Figure 36 shows the regional population in 1977 in each crop vs °D > 48. The correspondence between predicted and observed is fairly good except at three points. The field data show a large drop in population at around 350 to 400°D. This has already been discussed in relation to weather factors in an earlier section. The decline may be related to cool weather, but it is not certain. The second point of discrepancy is for R-wheat from 600 to 700°D. This crop did not exhibit the rapid decline in population which S-wheat experienced. The reason for this is unclear, but may be due to a difference in the rate of crop maturation. Finally, the populations in all crops remained too high at the end of the season in the model. This is probably due to a late-season acceleration in mortality and crop senescence in the field but unaccounted for by the model.

Figure 37 shows the results of the 1976 simulation. The same parameter values were used except T, the sum of the mean overwintering densities in five habitats, was 6.66, OVRED, the reduction in the oviposition rate in R-wheat, was 0.58 as observed in 1976, and DINCR was set at 2.0. The adult emergence curve was shifted 50°D > 48 later than standard, the wheat growth curve was shifted 200°D > 42 earlier, and the oat growth curve was shifted 30°D > 42 earlier to establish the proper timing of these events as discussed above. No evaluation of the 1976 results were made other than to note the fairly good correspondence between observed and predicted populations in Figure 37. All further discussion of validation applies to the 1977 simulation.

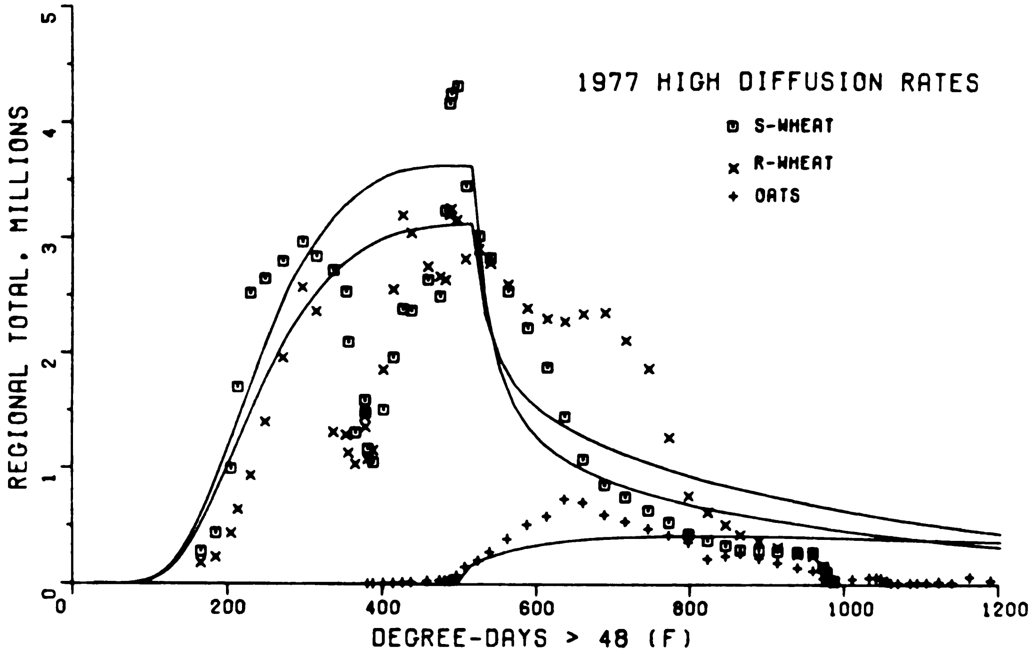


Fig. 36.--Total regional adult population in each crop in 1977 vs °D > 48, with simulation results using standard parameter values and high diffusion rates.

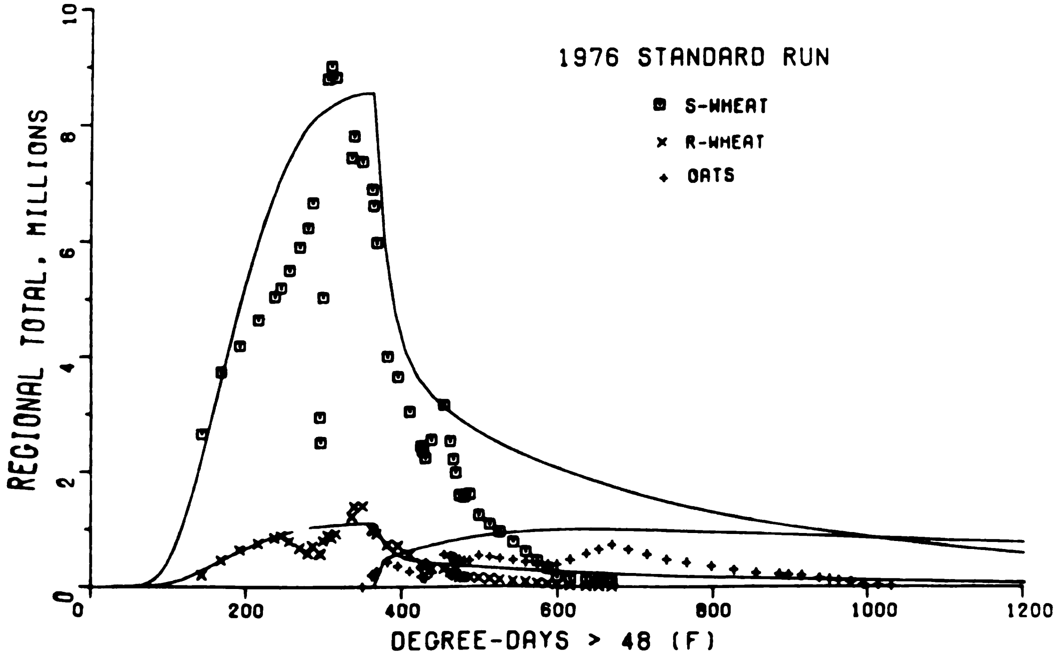


Fig. 37.--Observed and predicted total regional adult population in each crop in 1976 vs °D > 48.

The high value (10.0) required for DINCR in order to reduce the population in R-wheat sufficiently was surprising, since no such difference in the diffusion rates for R-wheat and S-wheat was observed in the field studies. The effect of decreasing the absorptivity of R-wheat is examined below.

Table 16 lists the observed and predicted values for some validation criteria. The correspondence is very good for most variables on the regional scale except in oats, where the seasonal totals are too high but the peak population is too low (this is also evident in Figure 36).

For the individual fields, however, the model generally fails to predict densities accurately. In particular, the wide range of densities found in the field is not duplicated by the model. For example, actual adult densities in S-wheat ranged from 44 to 246 adult-°D/ft^2, while the model produced densities ranging only from 66 to 122 (Figure 38). The coefficient of variation in adult densities was 55.1% in the field, but only 13.8% in the model. For S-wheat at least, there was a significant correlation between observed and predicted densities of both adults and eggs ($r = .435$, $p = .03$ for adults, and $r = .395$, $p = .05$ for eggs). In this crop the model was correct in its identification of the field with the highest adult density, and nearly correct about the field with the lowest density. For the other crops, however, the model failed entirely to predict appropriate densities.

That the mean densities produced by the model are fairly accurate, that there was a significant correlation, although slight,

Table 16.--Observed and predicted values of several validation criteria for run 11 of the simulation model (1977, high diffusion rates).

		S-wheat		R-wheat		Oats	
		obs.	model	obs.	model	obs.	model
I.	Seasonal Totals						
	Adult-°D/Region ($x10^9$)	1.25	1.61	1.35	1.63	.242	.388
	Adult-°D/Acre ($x10^6$)	3.59	4.03	2.26	2.71	3.10	4.85
	Eggs/Region ($x10^8$)	1.24	1.78	0.91	1.26	.427	.686
	Eggs/Acre ($x10^5$)	3.57	4.45	1.53	2.10	5.47	8.57
	Eggs/Adult-°D	.100	.110	.068	.078	.176	.177
II.	Regional Totals						
	Peak adults ($x10^6$)	4.32	3.63	3.27	3.12	.889	.423
	°D > 48 at peak	496	496	488	496	636	816
III.	Individual Fields, Seasonal Production						
	No. fields	25		37		7	
	Min. Adult-°D/ft^2	44.0	66.3	24.4	50.4	12.7	103.
	Max. Adult-°D/ft^2	246.	122.	115.	74.3	187.	125.
	$\bar{x}$ Adult-°D/ft^2	88.6	97.2	50.8	62.1	86.0	113.
	C.V. (%)	55.1	13.8	45.6	8.50	77.8	6.69
	r_{xy}	.435*		.162		.201	
	Min. Eggs/ft^2	3.72	7.41	0.87	3.80	1.65	18.4
	Max. Eggs/ft^2	42.1	13.6	10.6	5.80	43.0	22.1
	$\bar{x}$ Eggs/ft^2	9.94	10.7	3.49	4.82	13.1	19.9
	C.V. (%)	87.4	13.1	66.2	8.94	109.	6.24
	r_{xy}	.395*		.081		-.430	

*$p < .05$

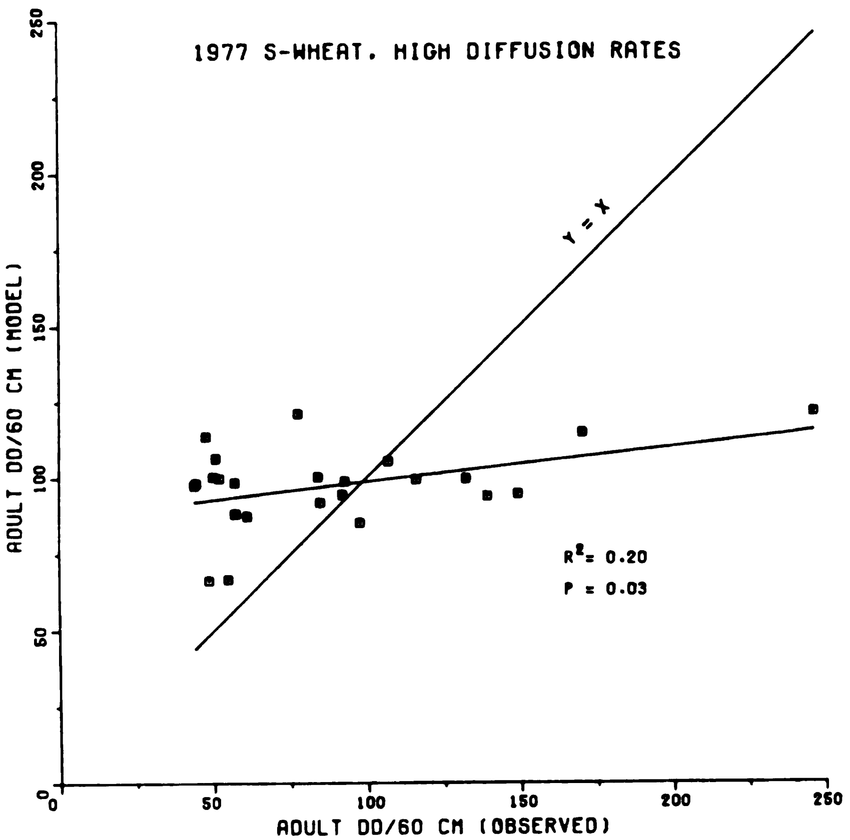


Fig. 38.--Observed and predicted adult densities in individual S-wheat fields in 1977.

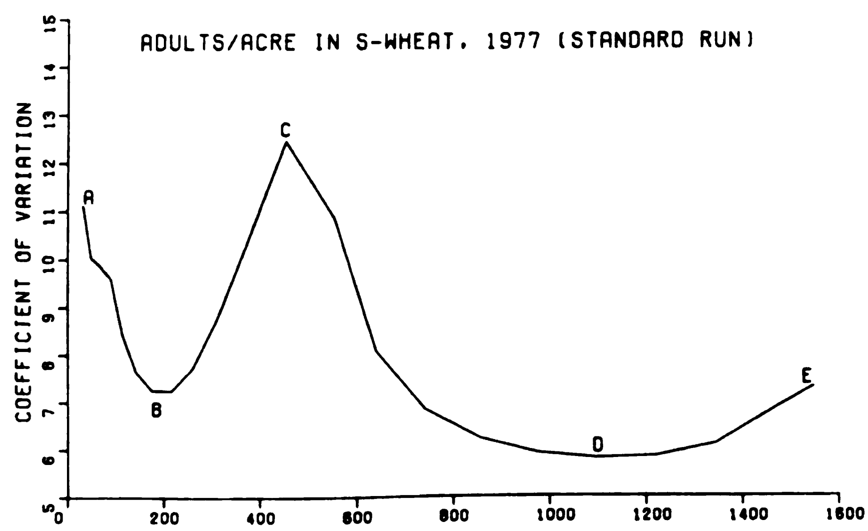


Fig. 39.--The coefficient of variation of predicted adult densities in S-wheat fields through the season.

between observed and predicted densities in S-wheat, and that by the other validation criteria the model performs fairly well all suggest that the model may be basically correct. It simply fails to account for the between-field variation in densities observed, particularly for fields with high densities.

There are two possible reasons why the model's predicted densities are too uniform. The first has to do with the nature of the dispersal process. As noted earlier, the effect of dispersal is to homogenize the effect of local uniqueness. While dispersal permits nearby population sources (such as a fence row) to contribute to a field's high density, continued dispersal tends to smooth out spatial variation. This is illustrated in Figure 39, which shows the coefficient of variation (C.V.) of predicted adult densities in S-wheat fields as it changes through the season (these are simulation results, not observed values). The C.V. initially declines (A to B) due to dispersal homogenizing the original differences in density related to the spatial distribution of overwintering sites. It then increased beginning at the time of peak emergence (B) to a maximum at the time of highest field populations (C). This may be due to the effects of continued emergence from the heterogeneous overwintering sites again overcoming the smoothing effect of dispersal, as the emigration rate from the host crops declines with increasing crop height. When the exodus from wheat begins, the high diffusion rate again homogenizes densities (C to D) until the C.V. reaches a minimum (D). The subsequent increase from D to E seems to be related to the effects of neighboring habitats. A nearby oat field, for example, acts to decrease a wheat field's population because it acts as a sink. With the declining diffusion rate in oats as they get taller, beetles entering that crop will remain, and not reenter neighboring wheat. A nearby dense woodlot, on the other hand, acts as a barrier and serves to preserve higher densities in the wheat field. These last ideas were confirmed by an examination of the habitat surrounding fields with particularly low or high predicted densities. Thus, there are two opposing forces at work regulating rates of population buildup and decline:dispersal, which has an homogenizing influence, and local uniqueness, which has the opposite effect. The high diffusion rates used in the simulation to drive beetles out of the nonhost habitats and into small grains may be responsible for excessive uniformity in the resulting densities. This is examined in the next section.

A second possible reason for the failure of the model to predict an adequate range of densities is also related to the property of local uniqueness. As noted earlier, between-field differences in crop height were not incorporated into the model. In fact, the only contributors to local uniqueness that were incorporated were differences in the habitats surrounding the fields. There may be other attributes of fields with high density which were not considered in the model. Four possibilities are (1) the relative crop maturity (planting date, growth rate) of the field; (2) some environmental condition (such as soil type, topography, soil moisture, wind patterns) or interaction not accounted for by the model; (3) heterogeneity, or aggregation, in the overwintering populations <u>within</u> a given habitat, resulting from the existence of "hot spots" of high beetle density created by chance, by aggregation behavior of the beetle, or by specific combinations of habitats being particularly favorable overwintering sites; and (4) density dependent effects. Levin (1976, p. 294) notes that "density-dependent factors in dispersal or recolonization success can lead . . . to spatio-temporal patterning." Several of these factors were checked for the 12 S-wheat fields with the highest observed adult densities in 1977. These fields were not atypical with respect to soil type, slope, or crop height at any point in the season. The hierarchical clustering discussed earlier showed no grouping together of these 12 fields based on the measured habitat features.

Alternatives to Random Dispersal

As mentioned above, the high diffusion rates used in the simulation may have led to the homogeneous resultant densities. To test this idea, the diffusion rate was lowered to 4000 in^2/min in nonhost cropland and in oats prior to germination, and to 6000 in woods. The absorptivity of nonhost cropland was changed to 0.5. At the critical height in wheat, the diffusion rate was changed to 6000 and the absorptivity was dropped to 0.25. These measures were intended to reduce the proportion of the population in nonhost habitats, thereby maintaining appropriate numbers in the host crops, while permitting the use of lower dispersal rates in an attempt to lessen the homogenizing influence of dispersal. The result, instead, was a *smaller* coefficient of variation of adult densities in S-wheat fields (13.4%), and a lower, now insignificant, correlation between observed and expected densities (.381). Furthermore, these new parameter values led to a poorer match of model output to observation for the regional total in oats, and a smaller difference between the peak population in S-wheat and R-wheat (Figure 40).

The effect of making the host crops attractive to the cereal leaf beetle was examined by increasing the absorptivity of S-wheat and oats to 2.0, and of R-wheat to 1.5. The absorptivity of nonhost cropland was again set at 0.5. The diffusion rate in cropland was lowered to 2000, and in woods to 4000. At the critical wheat height the absorptivity of S-wheat and R-wheat was changed to 0.25 and the diffusion rate to 4000. The result (Figure 41) was a better fit of the population total curves to observed values in S-wheat and R-wheat, but a much worse fit in oats. The C.V. of adult densities in S-wheat was slightly higher (15.5%), but the correlation between actual and predicted adult densities was lower still (.318).

In conclusion, reducing the diffusion rate did not lead to less homogeneity in adult densities in the host crops. Making other habitats less absorptive and making the host crops more attractive did increase the number of beetles found in small grains, but at the expense of reduced correspondence between observed and predicted densities in the individual fields. The simplest assumption regarding dispersal among the various habitats, namely, random diffusion, seems adequate to account for regional population patterns, and gives better single-field predictions than the assumptions of repulsion from nonhosts or attraction to hosts. All subsequent simulations were run

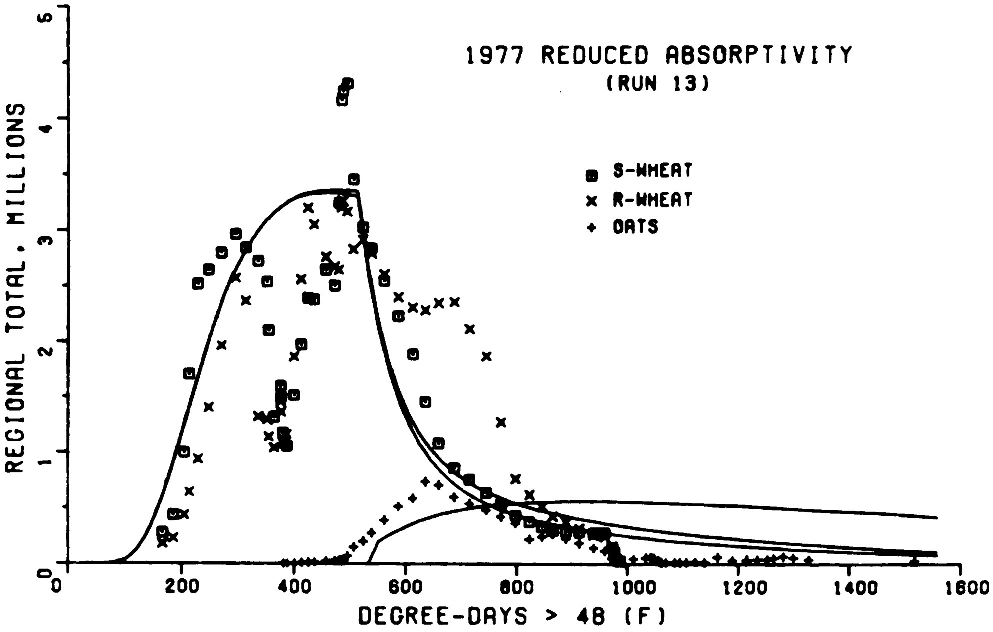


Fig. 40.--Total regional adult population in each crop in 1977, with simulation results using reduced absorptivities and lower diffusion rates in nonhost habitats.

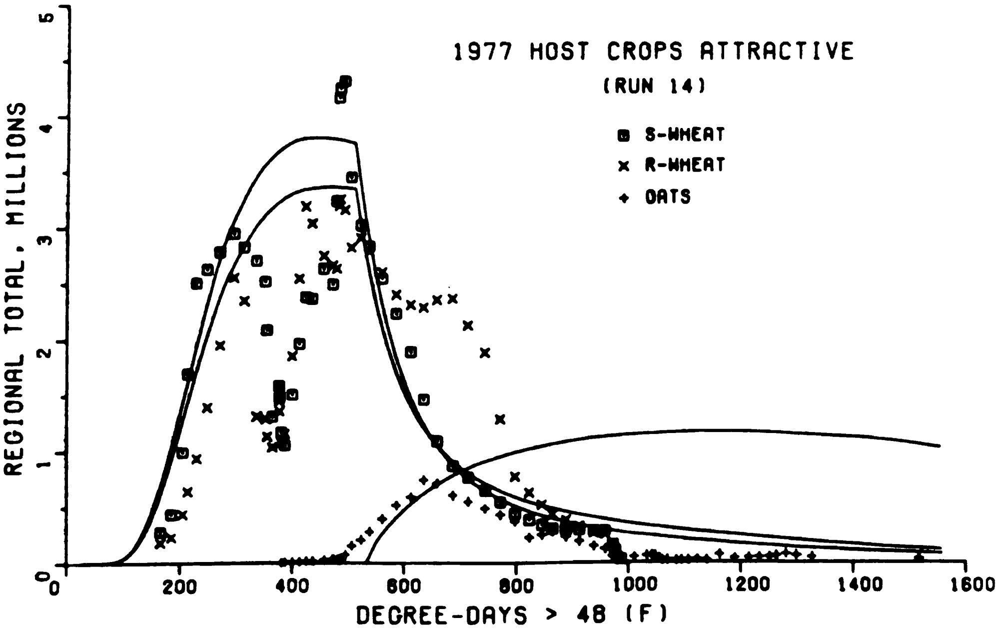


Fig. 41.--Total regional adult population in each crop in 1977, and simulation results with host crops attractive and diffusion rates reduced in other habitats.

using the neutral model with a high diffusion rate (8000 in^2/min) in the nonhost habitats.

Environmental or temporal features other than those incorporated into the model which increase a field's local uniqueness, or spatial variation in the density of overwintering beetles within habitats must be responsible for the great range in densities observed in the field.

SIMULATIONS

The Effect of Resistant Wheat

One of the major objectives of the U.S.D.A. pubescent wheat pilot project conducted at Galien, MI is to determine what impact planting large acreages of resistant wheat will have on the number of cereal leaf beetles in oats. The proportion of the wheat acreage which was resistant was increased from 0% in 1975 to 13% in 1976, 63% in 1977 and nearly 100% in 1978. It was hoped that the effect of this change, if any, on the densities in oat and S-wheat fields could be assessed. The problem with this approach is that it is not a controlled experiment. Besides the proportion of wheat which was resistant, a number of other factors changed over the years. These include weather conditions, the regional CLB population level, the acreages and spatial patterns of crops, and even the variety of resistant wheat used. The advantage of simulation is that the wheat can be made susceptible or resistant while everything else is held constant: a controlled experiment can be achieved.

The 1977 standard simulation was used to evaluate the effect of planting all S-wheat vs planting all R-wheat. Only the parameters OVRED and DINCR were changed (from 1.0 to 0.68 and from 1.0 to 10.0, respectively). The acreage of wheat was 1000 A, the acreage of oats was 80 A.

Comparing the two runs, the mean egg density in wheat was reduced from 9.69 to 5.03 eggs/ft^2 by converting to R-wheat. The level of adult activity in wheat was reduced from 88.1 to 64.8 adult-°D/ft^2. It might be expected that these displaced adults would end up in oats. Surprisingly, the density of adults and eggs in oats actually <u>decreased</u> when R-wheat was planted! The mean egg density went from 18.7 to 18.5. While this was not a statistically significant change ($t = .325$, 7 df), the direction of change was the opposite of what was expected.

This remarkable result is actually easily explained in terms of spatial and temporal patterns. Most of the oat fields in 1977 were planted very near a wheat field (of one type or another). Beetles enter S-wheat and accumulate there before oats emerge from the ground. By the time the exodus of beetles from wheat occurs, however, oats are present.

The dispersing adults readily move from the maturing wheat to the nearby oats, resulting in high densities in oats. If all wheat is resistant, however, there are fewer adults accumulating in the wheat; they are more likely to disperse out of the R-wheat before oats emerge. By the time oats are present and the wheat matures, there is not a large, concentrated source of migrants near the oats. Instead, the beetles are spread throughout the environment, and the result is lower densities in oats.

To test this hypothesis further, two pairs of oat fields were examined more closely in the simulation as the wheat was changed from susceptible to resistant. One member of each pair was located directly between two wheat fields, while the other member, less than 1/2 mile away, had no wheat directly adjacent. (The field numbers are 136 and 235 for the between-wheat fields, and 711 and 612 for the away-from-wheat fields.) As the wheat was changed from S to R, the adult density in the two oat fields located between wheat fields decreased 2 to 3%, while in the other two oat fields the adult density increased 1 to 3%. The increase in density in oat fields not having wheat neighbors might be expected since the number of beetles dispersing in the environment would be greater when R-wheat is planted.

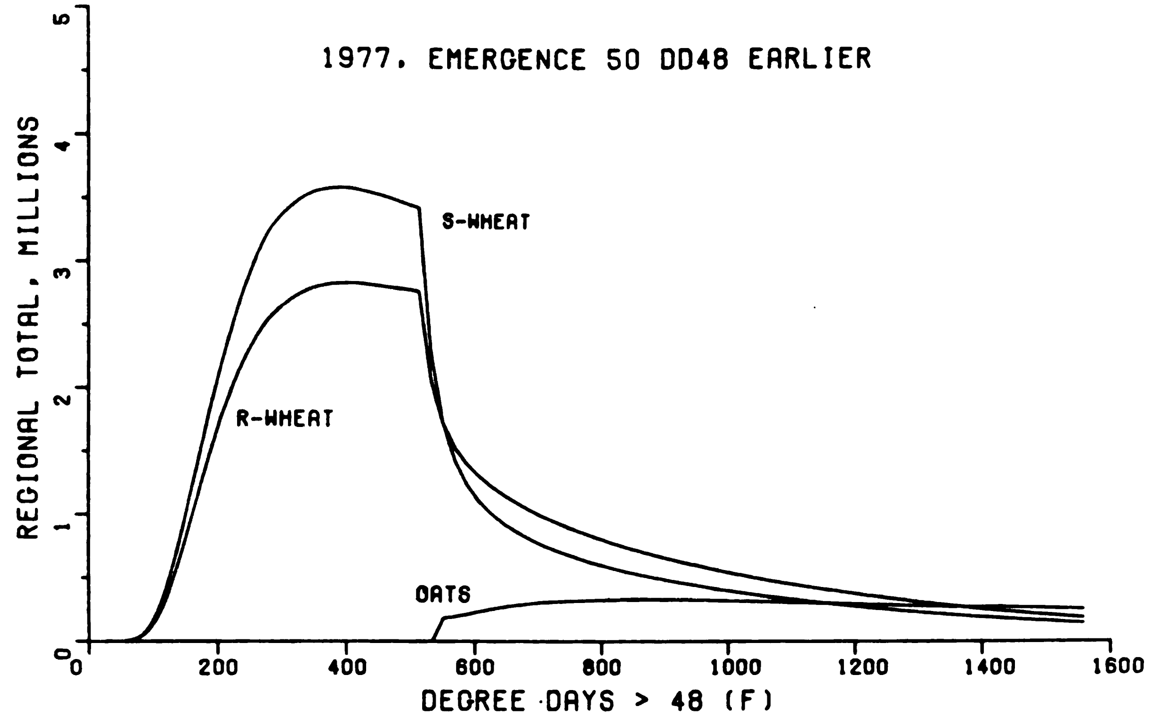
As a further confirmation of the influence of wheat neighbors, actual adult densities in oats in 1977 were checked. Of eight oat fields, the three with the highest adult densities were located directly between two wheat fields. Four others, with significantly lower densities, had no wheat neighbors directly adjacent, while one field with one wheat neighbor was intermediate in density between the other two groups.

Temporal Patterns

CLB Emergence

Figures 42 and 43 show the effect of shifting emergence 50°D > 48 earlier or later on total regional densities in each crop.

Early emergence results in higher adult and egg densities in S-wheat, lower adult density in R-wheat, and higher egg density in R-wheat. Less activity is seen in oats. With later emergence, opposite effects are seen.



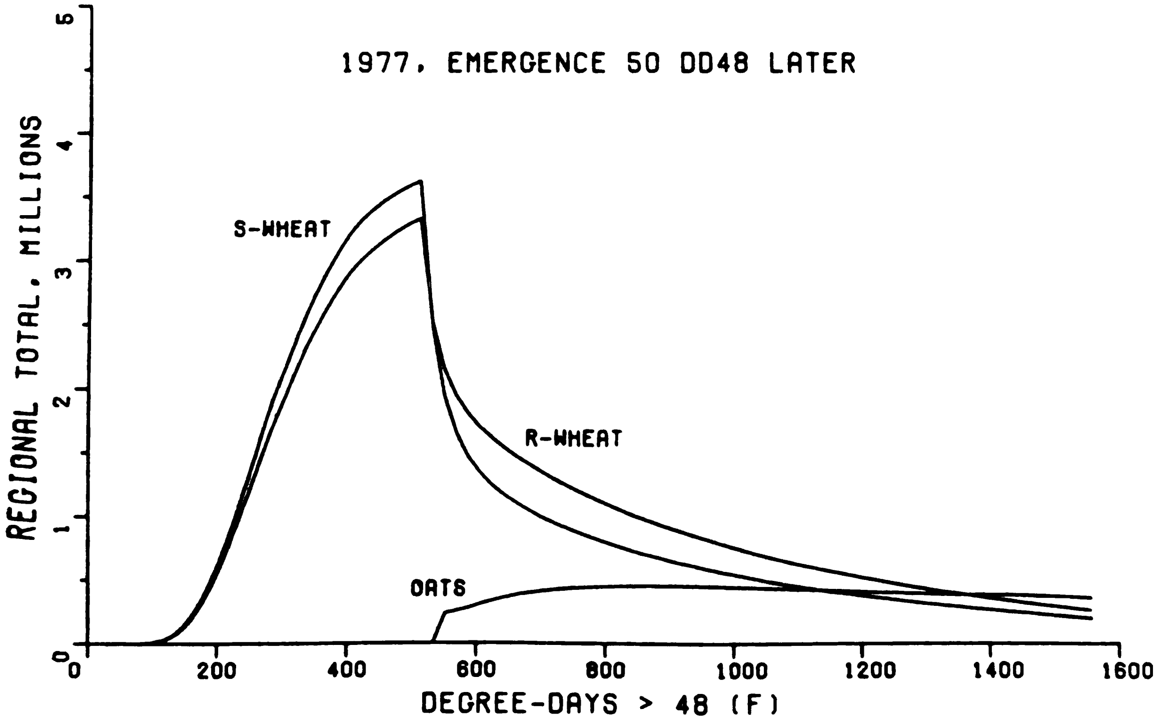


Fig. 42-43.--CLB emergence shifted 50°D > 42 earlier and later.

These results are interpretable in light of the higher D value in R-wheat interacting with crop height. In S-wheat more adult activity is expected with earlier emergence, but in R-wheat the longer exposure to short wheat with a consequently higher diffusion rate drives proportionately more beetles out of this crop. The higher egg densities result from a higher mean eggs/female value for the season when emergence is earlier. The reason for this is not clear, but may be related to beetles aging less rapidly early in the season and therefore ovipositing at a higher rate. The interactions of temperature, sexual maturation, aging, oviposition rate and mortality are complex.

Planting Date of Oats

Earlier oats affects the population in wheat very little, but increases the population in oats. Therefore when oats are planted early a greater portion of the total beetle activity will take place in that crop. The small effect on wheat may be due to the very low acreage of oats in 1977 at Galien, and in the simulation. Late-planted oats has the opposite effect.

Shifting the oats 100°D > 42 earlier increased the egg density in oats 6%, while delaying the oats 100°D reduced the egg density 21%. 100°D is about one week in mid May. The reason for the great reduction in egg density when planting was delayed is that oat seedlings then emerged after the exodus from wheat (Figures 44, 45). Delayed planting would appear to be a valuable management tool under the right conditions. Other interactions, such as reduced soil water

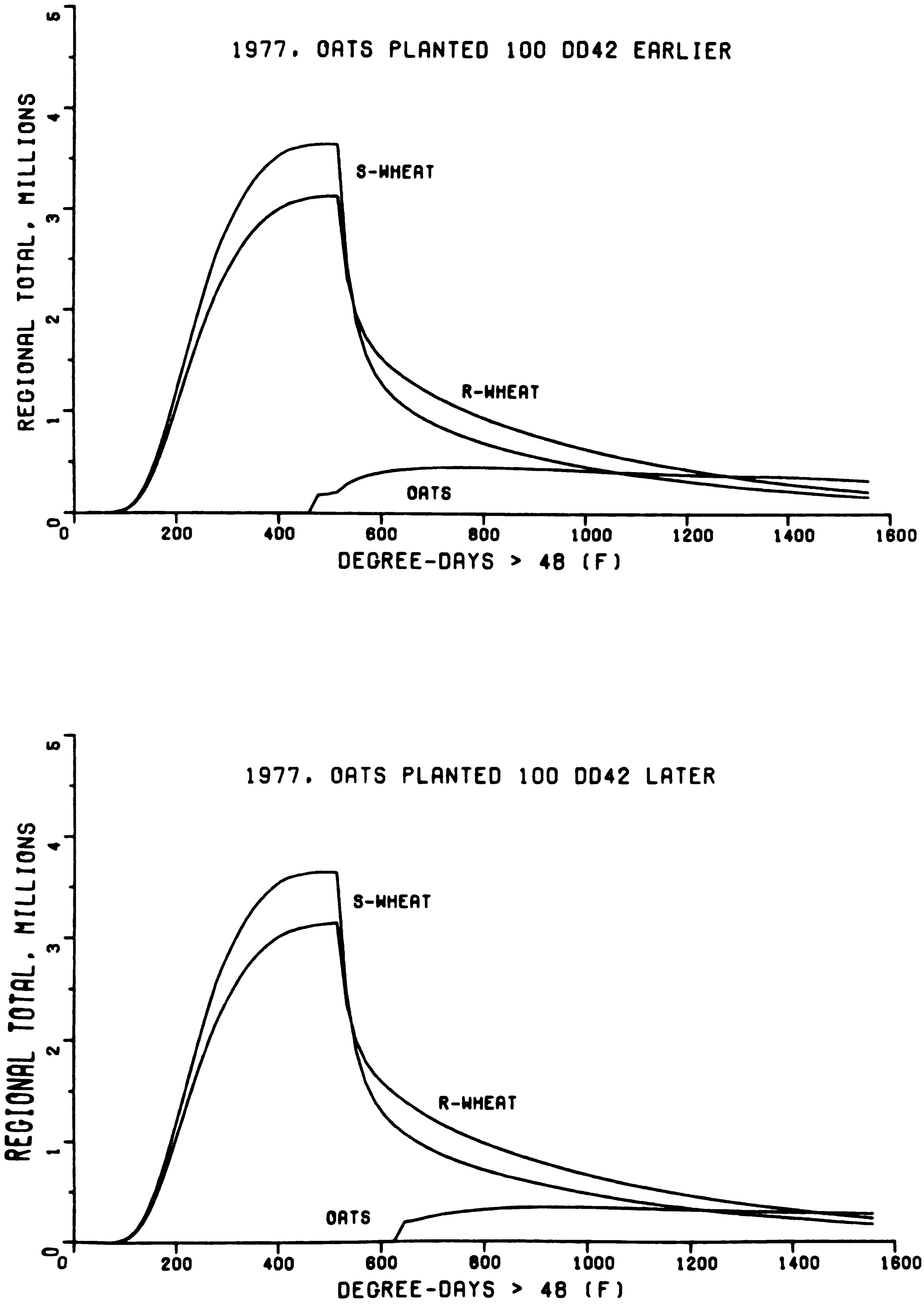


Fig. 44-45.--Oats planted 100°D > 42 earlier and later.

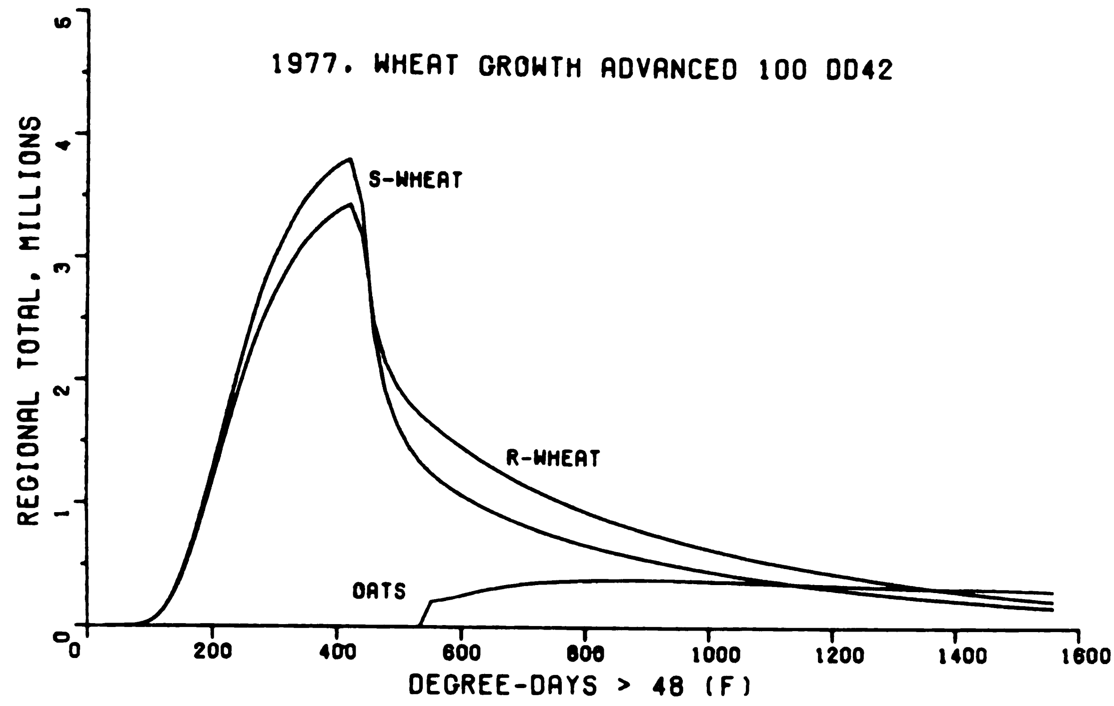
availability, and increased risk of pre-aestival feeding by adult beetles with very late-planted oats, must also be considered.

Wheat Growth

When the wheat growth curve is advanced 100°D > 42, the peak adult density in S-wheat and R-wheat is increased but the seasonal total activity is reduced (Figure 46). This is because the wheat matures and becomes unsuitable sooner after the beetles emerge from overwintering. The effect on the population in R-wheat is less because of the interaction of crop height and diffusion rate. The taller crop slows the rate of leaving the field, and higher densities are attained. This is relatively more important in R-wheat due to the higher diffusion rate in this crop.

A delayed wheat growth curve (Figure 47) resulted in a higher adult density in S-wheat, but lower in R-wheat. Again, the interaction of crop height and beetle diffusion rate led to a high emigration rate in the relatively shorter crop, and this was more important in R-wheat.

The effect on the population in oats was very similar for both early and late wheat: the density decreased. In the former case the beetles began to leave wheat before oats were available, while in the latter case beetles stayed in wheat longer instead of moving to oats. This points out the delicate relationships involved here; and perhaps explains past difficulties in understanding the role of crop synchronies in determining the relative abundance of the CLB. The maximum CLB densities in oats can be expected when



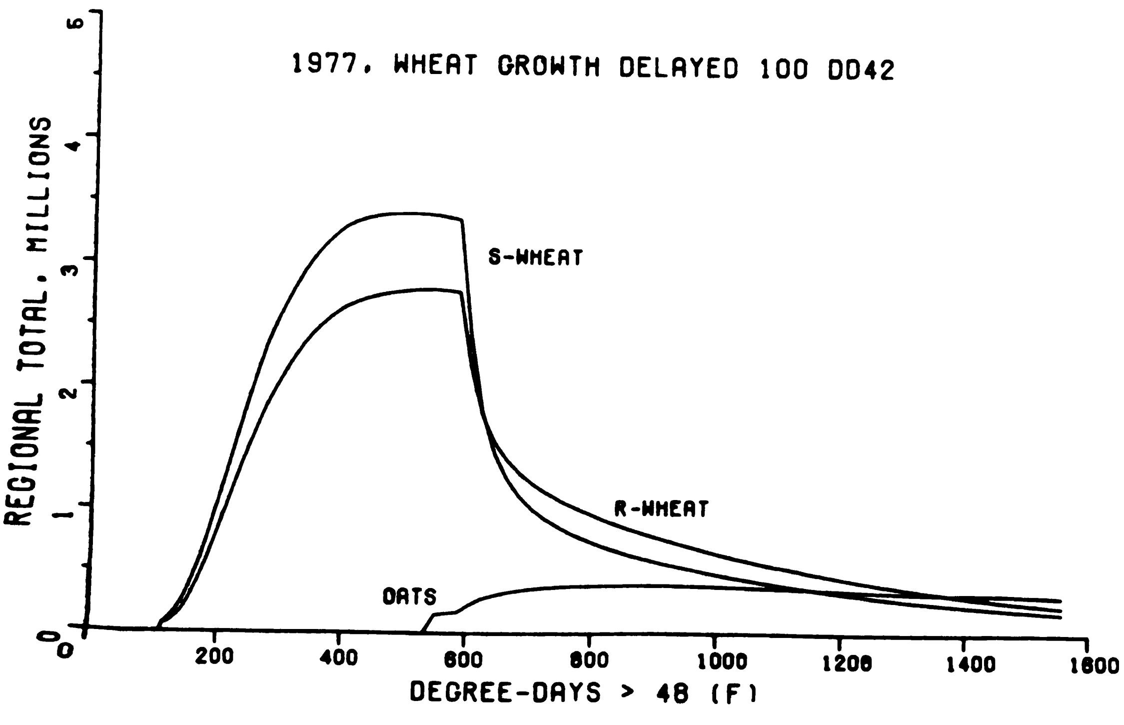


Fig. 46-47.--Wheat growth advanced and delayed 100°D > 42.

oats emerge just as nearby wheat fields become unsuitable. When the synchrony of the crops is altered in either direction (farther apart or closer together in time), the transfer from wheat to oats will be reduced. Spatial effects interact with this because it will be the oat fields nearest wheat fields which are affected most by changes in the temporal synchronies. As with the planting of all resistant wheat, oat fields not near wheat may have higher densities when wheat growth is advanced and that crop is less suitable.

Spatial Patterns

Simulations on the effect of spatial patterns included runs examining the effect of altering the absolute acreage planted to host crops, of altering the relative amount of winter and spring grains, of dividing a fixed acreage of wheat into fields of various sizes, of altering the shape of fields of a given acreage, and of altering the location of fields with respect to wood lots and other fields. Resistant wheat was not involved in any of these simulations. Each of the experiments was replicated two or three times by randomly selecting which cells would have their crop type changed in the acreage simulations, and the location of fields in the field-size and shape simulations. Fields were deliberately located for the field-location simulation, but three fields of each location type were selected. Maps showing the spatial configuration of each experiment are found in Appendix I.

Absolute Acreages

Under standard conditions, the acreage of wheat was 1000 a, and of oats 80a. Three simulations each of doubling and halving these acreages were carried out. The mean values of adult and egg total populations and densities in the 2x and 1/2x situations will be compared.

When acreages were changed from 1/2x to 2x standard (increased fourfold), the total adults and eggs in wheat increased 3.24x and 3.21x, respectively. In oats the increases were 3.28x and 3.31x for total adults and total eggs. Densities were reduced by this change in acreage by factors of .81 for both adults and eggs in wheat, and .75 for both stages in oats.

These results show that an increase in acreage is matched by an almost equal increase in the total population. There is a small effect of "dilution," however, as shown by the decreases in density. The results suggest that a large portion of the population is not found in the host crops at any one time, but is dispersing between fields. When more host crop acreage is available, beetles are more likely to enter it, and a proportionately greater amount of their total activity takes place in the crop.

These results are supported by the observation at Galien in 1976 and 1977 that only a fraction of the total number of beetles estimated to have emerged from overwintering can be accounted for in the grain fields at the time of peak regional density. For example, in 1977 the sum of the mean densities in five overwintering habitats was 6.61. This sum was then distributed among the five habitats according to the frequency distribution developed above (Table 15), and the resulting estimates of density in each habitat were multiplied by the total acreage of that habitat in the region (given in section on Spatial Analyses, above). The resulting estimate of the total population emerging from 5 April to 12 May was 46 x 10^6 beetles. However, on 11 May the peak regional population total in small grains was only 7.6 x 10^6, about one sixth the number expected. The 1976 field data show a similar discrepancy. To be sure, there are sampling errors involved in both estimates, and a portion of the emerging population will have died over the interval involved, but the data support the above simulation result.

Since the crop ratio remained unaltered while the acreages were changed, neither the ratios of totals nor densities in oats to wheat changed for either adults or eggs.

Relative Acreages

The crop ratio (wheat to oats) was changed in a series of simulations by increasing the oat acreage 2x, 4x and 8x from the standard value of 80 acres while the wheat acreage was held constant at 1000 a.

With each doubling of the oat acreage, the total population in oats just about doubled, but densities of both adults and eggs remained quite constant, declining significantly only when the oat acreage was 8x the standard value and the population began to be "diluted" in this large acreage.

The total number and density of adults and eggs declined in wheat as the oat acreage increased, at first slightly but then increasingly so as the oat acreage became a significant portion of the total.

The ratio T_o/T_w, discussed earlier in the Analysis of Crop Preference, increased as the crop ratio declined, but the ratio E_o/E_w remained relatively constant. These results are as expected for random dispersal, no fixed crop preference, and constant relative quality of the two crops.

Field Size and Shape

Only wheat fields (susceptible) were involved in the following simulations. Four experiments altering the size of square fields were carried out, with two random replications of each. The locations of fields were randomly selected from long lists of possible locations (there are more possible locations for 10-acre fields than for 160-acre fields due to the presence of wood lots, etc.). The numbers and sizes of fields used were six 160-acre fields (Σ = 960 a), eleven 90-acre fields (Σ = 990 a), twenty-four 40-acre fields (Σ = 960 a), and ninety-six 10-acre fields (Σ = 960 a). In effect, a fixed acreage of wheat was increasingly partitioned and dispersed.

The results can be simply stated: as the field size increased, the density of adults and eggs decreased. The mean adult density in the 160-acre fields was 25% lower than in 10-acre fields; the egg density was 22% lower.

Elongate 90-acre fields were compared to square 90-acre fields by "planting" wheat in fields .125 mi wide and 1.125 mi long (1 x 9 cells). These absurdly impractical fields were located as nearly as possible in the same places as the square fields (see maps, Appendix I). The mean adult density was 11% higher in elongate fields, while the mean egg density was 9% higher.

The field size and shape simulations suggest that high cereal leaf beetle densities are promoted by having fields with relatively more "edge." Conversely, lower densities might be maintained by adopting the practice of planting larger fields. The reason for the edge effect is two-fold. First, large fields reduce the amount of favored overwintering habitat in the area. Central portions of large fields will be more distant from overwintering habitats and the edge portions will have such sources of infestation on only one side. Second, since diffusion rates are higher in the noncrop environment surrounding a field, these habitats act as sources, while the host crops, in which beetles have lower diffusion rates, act as sinks. Nonhost habitats therefore convey dispersing beetles to the fields, but the central portions of large fields are buffered from this effect.

Lecigne and Roehrich (1977) found that colonization of wheat fields by the CLB begins at the edges, but the insects are in the middle of the field when they lay their eggs. Therefore the larval infestation was greater in the center. The results of the current simulation do not agree with Lecigne and Roehrich's findings in that regard. For 90-acre and 160-acre fields, the inner cells had lower egg densities than the outer.

I would agree with their conclusion, however, that the population of the CLB is "promoted by the juxtaposition of cereal-fields and forests."

Field Locations

In an earlier section I indicated that wheat fields located near oat fields might have lower total seasonal populations, while wheat fields surrounded by woods might have higher densities. My reasoning was that an oat field would act as a sink, accepting more immigrants than it gave back. Dense woods around a field should act as a barrier to dispersal, holding the population in the area. In general it would be interesting to compare the effect of planting fields in several different types of locations.

The field location simulation involved "planting" wheat fields in five different situations: (A) surrounded on two or more sides by sparse woods, (B) with sparse woods on one side only, (C) surrounded on two or more sides by dense woods, (D) with dense woods on one side only and (E) not near woods of any kind. Ten-acre wheat fields were placed in six examples of each of the above categories. Ten-acre oat fields were planted next to three of the wheat fields in each category, and three more were planted away from wheat. A total of 30 wheat and 18 oat fields were therefore systematically located within the habitat matrix of the Galien study area.

An analysis of variance of the resulting adult densities in wheat gave the following results. There were significant ($p < .02$) effects of both the wood lot and oat factors, but there was no interaction of these factors. Specifically, wheat fields with oat neighbors had lower seasonal adult densities. The ranking of the five location categories in order of increasing adult density was C, D, E, A, B.

Wheat fields surrounded by dense woods (C) had significantly lower densities than those with sparse woods on one or more sides (A, B), and fields with dense woods on one side only (D) had lower densities than fields with sparse woods on one side only (B) (Duncan's new multiple range test, 5% level, Steele and Torrie 1960).

Among the oat fields, there were no significant differences in adult density related to location, although fields not planted near wheat had the lowest mean density.

DISCUSSION

Two distinct types of information which an operational pest management (PM) program requires for management decisions to be made are the time at which a relevant biological event will occur, and the magnitude of the event. For example, the necessary information might be the peak larval density of a pest and the time at which peak density occurs. While models of the pest system under consideration may ultimately provide estimates of these, such models will usually depend on other, earlier information for initialization. Initial field observations put a model "on track," in both timing and magnitude, with events in the field.

Fulton (1978) discussed the role of egg and larval sampling in initializing his within generation model of the cereal leaf beetle for pest management decision-making. Biological monitoring is one of the more costly and time consuming components of an implemented PM system. The spatiotemporal model developed here, if totally successful, would have contributed to this need by providing the information necessary to initialize a within-generation model such as Fulton's, or at least by reducing the cost of biological monitoring. It was hoped that the adult model would help to identify the influence of specific spatial and temporal structures of the environment on the distribution and abundance of the adult beetle. A knowledge, then, of such features as the relative acreage and developmental synchrony of different host crops for a large region, and each field's crop variety, relative maturity, acreage and proximity to beetle overwintering habitats and other fields, might have enabled predictions to be made of potential pest populations through space and time. The model would thus have served to at least identify those fields with a potential pest problem. Sampling by scouts to initialize a detailed within-generation model could be restricted to these fields, or the growers responsible for the specific fields could be alerted to monitor the pest population level. In effect, a realistic model of adult distribution and abundance might reduce the sampling effort required for the pest management program and buy time for decision making by providing earlier predictions of pest density.

While the model developed here failed to predict densities in specific fields, or even to broadly classify the fields into high and low density groups, based on simulation results general statements about the role of certain spatial structures of the environment in determining the density of beetles in a field might be made. These generalizations are unlikely to be of much help in deciding where sampling to monitor pest populations should be done, but might serve as recommendations for designing a regional crop system that would minimize the probability of seeing damaging numbers of cereal leaf beetles. The simulations carried out suggest that large fields, of a shape which minimizes the "edge development" index, will have lower densities of beetles. Winter grain fields should not be located near prime overwintering habitats, such as sparse woods, but should take advantage of the low source populations and barrier to dispersal offered by dense woods. Lower densities might be achieved by locating fields where dense woods occupies as many borders of the field as possible. Oat fields should not be planted immediately adjacent to wheat, unless the wheat is of a resistant variety, in which case it seems some advantage might be gained by planting the oats right next to the wheat.

The density of CLBs in oats appears to be little affected by changes in the absolute or relative acreage of oats in the region. This is in large part due to the large reserve population of beetles in the nonhost crop environment. The existence of this reservoir, predicted by the model, needs to be confirmed. Support for the idea comes from calculations showing that in 1976 and 1977 at Galien most of the overwintering population was not accounted for by beetles in the grain fields at any one time, although Ruesink (1972) and Casagrande (1975) did not find this to be the case from 1971 to 1974 at Gull Lake. The experiment of Wells (1967), in which spraying all the wheat fields in a township did not reduce the population later found in oats as compared to controls, also supports the argument for a large population of inter-field transients. The existence of this extra-field population is not merely a result of there being acceptable nongrain host plants in the environment; it is a result of the spatial separation of fields and the nature of a diffusion process. Time lags involved in inter-field dispersal result in fewer beetles being found in the fields at any one time. Further studies on the role of the nonhost environment in the population dynamics of the cereal leaf beetle seem warranted.

The successful prediction of densities in specific fields might be improved by a better understanding of the factors involved in defining the local uniqueness of a field. The role of variations in relative crop maturity, microclimate, wind patterns, and initial source populations all need to be better defined, and may improve the predictability of field densities. "Hot spots" of high density in overwintering sites may be a result of patterns of summer adult dispersal in the previous year, but almost nothing is known about this portion of the beetles' life cycle. The influence of environmental conditions, the physical structure of the crop, and the host plant's physiological state on the diffusion rate of adults is an area of research that also demands attention.

With regard to the timing of events, the other type of information needed to initialize pest management models, the spatiotemporal model developed here makes a more substantial contribution. Fulton (1978) discovered that in order for his cereal leaf beetle model to be correctly synchronized with field events it was necessary to know when the adults moved from wheat to oats. In the context of the hypothesis of random dispersal set forth above, the problem may be restated as determining when the rate of emigration from wheat increases dramatically. This may be related to maturation of the crops, and needs to be investigated further.

Many explanations have been suggested for the relative numbers of beetles found in winter and spring grains in particular years.

Ruesink (1972, p. 65) proposed a fixed preference of individuals for one grain or the other, but then said that the portion of the population entering winter grains depends on the size of the plant as it comes through the winter. Gage (1972, p. 78) noted that very low densities of CLBs in wheat may occur when wheat is planted early. Casagrande (1975, p. 51) suggested planting both winter wheat and spring oats late to increase the portion of the population infesting wheat. Contrary to Ruesink's statement, Casagrande (1975, p. 41) found no relationship between the early height of wheat and the relative densities in winter and spring grains, and no relationship between relative beetle densities and the acreage of oats. Casagrande (1975, p. 46) then proposed a model relating the proportion of the population in winter grains to the regional beetle density, but as was shown above, 11 years of data from Gull Lake fail to support this idea. The spatiotemporal model developed here relates the observed proportion of beetles in each crop, and the apparent movement from wheat to oats, very simply to the relative synchronies of CLB emergence, winter grain development, and oat planting date. Although the underlying model is simple, variations in the timing of these events, the diffusion rate of the beetle and the spatial configuration of the crop system result in a complex array of patterns of distribution and abundance. Initial observations to synchronize a pest management model with field events should be aimed at identifying the temporal positioning of beetle emergence, wheat growth in particular fields, and the expected planting date of oats.

As shown above by simulation, densities in oats might be minimized by either increasing <u>or</u> <u>decreasing</u> the temporal separation of wheat and oat growth. The synchronies might also be manipulated by selecting varieties with long or short growing seasons: for example, late-maturing wheat and early-maturing oats. These possibilities for managing temporal patterns, as well as the impact such manipulations might have on other components of the crop system, such as the Hessian fly, parasite species, grain yield, etc. need to be investigated further.

SUMMARY AND CONCLUSIONS

Population dynamics as a science deals with the distribution and abundance of organisms, yet too often the emphasis is on "abundance." Whenever dispersal plays a part in a species' life history, the contribution of the dispersal process to the population's dynamics may be major and must be considered. Only a spatiotemporal approach will lead to an understanding of both the population's spatial distribution and changes, through time, in its abundance at a particular place.

Preliminary analyses showed that survival and redistribution during the adult stage was the factor most associated with year to year fluctuations in the density of cereal leaf beetle larval populations in research plots at Gull Lake. Efforts to understand this situation led to the identification of broad classes of influences--general (regional) and unique (site-specific)--producing temporal and spatial variations in density. Dispersal interacts with this array of factors, increasing the effects of some and reducing the effects of others.

It has been suggested by one worker (Ruesink 1972) that individual cereal leaf beetles have a preference for either winter wheat or spring oats, and that movement between these crops is minimal. A more common assumption has been that beetles move sequentially from wild grasses to winter wheat and then to spring oats. A new model was proposed, here, of beetles moving at random between fields, entering them as they are encountered. The number of beetles in a field at any particular time is a net result of immigration and emigration rates. The rate of entering a field is a function of the spatial distribution and nature of overwintering sites and other fields nearby, and the relative length of the field's boundary. The rate of leaving the field depends on the suitability of conditions within the field. The spatial distribution of beetles among fields is related to general features of the region such as the relative acreages and developmental synchronies of the different host crops.

This hypothesis was examined by analyzing existing data and by conducting new field investigations, and, in general, was supported by these findings. The precise relationships between environmental features and density in individual fields are difficult to define; the factors leading to high density may be many and complexly interrelated, and are likely to vary from one year to the next as temporal and spatial patterns change.

A simulation model of cereal leaf beetle spatiotemporal dynamics was developed, and was found to perform fairly well in validation runs comparing its output to observations made near Galien, MI in 1976 and 1977. Alternatives to the assumption of random interfield dispersal were evaluated and did not increase the validity of the model. The major shortcoming of the model is that it fails to generate sufficient between-field variation in densities. This is thought to be due to not having incorporated enough features defining the local uniqueness of each field.

Interesting simulation results were that the conversion of all wheat acreage to a resistant variety need not increase the density of beetles in oats; that advanced, as well as delayed, growth of wheat may reduce the density of beetles in oats, depending on the planting date of oats and the timing of the emergence of beetles from overwintering; that an increase in total acres planted may lead to an increase in the total number of beetles observed in small grains, with little reduction in density; that small or elongate fields might be expected to have higher beetle densities than large, square fields; and that wheat fields surrounded by dense woods and having oat neighbors will have lower densities than wheat fields near sparse woods without adjacent oats.

The model, in its present form, will be of little use in an operational mode for pest management purposes, but has been quite successful as a research tool. The model describes, in a new way, the relationship between the cereal leaf beetle, its host crops and the spatial and temporal structure of its environment. In so doing, it resolves many past conceptual difficulties and provides many new challenges. The possibilities for using the model to investigate theoretical questions of spatiotemporal population dynamics, to explore the response of the existing crop system to perturbations and control measures, and as an aid in creating new system designs are limitless and exciting.

LITERATURE CITED

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Anderberg, M. R. 1973. Cluster Analysis for Applications. Academic Press.

Andrewartha, H. G. and L. C. Birch. 1954. The Distribution and Abundance of Animals. U. of Chicago Press.

Arnold, G. W. and C. T. deWitt (eds.). 1976. Critical Evaluation of Systems Analysis in Ecosystems Research and Management. Centre for Agric. Publ. and Docu., Wageningen, the Netherlands.

Bailey, N. T. J. 1968. Stochastic birth, death and migration processes for spatially distributed populations. Biometrika 55(1): 189-98.

den Boer, P. J. 1968. Spreading of risk and stabilization of animal numbers. Acta Biotheor. 18: 165-94.

den Boer, P. J. 1971. Stabilization of animal numbers and the heterogeneity of the environment: the problem of the persistance of sparse populations. In: Dynamics of Populations 1970, P. J. den Boer and G. R. Gradwell (eds.), Centre for Agric. Publ. and Docu., Wageningen, the Netherlands. Pp. 77-97.

Birch, L. C. 1971. The role of environmental heterogeneity and genetical heterogeneity in determining distribution and abundance. In: Dynamics of Populations 1970, pp. 109-128.

Bliss, C. I. and R. A. Fisher. 1953. Fitting the negative binomial distribution to biological data, and Note on the efficient fitting of the negative binomial. Biometrics, June 1953: 176-200.

Cartwright, B., R. E. Eikenbary, and R. D. Morrison. 1977. Evaluation of equations describing dispersal of the released coccinellid Menochilus sexmaculatus. Paper presented at national meeting Entomol. Soc. Amer., Nov. 30, 1977, Washington, D.C.

Casagrande, R. A. 1975. Behavior and survival of the adult cereal leaf beetle, Oulema melanopus (L.). Ph.D. Thesis, Michigan State University.

Casagrande, R. A. and D. L. Haynes. 1976a. An analysis of strip spraying for the cereal leaf beetle. Environ. Entomol. 5: 612-20.

Casagrande, R. A. and D. L. Haynes. 1976b. The impact of pubescent wheat on the population dynamics of the cereal leaf beetle. Environ. Entomol. 5: 153-159.

Casagrande, R. A., W. G. Ruesink, and D. L. Haynes. 1977. The behavior and survival of adult cereal leaf beetles. Ann. Entomol. Soc. Amer. 70: 19-30.

Castro, T. R. 1964. Natural history of the cereal leaf beetle, *Oulema melanopa* (L.), and its behavior under controlled environmental conditions. Ph.D. Thesis, Michigan State University. 121 pp.

Clark, P. J. and F. C. Evans. 1954. Distance to nearest neighbor as a measure of spatial relationships in populations. Ecology 35(4): 445-53.

Cochran, W. G. 1963. *Sampling Techniques*. 2nd ed. John Wiley & Sons, Inc. 413 pp.

Eberhardt, L. L. 1970. Correlation, regression, and density dependence. Ecology 51(2): 306-310.

Finney, D. J. 1971. *Probit Analysis*. 3rd ed. Cambridge U. Press. 333 pp.

Fulton, W. C. 1975. Monitoring cereal leaf beetle larval populations. M.S. Thesis, Michigan State University. 108 pp.

Fulton, W. C. 1978. The development of a model for use in the on-line control of the cereal leaf beetle (*Oulema melanopus* (L.)). Ph. D. Thesis, Michigan State University.

Fulton, W. C. and D. L. Haynes. 1975. Computer mapping in pest management. Environ. Entomol. 4: 357-60.

Fulton, W. C. and D. L. Haynes. 1977a. The influence of population maturity on biological monitoring for pest management. Environ. Entomol. 6: 174-80.

Fulton, W. C. and D. L. Haynes. 1977b. The use of regression equations to increase the usefulness of historical temperature data in on-line pest management. Environ. Entomol. 6: 393-99.

Gage, S. H. 1972. The cereal leaf beetle, *Oulema melanopus* (L.), and its interaction with two primary hosts: winter wheat and spring oats. M.S. Thesis, Michigan State University.

Gage, S. H. 1974. Ecological investigations on the cereal leaf beetle, *Oulema melanopus* (L.), and the principal larval parasite, *Tetrastichus julis* (Walker). Ph.D. Thesis, Michigan State University.

Gallun, R. L., R. Ruppel, and E. H. Everson. 1966. Resistance of small grains to the cereal leaf beetle. *J. Econ. Entomol.* 59: 827-829.

Guppy, J. C. and D. G. Harcourt. 1978. Effects of temperature on development of the immature stages of the cereal leaf beetle, *Oulema melanopus* (Coleoptera: Chrysomelidae). *Can. Entomol.* 10: 257-63.

Gutierrez, A. P., W. H. Denton, R. Shade, H. Maltby, T. Burger, and G. Moorhead. 1974. The within field dynamics of the cereal leaf beetle (*Oulema melanopus* (L.)) in wheat and oats. *J. Anim. Ecol.* 43: 627-40.

Haynes, D. L. 1973. Population management of the cereal leaf beetle. Insects: studies in population management; Ecolog. Soc. Australia, Memoirs 1, Canberra.

Haynes, D. L., R. K. Brandenburg, and D. P. Fisher. 1973. Environmental monitoring network for pest management systems. *Environ. Entomol.* 2: 889-99.

Helgesen, R. G. 1969. The within-generation population dynamics of the cereal leaf beetle, *Oulema melanopus* (L.). Ph.D. Thesis, Michigan State University.

Helgesen, R. G. and D. L. Haynes. 1972. Population dynamics of the cereal leaf beetle, *Oulema melanopus* (Coleoptera: Chrysomelidae): A model for age specific mortality. *Can. Ent.* 104: 797-814.

Holling, C. S., D. D. Jones, and W. C. Clark. 1975. Spruce budworm/ forest management. Workshop progress report PR-5, Inst. Resour. Ecol., U. of British Columbia, Vancouver.

Holling, C. S., D. D. Jones, and W. C. Clark. 1976. Ecological policy design: lessons from a study of forest/pest management. Inst. Resour. Ecol. Report R-6-B, U. of British Columbia, Vancouver.

Hoxie, R. P. and S. G. Wellso. 1974. Cereal leaf beetle instars and sex, defined by larval head capsule widths. *Ann. Ent. Soc. Amer.* 67: 183-86.

Hoxie, R. P., S. G. Wellso, and J. A. Webster. 1975. Cereal leaf beetle response to wheat trichome length and density. *Environ. Entomol.* 4: 365-70.

Huffaker, C. B. 1958. Experimental studies on predation: dispersion factors and predator-prey oscillations. *Hilgardia*, 27: 343-83.

Iwao, S. 1971. Dynamics of numbers of a phytophagus lady-beetle, Epilachna vigintioctomaculata, living in patchily distributed habitats. In: Dynamics of Populations 1970, pp. 129-147.

Jackman, J. A. 1976. A quantitative description of oat growth with cereal leaf beetle populations. Ph.D. Thesis, Michigan State. University. 172 pp.

Jantz, O. K. 1965. Cereal leaf beetle field attractant tests during 1965. Special report W-209. USDA, ARS and Mich. Agric. Expt. Stn. (unpubl.).

Jokinen, D. P. 1978. The effect of pubescent wheats on the population dynamics of the cereal leaf beetle. 4th Ann. Grant Report for USDA, ARS Project No. 3302-14800-001.

Karlin, S. and H. M. Taylor. 1975. A first course in stochastic processes. 2nd ed. Academic Press. 557 pp.

Kitching, R. 1971. A simple simulation model of dispersal of animals among units of discrete habitats. Oecologia (Berl.) 7: 95-116.

Kramer, P. J. 1969. Plant and soil water relationships: a modern synthesis. McGraw Hill. 482 pp.

Lecigne, P. and R. Roehrich. 1977. Cereal leaf beetle Oulema melanopus (Coleoptera, Chrysomelidae). Determination of adult population displacement. Rev. Zool. Agric. Pathol. Veg. 76(3): 71-76.

Lee, K. Y., R. O. Barr, S. H. Gage, and A. N. Kharkar. 1976. Formulation of a systems model for insect pest control--the cereal leaf beetle problem. J. Theor. Biol. 59: 33-76.

Levin, S. A. (ed.). 1975. Ecosystem analysis and prediction. Soc. Indus. Appl. Math. 337 pp.

Levin. S. A. 1976. Population dynamic models in heterogeneous environments. Ann. Rev. Ecol. Syst. 7: 287-310.

Levin, S. A. and R. T. Paine. 1974. Disturbance, patch formation, and community structure. Proc. Nat. Acad. Sci. 71(7): 2744-47.

Lloyd, M. 1967. Mean crowding. J. Anim. Ecol. 36: 1-30.

Logan, P. 1977. Development of improved density estimators for larvae of the cereal leaf beetle, Oulema melanopus (L.). Ph.D. Thesis, Michigan State University.

MacLeod, J. and J. Donnelly. 1960. Natural features and blowfly movement. J. Anim. Ecol. 29: 85-93.

Manetsch, T. J. and G. L. Park. 1977. Systems analysis and simulation with applications to economic and social systems. Parts I & II. 3rd Ed. Dept. Elec. Eng. Sys. Sci. Michigan State University, East Lansing.

Morris, R. F. (ed.). 1963. The dynamics of epidemic spruce budworm populations. Mem. Entomol. Soc. Can. No. 31.

MSU. 1970. Cereal leaf beetle research 1962-69. Res. Rpt. 113, Farm Sci. Mich. State Univ. Agr. Exp. Stn. East Lansing. 20 pp.

Nie, N. H., C. H. Hull, J. G. Jenkins, K. Steinbrenner, and D. H. Bent. 1975. Statistical Package for the Social Sciences. 2nd Ed. McGraw-Hill.

Patil, G. P., E. C. Pielou, and W. E. Waters (eds.). 1971. Statistical Ecology. Penn. State U. Press, University Park. 3 volumes.

Patten, B. C. (ed.). 1972. Systems Analysis and Simulation in Ecology. Academic Press, New York. 4 volumes.

Pielou, E. C. 1974. Population and Community Ecology. Gordon and Breach Science Publ. 424 pp.

Pielou, E. C. 1977. Mathematical Ecology. John Wiley & Sons. 385 pp.

Pimentel, D., W. P. Nagel, and J. L. Madden. 1963. Space-time structure of the environment and the survival of parasite-host systems. Amer. Naturalist 97(894): 141-67.

Poole, R. W. 1974. An Introduction to Quantitative Ecology. McGraw-Hill.

Richardson, R. H. 1970. Models and analyses of dispersal patterns. In: Mathematical Topics in Population Genetics. K. Kojima (ed.). Springer-Verlag, New York. Pp. 79-103.

Robinson, P. 1954. The distribution of plant populations. Annals of Bot., N.S. 18(69): 35-45.

Ruesink, W. G. 1972. The integration of adult survival and dispersal into a mathematical model for the abundance of the cereal leaf beetle, Oulema melanopus (L.). Ph.D. Thesis, Michigan State University.

Ruesink, W. G. and D. L. Haynes. 1973. Sweepnet sampling for the cereal leaf beetle, Oulema melanopus. Environ. Entomol. 2: 161-72.

Salisbury, F. B. and C. Ross. 1969. Plant Physiology. Wadsworth Publishing Co., Inc. 747 pp.

Sampson, R. J. 1975. Surface II Graphics System. Kansas Geological Survey. Lawrence, Kansas.

Sawyer, A. J. 1976a. The effect on the cereal leaf beetle of planting oats with a companion crop. M.S. Thesis, Michigan State University.

Sawyer, A. J. 1976b. The effect of pubescent wheats on the population dynamics of the cereal leaf beetle. 2nd Ann. Grant Report for USDA, ARS Project No. 3302-14800-001.

Sawyer, A. J. 1978. The effect of pubescent wheats on the population dynamics of the cereal leaf beetle. 3rd Ann. Grant Report for USDA, ARS Project No. 3302-14800-001.

Sawyer, A. J. and D. L. Haynes. 1978. Allocating limited sampling resources for estimating regional populations of overwintering cereal leaf beetles. Environ. Entomol. 7: 62-66.

Sawyer, A. J. and D. L. Haynes. 1979. On the nature of errors involved in estimating stage-specific survival rates by Southwood's method for a population with overlapping stages. In prep. for Res. Popul. Ecol.

Schillinger, J. A. and R. L. Gallun. 1968. Leaf pubescence of wheat as a deterrent to the cereal leaf beetle, Oulema melanopus. Ann. Entomol. Soc. Amer. 61: 900-903.

Scotter, D. R., K. P. Lamb, and E. Hassan. 1971. An insect dispersal parameter. Ecology 52(1): 174-77.

Searle, S. R. 1971. Linear models. John Wiley & Sons, Inc. 532 pp.

Sneath, P. H. A. and R. R. Sokal. 1973. Numerical Taxonomy. W. H. Freeman & Co. 573 pp.

Sokal, R. R. and J. Rohlf. 1969. Biometry. W. H. Freeman and Co. 776 pp.

Southwood, T. R. E. 1966. Ecological methods, with particular reference to the study of insect populations. Methuen, London.

Steele, R. G. D. and J. H. Torrie. 1960. Principles and procedures of statistics. McGraw Hill. 481 pp.

Taylor, L. R. 1961. Aggregation, variance and the mean. Nature 189(4766): 732-735.

Tummala, R. L. and D. L. Haynes. 1977. On-line pest management systems. Environ. Entomol. 6: 339-49.

Tummala, R. L., W. G. Ruesink, and D. L. Haynes. 1975. A discrete component approach to the management of the cereal leaf beetle ecosystem. Environ. Entomol. 4: 175-86.

Van Den Brink, C., N. D. Strommen, and A. L. Kenworthy. 1971. Growing degree days in Michigan. Res. Rpt. 131, Farm Sci. Mich. State Univ. Agr. Exp. Stn. East Lansing. 48 pp.

Varley, G. C. and G. R. Gradwell. 1970. Recent advances in insect population dynamics. Ann. Rev. Entomol. 15: 1-24.

Voute, A. D. 1971. Presidential address for the advanced study institute on "Dynamics of Numbers in Populations." In: Dynamics of Populations 1970, pp. 19-28.

Watson, A. 1971. Key factor analysis, density dependence and population limitation in red grouse. In: Dynamics of Populations 1970, pp. 548-64.

Watt, K. E. F. 1961. Mathematical models for use in insect pest control. Can. Entomol. Supplement 19.

Watt, K. E. F. 1962. Use of mathematics in population ecology. Ann. Rev. Entomol. 7: 243-60.

Watt, K. E. F. 1966. The nature of systems analysis. In: Systems Analysis in Ecology. K. E. F. Watt (ed.). Academic Press, New York, pp. 1-14.

Watt, K. E. F. 1968. Ecology and Resource Management, a Quantitative Approach. McGraw-Hill, New York.

Webster, J. A. 1977. The cereal leaf beetle in North America: breeding for resistance in small grains. Ann. N.Y. Acad. Sci. 287: 230-37.

Webster, J. A., S. H. Gage, and D. H. Smith, Jr. 1973. Suppression of the cereal leaf beetle with resistant wheat. Environ. Entomol. 2: 1089-1091.

Welch, P. S. 1948. Limnological Methods. McGraw Hill. 381 pp.

Wells, M. T. 1967. Evaluation of methods of chemical control of the cereal leaf beetle (Oulema melanopus, L.) with respect to an integrated plan. M.S. Thesis, Michigan State University East Lansing. 55 pp.

Wellso, S. G. 1972. Reproductive systems of the cereal leaf beetle. Comparison of morphology during seasonal development. *Ann. Entomol. Soc. Amer.* 65: 945-49.

Wellso, S. G. 1973. Cereal leaf beetle: larval feeding, orientation, development, and survival on four small-grain cultivars in the laboratory. *Ann. Entomol. Soc. Amer.* 66: 1201-08.

Wellso, S. G. 1974. Aestivation in relation to oviposition initiation in the cereal leaf beetle. *In*: Scheving, L. E., F. Halberg, and J. E. Pauly (eds.). *Chronobiology*: 597-601. Igaku Shoin, Ltd., Tokyo.

Wellso, S. G. 1976. Cereal leaf beetle: feeding and oviposition on winter wheat and spring oats. *Environ. Entomol.* 5: 487-91.

Wellso, S. G. 1978. Feeding differences by pre- and postaestival cereal leaf beetles on first and third blades of seedling corn. *Environ. Entomol.* 7: 265-69.

Wellso, S. G., R. V. Connin, and R. P. Hoxie. 1973. Oviposition and orientation of the cereal leaf beetle. *Ann. Entomol. Soc. Amer.* 66: 78-83.

Wellso, S. G. and C. E. Cress. 1973. Intraspecific competition of the cereal leaf beetle reduced through spatial separation of eggs and feeding. *Environ. Entomol.* 2: 791-2.

Wellso, S. G., W. G. Ruesink, and S. H. Gage. 1975. Cereal leaf beetle: relationships between feeding, oviposition, mating, and age. *Ann. Entomol. Soc. Amer.* 68: 663-68.

Wiens, J. A. 1976. Population responses to patchy environments. *Ann. Rev. Ecol. Syst.* 7: 81-120.

Wilson, M. C. and R. E. Shade. 1966. Survival and development of the cereal leaf beetle, *Oulema melanopus* (Coleoptera: Chrysomelidae), on various species of Gramineae. *Ann. Entomol. Soc. Amer.* 59: 170-73.

Wolfenbarger, D. 1975. *Factors Affecting Dispersal Distances of Small Organisms*. Exposition Press, Hicksville, N.Y.

Wong, P. K. 1978. *Mathematical methods and models in biology*. Department of Mathematics, Michigan State University, East Lansing.

Yun, Y. M. 1967. Effects of some physical and biological factors on the reproduction, development, survival, and behavior of the cereal leaf beetle, *Oulema melanopus* (L.) under laboratory conditions. Ph.D. Thesis, Michigan State University. 153 pp.

APPENDIX A

OPTIMIZATION PROGRAM FOR
1977 COMPARTMENTAL ANALYSIS

```
      PROGRAM OPT(OUTPUT,TAPE1,INPUT)
      REAL M
      DIMENSION DEG(36),X1OBS(36),X2OBS(36),X3OBS(36)
      DATA DEG/496.,507.,524.,539.,562.,587.,613.,636.,660.,688.,
     +715.,745.,772.,798.,823.,846.,865.,889.,913.,939.,959.,973.,
     +977.,987.,1011.,1033.,1042.,1048.,1056.,1061.,1070.,1086.,
     +1095.,1107.,1123.,1140./
      DATA X1OBS/4.316,3.452,3.021,2.833,2.545,2.232,1.888,1.46,1.087,
     +.863,.759,.644,.54,.438,.381,.338,.302,.296,.289,
     +.282,.28,.151,.108,.029,0.,0.,0.,0.,0.,0.,0.,0.,0.,0.,0.,0./
      DATA X2OBS/3.164,2.826,2.911,2.79,2.605,2.404,2.312,
     +2.288,2.353,2.364,2.124,1.88,1.282,.771,.627,.521,.432,
     +.378,.323,.264,.25,.162,.084,.023,0.,0.,0.,0.,0.,0.,0.,0.,0.,0.
     +,0./
      DATA X3OBS/.073,.151,.204,.278,.392,.515,.590,.74,
     +.712,.603,.547,.484,.428,.369,.223,.248,.269,.229,
     +.190,.146,.119,.055,.041,.038,.049,.058,.063,.055,
     +.031,.017,.015,.016,.017,.018,.024,.017/
C MEAN VALUES OF X1 (S-WHEAT),X2 (R-WHEAT) AND X3 (OATS)
C OVER 37 DAYS IN 1977 FROM 488 TO 1140 DD > 48 (F)
      X1BAR=0.886
      X2BAR=1.040
      X3BAR=0.218
      DT=0.2
1     T=488.
      N=652
      ND=1
      U=0.
      REWIND 1
      READ*,M,A12,A13,A21,A23,A31,A32
      IF(M.EQ.9.0)STOP
      IT=FLOAT(N)/DT+1.
C INITIALIZE STATES AND RATES
      X1=4.249
      X2=3.257
      X3=0.032
C     READ*,X2
      WRITE(1,102)T,X1,X2,X3,X1,X2,X3
      R1=-(M+A31+A21)*X1+A12*X2+A13*X3
      R2=A21*X1-(M+A12+A32)*X2+A23*X3
      R3=A31*X1+A32*X2-(M+A13+A23)*X3
C LOOP OVER DEGREE-DAYS
      DO 10 I=1,IT
      T=T+DT
      DD=IFIX(T+.005)
C UPDATE STATES
C PREDICTOR (EULER)
      X1P=X1+DT*R1
      X2P=X2+DT*R2
      X3P=X3+DT*R3
```

```
      R1P=-(M+A31+A21)*X1P+A12*X2P+A13*X3P
      R2P=A21*X1P-(M+A12+A32)*X2P+A23*X3P
      R3P=A31*X1P+A32*X2P-(M+A13+A23)*X3P
C CORRECTOR (TRAPEZOIDAL RULE)
      X1=X1+DT/2.*(R1+R1P)
      X2=X2+DT/2.*(R2+R2P)
      X3=X3+DT/2.*(R3+R3P)
C UPDATE RATES
      R1=-(M+A31+A21)*X1+A12*X2+A13*X3
      R2=A21*X1-(M+A12+A32)*X2+A23*X3
      R3=A31*X1+A32*X2-(M+A13+A23)*X3
C UPDATE OPTIMIZATION CRITERION ON SAMPLING DATES
      IF(DD.NE.DEG(ND))GO TO 10
      U=U+((X1-X1OBS(ND))**2)/X1BAR+((X2-X2OBS(ND))**2)/X2BAR+
     +((X3-X3OBS(ND))**2)/X3BAR
      WRITE(1,102)DEG(ND),X1OBS(ND),X2OBS(ND),X3OBS(ND),X1,X2,X3
102   FORMAT(7E10.4)
      ND=ND+1
10    CONTINUE
      PRINT 101,U
      GO TO 1
C     STOP
101   FORMAT(* U=*F15.4)
      END
```

APPENDIX B

DATA FOR FIELDS AT GALIEN IN 1976 AND 1977

Table B1. Adult and egg densities in small grain fields at Galien in 1976, with field acreages, cell assignments in spatial analysis, and hierarchical cluster membership based on environmental features.

Field	Acres	Cells[a]	Adult-°D[b]	Eggs[b]	Cluster
S-Wheat					
133	18	5-6,5	10.20	1.82	4
136	18	7-8,5	29.71	5.15	4
145	5	5,4	24.99	2.76	4
214	21	1-2,9	5.71	1.33	5
217	5	2,12	28.55	4.16	2
222	10	4,13	28.25	2.62	2
225	60	1,15 2,15-16 3,15-16 4,16	13.93	1.99	4
231	33	5,16 6,15-16	47.20	4.69	4
241	10	7,12	115.21	6.42	2
311	19	1-2,18	24.83	2.97	4
313	70	2,17 3,17-19 4,17-19	19.06	2.56	4
333	8	5,23	29.43	2.62	5
334	14	7,23	82.33	8.85	5
336	7	6,23	21.17	2.73	5
343	14	6,17	11.94	1.56	4
345	10	7,17	23.60	3.62	4
415	12	2,25	36.25	2.25	2
421	10	2,29	106.20	11.94	2
431	34	6-8,32	203.24	28.35	3
432	11	7,30	186.75	36.44	3
525	5	12,30	53.57	3.35	5
637	17	13,21-22	48.42	2.98	5
644	5	16,17	25.44	2.92	3
713	15	10,9-10	43.29	4.66	2
729	7	11,16	70.39	18.43	2
747	11	13,9	73.10	6.16	2
811	18	9,3-4	19.76	2.95	4
812	15	10,3-4	11.32	1.31	4
813	15	11-12,4	42.84	3.14	5
821	20	9-10,5	36.49	2.75	4
822	5	12,5	53.25	6.30	5
843	10	13,2	20.85	3.40	5
911	14	17,3	13.52	1.55	2
924	5	17,8	18.17	2.50	2
933	10	23,8	65.53	6.81	3
1017	5	17,12	33.08	3.83	3
1115	55	17,19-20 18,19-20 19,19-20	33.79	2.64	4
1144	22	24,17-18	12.74	1.12	2

Table B1. Continued.

Field	Acres	Cells[a]	Adult-°D[b]	Eggs[b]	Cluster
1214	30	17,28 18,27-28	27.03	2.13	5
1222	7	19,31	10.94	11.00	1
1224	20	17-18,30	21.69	2.25	5
1227	6	20,31	8.65	0.69	1
1311	30	27,27 28,26-27	19.10	2.13	5
1410	16	7-8,1	25.54	2.49	4
1411	25	26,18 27,18-19	14.95	1.82	3
1511	20	28,10-11	65.57	13.21	5
1514	12	25,9	53.97	5.32	5
1542	7	30,11	44.25	12.06	5
1548	15	32,8-9	116.37	14.04	5
1625	12	26,7	93.51	17.28	5
R-Wheat					
611	20	10,19-20	26.70	1.68	2
625	20	10,21-22	46.51	3.51	2
632	20	15,21-22	63.03	3.66	2
726	12	9,13	60.50	5.06	1
1014	15	19-20,11	62.39	4.12	1
1023	10	17,14	33.72	3.59	1
1122	18	17,21-22	23.45	1.94	2
1124	20	19,21-22	21.97	2.49	2
Oats					
136	12	8,6	58.17	21.00	-
149	12	8,2	27.29	8.08	-
236	15	7-8,16	57.77	16.67	-
246	12	8,12	57.63	31.37	-
337	8	6,23	52.74	33.19	-
346	20	7,18-19	17.71	8.08	-
524	8	12,32	140.09	44.80	-
612	20	9-10,18	11.02	2.64	-
1024	18	17-18,14	22.60	8.36	-
1135	5	23,22	0.96	1.16	-
1228	7	20,31	50.13	7.16	-
1547	8	30,11	119.90	28.68	-

[a] rows,columns

[b] seasonal total per ft^2

Table B2. Adult and egg densities in small grain fields at Galien in 1977, with field acreages, cell assignments in spatial analysis, and hierarchical cluster membership based on environmental features.

Field	Acres	Cells[a]	Adult-°D[b]	Eggs[b]	Cluster
		S-Wheat			
125	28	3,7-8 4,8	97.73	4.32	2
149	12	8,1	44.58	6.54	-
218	16	3,10-11	57.52	6.83	2
225	56	1,15 2,15-16 3,15-16 4,16	54.84	4.50	4
227	4	1,10	48.65	5.45	4
322	25	3,22 4,21-22	61.13	10.47	4
427	6	1,16	57.19	5.62	1
513	8	10,26	47.86	4.43	2
615	4	9,21	52.12	6.87	4
626	2	9,22	131.83	26.56	4
731	7	16,13	50.08	4.78	3
735	6	16,15	57.25	4.24	3
747	11	13,9	245.67	22.74	2
833	12	16,5	77.79	7.55	3
933	6	24,9	115.66	10.61	3
1022	17	17-18,15	139.18	7.69	3
1042	21	22-23,11	84.22	10.33	3
1223	14	20,29	44.02	3.72	1
1511	16	29,10-11	149.25	15.20	4
1514	8	25,9	91.98	10.34	3
1524	2	28,12	92.88	7.10	3
1525	9	27,12	106.67	5.82	3
1533	14	31,15	51.02	7.15	3
1612	6	26,3	170.22	42.09	4
1636	22	32,6-7	84.79	7.68	4
		R-Wheat			
136	11	8,6	43.74	5.96	3
137	34	6,5 7,5-6	89.83	5.92	3
141	14	8,3	30.29	2.29	2
226	10	2,13	24.45	2.48	4
233	15	6,13-14	115.13	5.62	4
236	14	8,16	42.10	3.06	4
241	8	7,10	78.32	7.91	4
311	24	1-2,18	28.69	1.42	4
312	16	1-2,20	31.67	1.28	4
322	11	3,21	32.87	1.56	3
323	18	3,23-24	36.51	3.56	3
346	9	7,18	54.69	1.33	2

Table B2. Continued.

Field	Acres	Cells[a]	Adult-°D[b]	Eggs[b]	Cluster
348	15	5,17-18	102.44	7.55	2
413	7	3,27	26.54	0.94	1
416	2	4,26	33.92	1.08	1
421	12	2,29	29.71	2.24	1
425	21	1-2,31	51.01	2.58	1
441	17	5,27-28	31.72	1.79	1
522	15	9-10,30	86.64	5.34	4
535	38	13,30 14,29 15,29-30	45.79	1.35	4
536	22	14-15,31	27.34	0.87	4
625	12	12,22	24.73	2.32	4
722	13	9,14	74.00	6.04	4
742	19	13-14,12	62.60	6.66	4
744	10	16,12	72.59	3.69	4
818	13	9,1	40.87	4.82	4
1024	13	17,14	75.24	5.64	4
1131	19	20-21,21	46.42	2.20	4
1144	6	24,19	50.47	2.28	1
1212	7	17,26	25.00	2.37	3
1213	16	18-19,25	60.73	3.95	3
1216	5	17,25	45.02	2.89	3
1228	18	19-20,31	36.56	1.39	1
1312	24	26-27,26	61.56	3.03	4
1341	9	30,27	42.38	2.26	4
1412	27	26-28,21	49.09	2.52	4
1626	20	28,7-8	69.82	10.56	4
		Oats			
235	6	8,15	111.45	42.99	-
426	4	3,31	187.48	18.93	-
537	7	14,30	149.30	7.50	-
541	13	16,26	83.13	8.02	-
612	7	9,17	12.67	1.65	-
613	4	9,17	16.47	2.66	-
711	10	9,9	42.79	10.10	-

[a] rows,columns

[b] seasonal total per ft^2

APPENDIX C

REMOTE SENSING DATA

(Available on computer)

KEY

BD	Buildings	(no. of .4 a subcells)
WT	Water	"
SW	Sparse woods	"
DW	Dense woods	"
CL	Cropland	"
FR	Fencerows (ft)	
EW	Edge of woods (ft)	

Row	Col	BD	WT	SW	DW	CL	FR	EW
1	1	0	0	0	0	25	1340	0
1	2	0	0	0	0	25	650	0
1	3	0	0	0	0	25	650	0
1	4	0	0	0	0	25	1320	0
1	5	0	0	0	0	25	1320	0
1	6	0	0	0	9	16	400	1653
1	7	0	0	0	0	25	650	0
1	8	2	0	0	0	23	1005	0
1	9	0	0	0	0	25	1980	0
1	10	6	0	0	6	13	720	1450
1	11	5	0	0	2	18	260	555
1	12	0	0	5	4	16	1420	1095
1	13	0	0	0	12	13	924	1320
1	14	2	0	0	0	23	870	0
1	15	0	0	0	0	25	660	0
1	16	2	0	0	0	23	640	0
1	17	2	0	2	0	21	520	530
1	18	0	0	0	0	25	520	0
1	19	0	0	0	0	25	660	0
1	20	2	0	0	0	23	1120	0
1	21	2	0	0	0	23	1320	0
1	22	9	0	0	0	16	790	0
1	23	2	0	8	1	14	1915	0
1	24	0	0	3	0	22	1190	0
1	25	0	0	10	0	15	1755	0
1	26	0	0	10	0	15	650	0
1	27	0	1	0	0	24	790	0
1	28	3	0	6	4	12	650	1715
1	29	0	0	0	7	18	660	600
1	30	0	0	0	0	25	660	0
1	31	2	0	0	0	23	640	0
1	32	0	2	5	1	17	530	565
2	1	0	0	0	0	25	675	0
2	2	0	0	0	0	25	0	0
2	3	0	0	0	0	25	660	0
2	4	0	0	0	0	25	1320	0
2	5	0	0	0	0	25	660	0
2	6	0	0	0	0	25	660	0
2	7	0	0	0	0	25	1320	0
2	8	0	0	0	0	25	1270	0
2	9	0	0	0	0	25	660	0
2	10	0	0	0	0	25	1320	0
2	11	0	0	0	0	25	1320	0
2	12	0	0	7	0	18	1340	725
2	13	20	0	3	1	1	330	660
2	14	0	0	2	0	23	325	640
2	15	0	0	0	0	25	0	0
2	16	0	0	0	0	25	660	0
2	17	3	0	0	0	22	660	0
2	18	0	0	0	0	25	660	0

2	19	0	0	0	0	25	0	0
2	20	0	0	0	0	25	660	0
2	21	0	0	0	0	25	1300	0
2	22	4	0	0	0	21	595	0
2	23	1	0	0	0	24	1906	0
2	24	0	0	2	3	20	765	1040
2	25	0	2	2	0	21	0	645
2	26	0	4	11	0	10	975	1070
2	27	0	0	10	0	15	250	1570
2	28	0	0	13	6	6	0	1255
2	29	0	0	0	11	14	0	1065
2	30	0	0	0	0	25	650	0
2	31	0	0	0	0	25	0	0
2	32	0	7	4	0	14	0	0
3	1	0	0	0	0	25	395	0
3	2	0	0	0	0	25	1335	0
3	3	0	0	0	0	25	1980	0
3	4	0	0	0	0	25	1950	0
3	5	0	0	0	0	25	1350	0
3	6	0	0	0	1	24	1135	525
3	7	0	0	0	0	25	0	0
3	8	0	0	0	0	25	660	0
3	9	0	0	0	0	25	1320	0
3	10	0	0	3	0	22	0	670
3	11	0	0	3	0	22	620	790
3	12	0	0	0	0	25	1850	0
3	13	2	0	0	0	23	990	0
3	14	0	0	0	0	25	990	0
3	15	0	15	0	0	10	0	0
3	16	1	0	0	0	24	650	0
3	17	0	0	0	0	25	660	0
3	18	0	0	0	0	25	450	0
3	19	0	0	0	0	25	0	0
3	20	0	0	1	0	24	530	320
3	21	0	0	0	0	25	710	0
3	22	1	0	0	0	24	1420	0
3	23	0	0	2	0	23	435	190
3	24	0	0	3	12	10	0	860
3	25	0	4	12	5	4	0	730
3	26	0	7	6	10	2	140	490
3	27	0	0	0	0	25	200	0
3	28	0	0	6	9	10	0	975
3	29	0	0	6	19	0	0	0
3	30	0	0	17	3	5	0	1230
3	31	0	0	1	0	24	0	250
3	32	1	0	14	0	10	0	670
4	1	0	0	0	0	25	0	0
4	2	0	0	0	0	25	660	0
4	3	0	0	0	0	25	0	0
4	4	0	0	0	0	25	1320	0

4	5	1	0	0	0	24	1310	0
4	6	0	0	0	1	24	660	330
4	7	0	0	0	20	5	0	1820
4	8	0	0	0	7	18	0	825
4	9	0	0	0	0	25	660	0
4	10	0	0	0	25	0	0	1715
4	11	2	0	2	8	13	0	925
4	12	0	0	4	0	21	690	670
4	13	0	0	0	0	25	660	0
4	14	0	14	0	0	11	265	0
4	15	0	9	0	0	16	0	0
4	16	1	0	0	0	24	1340	0
4	17	0	0	0	0	25	1320	0
4	18	0	0	0	0	25	1450	0
4	19	0	0	0	0	25	660	0
4	20	0	0	0	14	11	265	1850
4	21	0	0	0	0	25	370	0
4	22	1	0	3	0	21	925	660
4	23	1	0	0	0	24	660	0
4	24	0	0	0	5	20	660	1245
4	25	0	0	0	25	0	0	0
4	26	0	0	0	21	4	224	1070
4	27	0	0	1	0	24	500	505
4	28	0	0	0	8	17	0	1035
4	29	0	0	0	25	0	0	0
4	30	0	0	0	23	2	130	380
4	31	0	0	0	3	22	655	1055
4	32	0	0	4	2	19	0	1780
5	1	0	0	0	0	25	0	0
5	2	0	0	0	0	25	660	0
5	3	0	0	20	5	0	480	2430
5	4	0	0	0	0	25	1970	0
5	5	0	0	0	0	25	660	0
5	6	0	0	0	0	25	0	0
5	7	0	0	0	1	24	0	260
5	8	0	0	0	18	7	160	830
5	9	0	0	7	0	18	0	725
5	10	0	0	25	0	0	0	750
5	11	0	0	9	6	10	0	1450
5	12	1	0	9	3	12	530	1190
5	13	0	0	0	3	22	1135	845
5	14	1	0	3	6	15	110	1740
5	15	0	0	1	16	8	0	755
5	16	0	0	2	0	23	660	410
5	17	0	0	0	0	25	660	0
5	18	0	0	0	0	25	660	0
5	19	0	0	0	0	25	130	0
5	20	0	0	0	0	25	790	0
5	21	0	0	0	3	22	1055	1080
5	22	0	0	0	7	18	660	1185

5	23	0	0	0	0	25	660	0
5	24	0	0	0	3	22	0	690
5	25	0	0	18	7	0	0	0
5	26	0	0	19	6	0	0	660
5	27	0	0	0	0	25	660	0
5	28	0	0	0	11	14	0	860
5	29	0	0	0	25	0	0	0
5	30	0	0	0	25	0	0	0
5	31	0	0	0	25	0	0	0
5	32	0	0	0	25	0	0	530
6	1	0	0	0	0	25	0	0
6	2	0	0	0	0	25	660	0
6	3	0	0	5	0	20	1320	0
6	4	0	0	0	0	25	1220	0
6	5	0	0	0	0	25	660	0
6	6	0	0	0	0	25	0	0
6	7	0	0	0	0	25	0	0
6	8	0	0	0	0	25	660	0
6	9	0	0	3	18	4	0	790
6	10	0	0	21	4	0	0	530
6	11	0	0	4	0	21	460	1310
6	12	0	0	0	0	25	1975	0
6	13	1	0	2	2	20	1715	1380
6	14	0	0	0	4	21	575	1835
6	15	0	0	0	0	25	660	0
6	16	0	0	0	0	25	1320	0
6	17	0	0	0	0	25	925	0
6	18	0	0	0	0	25	790	0
6	19	0	0	0	0	25	1715	0
6	20	0	0	0	0	25	660	0
6	21	0	0	0	0	25	1005	0
6	22	1	0	0	1	23	1055	460
6	23	1	0	0	0	24	925	0
6	24	0	0	13	5	7	0	1590
6	25	0	0	7	18	0	0	0
6	26	0	0	10	15	0	0	660
6	27	0	0	0	0	25	660	0
6	28	0	0	1	9	15	0	680
6	29	0	0	5	20	0	0	230
6	30	0	0	0	24	1	0	310
6	31	0	0	0	17	8	0	790
6	32	0	0	0	1	24	660	215
7	1	0	0	0	0	25	0	0
7	2	0	0	0	0	25	0	0
7	3	0	0	0	0	25	1965	0
7	4	0	0	0	0	25	1980	0
7	5	0	0	0	0	25	660	0
7	6	0	0	0	0	25	0	0
7	7	0	0	0	0	25	100	0
7	8	0	0	0	4	21	610	628

7	9	0	0	8	4	13	265	1260
7	10	0	0	8	0	17	0	755
7	11	0	0	1	0	24	0	0
7	12	0	0	0	0	25	660	0
7	13	0	0	1	0	24	0	0
7	14	0	0	0	13	12	0	1365
7	15	0	0	6	10	9	0	1451
7	16	1	0	0	0	24	0	0
7	17	0	0	0	0	25	660	0
7	18	0	0	0	0	25	330	0
7	19	0	0	0	0	25	1980	0
7	20	0	0	0	0	25	660	0
7	21	0	0	0	0	25	325	0
7	22	0	0	0	0	25	950	0
7	23	1	0	0	0	24	1500	0
7	24	1	0	0	11	13	650	830
7	25	0	0	0	21	4	0	650
7	26	0	0	5	20	0	0	660
7	27	0	0	8	0	17	660	1310
7	28	0	0	12	0	13	0	845
7	29	0	0	25	0	0	0	0
7	30	0	0	11	0	14	0	1395
7	31	0	0	2	19	4	0	475
7	32	0	0	0	0	25	660	0
8	1	2	0	0	0	23	1320	0
8	2	5	0	0	0	20	1060	0
8	3	1	0	0	0	24	1300	0
8	4	0	0	0	0	25	1890	0
8	5	1	0	0	0	24	1120	0
8	6	0	0	0	0	25	660	0
8	7	0	0	0	0	25	980	0
8	8	0	0	10	11	4	1000	635
8	9	1	0	8	8	8	330	1630
8	10	1	0	0	0	24	1095	0
8	11	4	0	0	0	21	2095	0
8	12	2	0	0	0	23	660	0
8	13	0	0	0	0	25	1320	0
8	14	2	0	0	0	23	1055	0
8	15	0	0	0	0	25	660	0
8	16	1	0	0	0	24	720	0
8	17	1	0	0	0	24	1320	0
8	18	1	0	0	0	24	1095	0
8	19	3	1	3	13	5	660	1980
8	20	2	0	0	0	23	660	0
8	21	0	0	0	0	25	1320	0
8	22	0	0	0	0	25	1320	0
8	23	6	0	0	0	19	800	0
8	24	0	0	2	0	23	1960	790
8	25	2	0	4	0	19	1490	980
8	26	0	0	0	25	0	0	0

8	27	4	0	2	0	19	2615	0
8	28	1	0	7	0	17	655	1360
8	29	0	0	11	0	14	660	885
8	30	0	0	7	0	18	500	1230
8	31	0	0	20	3	2	0	1650
8	32	0	0	2	0	23	1190	530
9	1	0	0	0	0	25	1200	0
9	2	0	0	14	5	6	660	1970
9	3	3	0	0	0	22	926	0
9	4	0	0	0	0	25	1320	0
9	5	0	0	0	0	25	660	0
9	6	2	0	0	0	23	400	0
9	7	0	0	0	0	25	660	0
9	8	2	0	10	3	10	400	2090
9	9	0	0	4	0	21	1135	980
9	10	1	0	9	0	15	240	1305
9	11	0	0	10	0	15	660	790
9	12	0	0	1	0	24	1320	330
9	13	0	0	2	0	23	645	585
9	14	0	0	1	1	23	1005	400
9	15	0	0	0	0	25	660	0
9	16	2	0	0	0	23	1190	0
9	17	0	0	0	0	25	1980	0
9	18	0	0	0	0	25	1980	0
9	19	0	0	0	0	25	1385	0
9	20	1	0	0	0	24	2440	0
9	21	1	0	3	0	21	1005	660
9	22	1	0	3	0	21	1584	685
9	23	0	0	1	0	24	1320	530
9	24	2	0	0	1	22	160	500
9	25	1	0	7	0	17	1425	1000
9	26	0	2	9	0	14	1015	1055
9	27	0	0	7	4	14	660	2110
9	28	2	1	1	0	21	1770	370
9	29	1	0	0	1	23	925	265
9	30	0	0	0	0	25	845	0
9	31	4	0	0	0	21	1120	0
9	32	0	0	0	0	25	1160	0
10	1	0	0	0	0	25	1320	0
10	2	0	0	2	15	8	360	1715
10	3	0	0	0	0	25	1315	0
10	4	0	0	0	0	25	660	0
10	5	0	0	0	0	25	0	0
10	6	0	0	0	0	25	0	0
10	7	0	0	0	6	19	495	950
10	8	1	0	0	6	18	1585	730
10	9	0	0	0	0	25	1310	0
10	10	0	0	0	0	25	460	0
10	11	0	0	14	3	8	265	1255
10	12	0	0	11	0	14	360	1870

10	13	1	0	4	4	16	1780	1040
10	14	0	0	2	16	7	0	1005
10	15	0	0	0	23	2	0	1230
10	16	0	0	0	3	22	1320	565
10	17	0	0	0	0	25	1585	0
10	18	0	0	1	0	24	675	625
10	19	0	0	0	3	22	275	825
10	20	0	5	0	0	20	1170	0
10	21	0	1	0	0	24	650	0
10	22	1	0	0	0	24	1595	0
10	23	1	0	0	0	24	790	0
10	24	0	0	9	1	15	130	1340
10	25	0	0	0	2	23	660	370
10	26	0	0	2	0	23	620	1190
10	27	0	0	5	0	20	0	805
10	28	0	0	0	0	25	1190	0
10	29	0	0	0	13	12	155	2375
10	30	0	0	0	4	21	0	0
10	31	0	0	0	0	25	1905	0
10	32	0	0	0	0	25	1350	0
11	1	0	0	0	0	25	660	0
11	2	0	0	0	0	25	660	0
11	3	0	0	0	0	25	1320	0
11	4	0	0	0	0	25	1320	0
11	5	0	0	0	0	25	600	0
11	6	0	0	0	0	25	660	0
11	7	0	0	0	0	25	660	0
11	8	0	14	3	0	8	660	0
11	9	0	0	0	0	25	1190	0
11	10	0	0	13	0	12	460	2245
11	11	0	0	0	0	25	745	0
11	12	0	0	8	0	17	1520	650
11	13	0	0	0	10	15	395	1590
11	14	0	0	13	8	4	0	925
11	15	0	0	16	2	7	0	1165
11	16	0	0	0	1	24	670	330
11	17	0	0	0	0	25	660	0
11	18	0	0	1	8	16	395	150
11	19	0	0	0	2	23	0	0
11	20	0	0	0	0	25	460	0
11	21	0	1	0	0	24	1315	0
11	22	1	0	0	0	24	1875	0
11	23	0	0	1	4	20	405	1370
11	24	0	0	0	1	24	0	460
11	25	0	0	16	3	6	120	1980
11	26	0	0	0	11	14	171	2680
11	27	0	0	12	0	13	200	1935
11	28	0	0	0	0	25	1320	0
11	29	0	0	0	8	17	0	1390
11	30	0	0	0	15	10	0	1360

11	31	0	0	0	1	24	0	305
11	32	0	0	0	0	25	4505	0
12	1	2	0	0	0	23	1200	0
12	2	0	0	3	0	22	1120	0
12	3	0	0	0	0	25	660	0
12	4	0	0	0	0	25	1980	0
12	5	0	0	0	0	25	1320	0
12	6	0	0	2	0	23	1370	850
12	7	0	0	10	0	15	130	1480
12	8	3	0	3	1	18	1188	815
12	9	1	0	0	0	24	1530	0
12	10	0	0	0	1	24	1980	330
12	11	0	0	0	2	23	0	925
12	12	1	0	0	8	16	690	2060
12	13	0	0	0	0	25	1980	0
12	14	0	0	6	4	15	530	805
12	15	0	0	8	16	1	0	390
12	16	1	0	3	4	17	0	920
12	17	1	0	0	0	24	645	0
12	18	0	0	0	8	17	265	950
12	19	0	2	0	0	23	530	0
12	20	0	0	0	0	25	1320	0
12	21	0	0	7	0	18	0	0
12	22	0	0	0	0	25	1055	0
12	23	2	1	0	3	19	460	845
12	24	0	0	0	1	24	0	360
12	25	0	0	4	0	21	1160	860
12	26	0	0	0	3	22	660	945
12	27	0	0	0	0	25	660	0
12	28	0	0	0	0	25	1320	0
12	29	0	0	0	1	24	1070	650
12	30	0	0	0	8	17	380	990
12	31	0	0	5	2	18	130	1480
12	32	0	0	1	2	22	3795	650
13	1	1	0	1	6	17	660	1090
13	2	0	0	0	7	18	130	900
13	3	0	12	0	8	5	660	1250
13	4	0	0	0	0	25	660	0
13	5	0	0	3	0	22	1310	480
13	6	0	0	2	10	13	1255	970
13	7	0	0	5	5	15	0	1175
13	8	1	0	13	0	11	530	1585
13	9	0	0	0	0	25	844	0
13	10	0	0	2	6	17	0	1105
13	11	0	0	5	20	0	0	0
13	12	0	0	0	4	21	660	1310
13	13	0	0	0	0	25	775	0
13	14	0	0	0	0	25	660	0
13	15	0	0	10	4	11	0	840
13	16	1	0	22	2	0	0	660

13	17	1	0	10	0	14	0	1670
13	18	0	0	2	0	23	0	1115
13	19	0	0	1	6	18	660	705
13	20	0	0	0	5	20	660	1120
13	21	0	0	9	4	12	290	720
13	22	0	0	4	2	19	685	1320
13	23	2	0	0	0	23	1120	0
13	24	0	0	0	0	25	1020	0
13	25	0	0	0	3	22	660	1055
13	26	0	0	0	0	25	660	0
13	27	0	0	0	0	25	0	0
13	28	0	0	3	14	8	0	1690
13	29	0	0	1	21	3	0	1055
13	30	0	0	3	0	22	660	485
13	31	0	0	0	0	25	885	0
13	32	0	0	0	0	25	1716	0
14	1	1	0	6	4	14	530	1980
14	2	0	0	5	11	9	0	685
14	3	0	0	0	19	6	0	935
14	4	3	0	5	0	17	145	1005
14	5	0	0	3	0	22	400	370
14	6	0	0	4	9	12	725	970
14	7	0	0	25	0	0	0	0
14	8	1	0	24	0	0	660	265
14	9	1	0	10	0	14	260	640
14	10	0	0	9	10	6	0	790
14	11	0	0	5	20	0	0	330
14	12	0	0	0	4	21	1320	785
14	13	4	0	6	9	6	0	2105
14	14	0	0	11	0	14	500	1980
14	15	0	0	3	0	22	640	800
14	16	0	0	25	0	0	0	1585
14	17	3	0	2	0	20	462	400
14	18	0	0	3	3	19	1255	1265
14	19	0	0	0	4	21	965	1930
14	20	0	0	0	7	18	145	765
14	21	0	1	0	0	24	1715	0
14	22	2	0	0	0	23	925	0
14	23	0	0	0	0	25	660	0
14	24	0	0	0	0	25	0	0
14	25	0	0	1	4	20	650	930
14	26	0	0	0	6	19	845	1385
14	27	0	0	0	15	10	0	725
14	28	0	0	0	2	23	765	790
14	29	0	0	0	0	25	0	0
14	30	0	0	0	0	25	660	0
14	31	0	0	0	0	25	660	0
14	32	1	0	0	0	24	1255	0
15	1	1	0	3	2	19	270	700
15	2	0	0	11	13	1	0	0

15	3	0	0	0	25	0	0	130
15	4	0	0	0	2	23	660	620
15	5	0	0	0	0	25	650	0
15	6	0	0	18	0	7	0	710
15	7	0	0	25	0	0	0	660
15	8	0	0	0	10	15	0	1410
15	9	1	0	24	0	0	0	1110
15	10	0	0	15	10	0	0	0
15	11	0	0	1	7	17	605	1470
15	12	0	0	0	0	25	1320	0
15	13	0	0	2	0	23	660	680
15	14	0	0	0	24	1	0	790
15	15	0	0	3	0	22	355	1120
15	16	2	0	3	2	18	0	990
15	17	0	0	0	19	6	380	1330
15	18	0	0	0	7	18	490	1635
15	19	0	0	6	4	15	420	965
15	20	0	0	0	0	25	1310	0
15	21	0	0	0	0	25	0	0
15	22	2	0	0	0	23	0	0
15	23	0	0	0	0	25	1320	0
15	24	0	0	0	0	25	660	0
15	25	0	0	0	0	25	0	0
15	26	0	0	0	0	25	0	0
15	27	0	0	2	9	14	265	1225
15	28	0	0	0	6	19	1320	830
15	29	0	0	0	0	25	0	0
15	30	0	0	0	0	25	660	0
15	31	0	0	0	0	25	200	0
15	32	0	1	4	0	20	460	1400
16	1	1	0	2	6	16	660	1980
16	2	2	0	1	4	18	1710	890
16	3	0	0	3	2	20	660	710
16	4	0	0	0	0	25	1320	0
16	5	0	0	0	0	25	1320	0
16	6	0	0	13	0	12	550	910
16	7	1	0	16	0	8	400	1320
16	8	1	0	0	0	24	1320	0
16	9	2	0	4	0	19	1290	500
16	10	0	0	14	3	8	265	1450
16	11	1	0	1	1	22	380	460
16	12	3	0	0	0	22	650	0
16	13	1	0	0	0	24	1160	0
16	14	3	0	2	8	12	795	1335
16	15	0	0	10	0	15	525	860
16	16	0	0	25	0	0	0	1320
16	17	1	0	2	10	12	870	2000
16	18	0	0	0	0	25	1320	0
16	19	3	0	0	0	22	150	0
16	20	1	2	0	0	22	1435	0

16	21	0	0	0	0	25	1140	0
16	22	2	0	0	0	23	525	0
16	23	0	0	0	0	25	1315	0
16	24	0	0	0	4	21	1320	845
16	25	0	0	0	0	25	660	0
16	26	1	0	0	0	24	0	0
16	27	1	0	0	0	24	395	0
16	28	0	0	0	0	25	1320	0
16	29	0	0	0	0	25	0	0
16	30	0	0	0	0	25	0	0
16	31	0	0	0	0	25	1120	0
16	32	0	0	0	0	25	1255	0
17	1	1	0	0	1	23	1320	430
17	2	0	0	0	0	25	1320	0
17	3	0	0	0	0	25	660	0
17	4	1	0	0	0	24	925	0
17	5	0	0	7	12	6	265	1715
17	6	0	0	8	2	15	790	700
17	7	0	0	6	1	18	1500	1625
17	8	0	5	5	0	15	1140	1055
17	9	2	3	4	0	16	1300	1255
17	10	4	0	0	0	21	1520	0
17	11	1	0	7	0	17	1065	2110
17	12	0	1	0	0	24	1585	0
17	13	0	0	0	0	25	1320	0
17	14	0	0	0	0	25	1320	0
17	15	0	0	0	0	25	660	0
17	16	0	0	0	0	25	990	0
17	17	2	0	1	1	21	1405	395
17	18	1	0	14	3	7	1030	2375
17	19	1	0	0	0	24	1200	0
17	20	1	0	0	0	24	1440	0
17	21	1	0	2	0	22	355	865
17	22	4	0	0	0	21	0	0
17	23	0	0	0	0	25	1320	0
17	24	0	0	0	0	25	1470	0
17	25	2	0	0	0	23	910	0
17	26	0	0	0	0	25	660	0
17	27	1	0	0	0	24	515	0
17	28	0	0	0	0	25	1320	0
17	29	3	0	0	0	22	595	0
17	30	1	0	0	0	24	540	0
17	31	1	0	0	5	19	1045	665
17	32	0	0	5	18	2	0	1585
18	1	0	0	0	9	16	435	1310
18	2	0	0	0	25	0	0	260
18	3	0	0	2	16	7	0	905
18	4	0	0	7	4	14	740	1710
18	5	0	0	8	17	0	0	1320
18	6	0	0	15	10	0	0	660

18	7	0	0	14	9	2	0	935
18	8	0	0	13	0	12	1460	0
18	9	0	0	1	0	24	1610	0
18	10	0	0	5	0	20	420	790
18	11	0	0	5	10	10	0	1300
18	12	0	0	1	5	19	530	1590
18	13	0	0	0	1	24	540	150
18	14	0	0	0	0	25	660	0
18	15	0	0	0	0	25	680	0
18	16	0	0	0	0	25	1120	0
18	17	0	0	0	0	25	0	0
18	18	0	0	14	4	7	687	1480
18	19	0	0	0	0	25	1320	0
18	20	0	0	0	0	25	660	0
18	21	0	0	2	0	23	1095	1010
18	22	3	0	0	0	22	1650	0
18	23	6	0	0	0	19	1565	0
18	24	0	0	0	0	25	1225	0
18	25	0	0	2	0	23	140	725
18	26	0	0	0	0	25	660	0
18	27	0	0	0	0	25	660	0
18	28	0	0	0	0	25	1320	0
18	29	0	0	0	0	25	660	0
18	30	0	0	0	0	25	0	0
18	31	0	0	1	1	23	320	335
18	32	0	0	15	4	6	0	1155
19	1	0	0	0	10	15	1050	425
19	2	0	0	1	4	20	100	1400
19	3	0	0	2	20	3	0	550
19	4	0	0	3	0	22	0	660
19	5	0	0	0	0	25	0	0
19	6	0	0	0	0	25	660	0
19	7	0	0	18	0	7	1320	0
19	8	0	0	7	7	11	410	1290
19	9	0	0	10	5	10	0	2415
19	10	0	0	1	0	24	2075	380
19	11	0	0	0	0	25	660	0
19	12	0	0	1	12	12	235	1545
19	13	0	0	0	25	0	0	1345
19	14	0	0	0	25	0	0	660
19	15	0	0	0	18	7	0	1425
19	16	0	0	0	14	11	805	1377
19	17	0	0	6	0	19	390	645
19	18	0	0	18	0	7	530	1573
19	19	0	0	0	0	25	1690	0
19	20	0	0	0	0	25	1320	0
19	21	0	0	0	0	25	0	0
19	22	2	0	0	0	23	820	0
19	23	0	0	0	0	25	1755	0
19	24	0	0	0	0	25	1470	0

19	25	0	0	0	0	25	1335	0
19	26	0	0	0	0	25	335	0
19	27	0	0	0	0	25	0	0
19	28	0	7	0	0	18	756	0
19	29	0	4	0	0	21	230	0
19	30	0	0	0	0	25	340	0
19	31	0	0	0	0	25	0	0
19	32	0	0	0	4	21	720	0
20	1	2	0	0	5	18	515	924
20	2	0	0	3	3	19	1450	1715
20	3	0	0	0	16	9	525	1450
20	4	0	0	0	4	21	1585	790
20	5	0	0	0	0	25	1320	0
20	6	2	0	0	0	23	1320	0
20	7	0	0	13	4	8	1585	1275
20	8	0	0	2	23	0	0	0
20	9	1	0	6	0	18	1340	1505
20	10	1	0	1	0	23	2180	420
20	11	0	0	0	0	25	1320	0
20	12	2	0	0	7	16	580	1635
20	13	0	0	1	24	0	0	1320
20	14	0	0	0	25	0	0	1345
20	15	0	0	0	0	25	0	0
20	16	0	0	0	4	21	935	790
20	17	0	0	3	10	12	0	1505
20	18	0	0	8	17	0	0	660
20	19	0	0	0	0	25	980	0
20	20	0	7	0	0	18	1075	0
20	21	0	0	0	0	25	1335	0
20	22	2	0	0	0	23	2605	0
20	23	0	0	0	0	25	1740	0
20	24	0	0	0	0	25	1460	0
20	25	0	0	0	0	25	800	0
20	26	0	0	0	0	25	1160	0
20	27	0	0	0	0	25	0	0
20	28	0	3	2	17	3	0	1900
20	29	0	2	0	0	23	0	0
20	30	0	1	0	0	24	130	0
20	31	0	0	0	0	25	0	0
20	32	0	0	3	10	12	0	1360
21	1	1	0	0	0	24	0	0
21	2	2	0	0	0	23	0	0
21	3	0	0	0	0	25	905	0
21	4	0	0	0	1	24	0	520
21	5	0	0	0	25	0	0	1320
21	6	0	0	6	19	0	0	1190
21	7	2	0	15	7	1	190	1250
21	8	0	0	0	25	0	0	360
21	9	0	9	1	12	3	0	1375
21	10	0	0	0	1	24	1340	540

21	11	0	0	0	0	25	1740	0
21	12	6	0	0	0	19	2072	0
21	13	1	0	0	0	24	510	0
21	14	0	0	0	0	25	920	0
21	15	0	0	0	2	23	565	0
21	16	0	0	0	0	25	650	0
21	17	2	0	0	0	23	800	0
21	18	1	2	3	13	6	0	1295
21	19	0	3	2	20	0	0	1490
21	20	0	1	0	24	0	0	1320
21	21	0	0	0	2	23	550	0
21	22	2	0	0	0	23	1180	0
21	23	0	0	0	0	25	1115	0
21	24	0	0	4	0	21	0	590
21	25	0	0	20	4	1	0	310
21	26	0	0	4	16	5	115	925
21	27	0	0	0	6	19	0	2400
21	28	0	0	13	12	0	0	315
21	29	0	0	0	14	11	0	1480
21	30	0	0	0	25	0	0	660
21	31	0	0	0	25	0	0	660
21	32	0	0	0	25	0	0	0
22	1	0	0	0	9	16	395	790
22	2	0	0	0	0	25	0	0
22	3	0	4	0	1	20	0	390
22	4	0	0	1	4	20	0	890
22	5	0	0	1	20	4	0	410
22	6	0	0	13	4	8	280	1610
22	7	4	3	11	0	7	420	680
22	8	1	0	19	5	0	0	700
22	9	0	2	14	9	0	0	795
22	10	0	0	0	4	21	1225	745
22	11	0	0	0	0	25	1290	0
22	12	1	0	0	12	12	1200	925
22	13	0	0	0	20	5	660	660
22	14	0	0	1	3	21	1280	700
22	15	0	0	0	3	22	1045	580
22	16	1	0	0	0	24	1335	0
22	17	0	0	0	0	25	1320	0
22	18	2	0	1	0	22	1450	210
22	19	1	0	0	5	19	790	660
22	20	0	0	1	5	19	1460	790
22	21	0	0	0	7	18	1525	1135
22	22	1	0	10	0	14	1375	1445
22	23	0	0	2	1	22	1110	937
22	24	0	0	7	12	6	0	765
22	25	0	0	3	20	2	0	330
22	26	0	0	0	25	0	0	0
22	27	0	0	0	25	0	0	120
22	28	0	0	0	25	0	0	0

22	29	0	0	10	15	0	0	0
22	30	0	0	0	19	6	0	775
22	31	0	0	0	6	19	0	980
22	32	0	0	4	15	6	0	1390
23	1	0	0	0	3	22	530	485
23	2	0	0	0	0	25	130	0
23	3	0	1	0	0	24	650	0
23	4	0	0	13	0	12	330	980
23	5	0	0	6	16	3	0	540
23	6	0	0	0	10	15	480	1005
23	7	0	0	5	4	16	0	1465
23	8	0	0	6	2	17	1200	725
23	9	0	0	0	1	24	410	240
23	10	0	0	0	0	25	1255	0
23	11	0	0	0	0	25	900	0
23	12	1	0	5	5	14	850	630
23	13	0	6	2	17	0	0	0
23	14	0	0	2	18	5	0	585
23	15	0	0	4	7	14	0	1300
23	16	0	0	0	8	17	0	830
23	17	0	0	12	0	13	225	1720
23	18	0	0	0	0	25	660	0
23	19	0	0	0	2	23	0	370
23	20	0	0	2	8	15	895	1670
23	21	0	0	0	18	7	160	1573
23	22	0	0	5	1	19	1912	1260
23	23	0	0	0	3	22	1680	890
23	24	0	0	2	4	19	0	2165
23	25	0	0	0	5	20	0	1040
23	26	0	0	0	25	0	0	130
23	27	0	0	3	22	0	0	0
23	28	0	0	0	25	0	0	0
23	29	0	0	2	23	0	0	0
23	30	0	0	5	19	1	0	260
23	31	0	0	8	14	3	0	565
23	32	0	0	4	7	14	0	995
24	1	0	0	0	0	25	790	0
24	2	0	0	0	8	17	660	2112
24	3	0	0	0	0	25	660	0
24	4	0	0	0	0	25	1085	0
24	5	0	0	0	5	20	0	1115
24	6	0	0	13	8	4	0	750
24	7	0	0	0	0	25	890	0
24	8	1	0	0	0	24	2175	0
24	9	0	0	1	5	19	435	1485
24	10	0	0	0	11	14	345	995
24	11	0	0	0	2	23	1450	685
24	12	0	2	2	4	17	1290	660
24	13	0	0	3	16	6	0	580
24	14	0	0	4	21	0	0	0

24	15	0	0	5	20	0	0	0
24	16	0	0	0	16	9	0	925
24	17	0	0	0	1	24	750	555
24	18	1	0	0	0	24	1030	0
24	19	0	0	0	5	20	900	705
24	20	3	0	0	1	21	675	696
24	21	0	0	0	4	21	0	620
24	22	0	0	0	0	25	0	0
24	23	0	0	0	0	25	825	0
24	24	0	0	0	0	25	1000	0
24	25	0	0	0	5	20	0	1530
24	26	0	0	5	16	4	0	1015
24	27	0	0	0	25	0	0	0
24	28	0	0	0	25	0	0	0
24	29	0	5	0	20	0	0	732
24	30	0	1	5	19	0	0	365
24	31	0	0	12	13	0	0	0
24	32	0	0	4	3	18	0	855
25	1	1	0	0	1	23	660	180
25	2	0	0	0	3	22	660	1200
25	3	2	4	0	0	19	0	0
25	4	0	0	0	0	25	660	0
25	5	0	0	0	0	25	0	0
25	6	0	0	2	0	23	0	440
25	7	0	0	0	0	25	1064	0
25	8	1	0	6	0	18	810	930
25	9	0	0	3	9	13	870	1490
25	10	0	0	0	20	5	315	2220
25	11	0	0	0	0	25	1320	0
25	12	1	0	0	1	23	2285	645
25	13	0	0	0	2	23	1625	395
25	14	0	0	3	17	5	160	805
25	15	0	0	10	15	0	0	0
25	16	0	0	9	16	0	0	530
25	17	0	0	16	5	4	0	1355
25	18	0	0	12	5	8	0	930
25	19	0	0	3	22	0	0	660
25	20	0	0	5	0	20	580	710
25	21	0	0	0	7	18	145	752
25	22	0	0	1	6	18	660	700
25	23	0	0	0	3	22	660	970
25	24	0	0	0	0	25	1450	0
25	25	0	7	0	0	18	0	0
25	26	0	0	4	10	11	150	725
25	27	0	1	1	23	0	0	855
25	28	0	13	0	12	0	0	695
25	29	0	6	15	4	0	0	875
25	30	0	18	4	0	3	480	855
25	31	0	1	5	0	19	490	540
25	32	0	0	0	0	25	0	0

26	1	0	0	3	6	16	660	1320
26	2	2	0	0	0	23	1320	0
26	3	3	0	0	0	22	1685	0
26	4	0	0	0	0	25	1320	0
26	5	0	1	0	0	24	1320	0
26	6	0	0	0	4	21	1320	510
26	7	0	0	0	10	15	1300	710
26	8	0	0	0	3	22	800	0
26	9	0	0	0	2	23	625	890
26	10	0	0	4	16	5	305	1965
26	11	0	0	0	0	25	660	0
26	12	0	0	0	0	25	2245	0
26	13	0	4	5	0	16	1140	400
26	14	0	2	8	13	2	0	315
26	15	0	0	10	15	0	0	0
26	16	0	0	1	24	0	0	0
26	17	0	0	25	0	0	0	0
26	18	0	1	13	4	7	0	1170
26	19	0	0	15	8	2	0	445
26	20	1	0	5	4	15	765	1914
26	21	0	0	0	8	17	1145	755
26	22	0	0	1	8	16	620	1395
26	23	0	0	3	1	21	790	780
26	24	0	0	1	0	24	1245	325
26	25	0	7	0	1	17	705	610
26	26	0	0	0	3	22	0	595
26	27	0	4	0	0	21	775	0
26	28	0	18	0	0	7	820	0
26	29	0	10	3	0	12	1410	715
26	30	0	0	2	0	23	0	425
26	31	0	0	0	0	25	1170	0
26	32	5	0	0	0	20	1250	0
27	1	0	0	12	13	0	460	1210
27	2	0	0	0	1	24	1950	270
27	3	0	0	0	0	25	2110	0
27	4	0	0	0	0	25	2000	0
27	5	0	1	0	0	24	0	0
27	6	0	0	1	10	14	0	840
27	7	0	0	0	24	1	0	190
27	8	2	0	0	5	18	1300	530
27	9	3	0	1	0	21	1175	310
27	10	0	1	5	0	19	0	850
27	11	0	0	2	0	23	1320	565
27	12	0	0	0	0	25	1940	0
27	13	0	0	11	3	11	1170	1245
27	14	0	2	13	10	0	0	180
27	15	0	3	2	20	0	0	0
27	16	0	0	17	8	0	0	0
27	17	0	0	25	0	0	0	0
27	18	0	0	8	2	15	0	990

27	19	0	0	4	0	21	0	590
27	20	2	0	0	0	23	2110	0
27	21	0	0	0	1	24	1140	300
27	22	0	0	0	6	19	0	1710
27	23	0	0	0	0	25	0	0
27	24	0	0	0	0	25	0	0
27	25	0	0	0	0	25	1600	0
27	26	0	0	0	0	25	0	0
27	27	0	0	0	0	25	660	0
27	28	0	0	0	0	25	0	0
27	29	2	0	0	0	23	1510	0
27	30	4	0	0	0	21	1520	0
27	31	0	0	0	0	25	1510	0
27	32	0	0	0	0	25	980	0
28	1	0	0	1	13	11	130	1450
28	2	0	0	0	10	15	0	1000
28	3	0	0	0	0	25	0	0
28	4	0	0	0	0	25	840	0
28	5	0	0	0	0	25	0	0
28	6	0	0	0	17	8	0	700
28	7	0	0	0	11	14	0	720
28	8	0	5	0	1	19	1710	400
28	9	0	3	9	13	0	0	445
28	10	0	1	6	3	15	840	925
28	11	0	0	0	0	25	1375	0
28	12	0	0	10	0	15	1240	1215
28	13	0	0	12	0	13	0	2175
28	14	0	0	8	15	2	0	655
28	15	0	0	15	5	5	0	685
28	16	0	1	17	0	7	0	860
28	17	0	0	14	0	11	0	1665
28	18	0	1	9	8	7	0	1340
28	19	0	0	6	12	7	0	1055
28	20	1	6	4	0	14	1225	1205
28	21	0	0	0	0	25	0	0
28	22	0	0	0	20	5	0	1320
28	23	0	0	0	0	25	200	0
28	24	0	0	0	0	25	1500	0
28	25	2	4	0	0	19	495	0
28	26	0	0	0	0	25	1380	0
28	27	4	0	0	0	21	1805	0
28	28	5	0	0	0	20	1520	0
28	29	3	0	0	0	22	1790	0
28	30	0	0	0	0	25	660	0
28	31	0	0	0	0	25	750	0
28	32	0	0	0	0	25	1015	0
29	1	0	0	0	22	3	0	560
29	2	0	0	0	25	0	0	660
29	3	0	0	0	0	25	350	0
29	4	0	0	0	0	25	1705	0

29	5	0	0	0	0	25	0	0
29	6	0	0	0	8	17	265	860
29	7	0	0	0	7	18	130	655
29	8	0	0	0	0	25	1305	0
29	9	0	0	8	0	17	975	1320
29	10	0	0	0	0	25	885	0
29	11	0	0	0	0	25	660	0
29	12	1	0	0	0	24	1520	0
29	13	0	0	2	0	23	0	820
29	14	0	0	4	14	7	0	2390
29	15	2	0	2	2	19	0	665
29	16	0	0	1	9	15	410	1200
29	17	1	0	8	0	16	530	1275
29	18	0	0	17	6	2	0	645
29	19	0	0	8	1	16	0	920
29	20	0	0	0	0	25	2295	0
29	21	0	0	0	0	25	675	0
29	22	0	0	0	12	13	135	1320
29	23	0	0	0	0	25	1545	0
29	24	1	0	0	0	24	315	0
29	25	5	0	0	0	20	1610	0
29	26	5	0	0	0	20	575	0
29	27	1	0	0	0	24	660	0
29	28	0	0	0	0	25	0	0
29	29	0	0	0	0	25	1320	0
29	30	0	0	0	0	25	660	0
29	31	0	0	0	0	25	660	0
29	32	0	0	0	0	25	0	0
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30	2	0	0	21	4	0	0	0
30	3	0	0	19	0	6	120	1055
30	4	0	0	0	0	25	1320	0
30	5	0	0	0	0	25	660	0
30	6	0	0	0	0	25	795	0
30	7	0	0	0	0	25	805	0
30	8	1	0	0	0	24	670	0
30	9	0	0	0	0	25	720	0
30	10	0	0	1	0	24	1780	696
30	11	0	0	0	0	25	1320	0
30	12	1	0	0	0	24	2495	0
30	13	0	0	0	0	25	1320	0
30	14	0	0	0	0	25	1690	0
30	15	0	0	0	2	23	1110	365
30	16	0	0	2	18	5	0	2350
30	17	1	1	2	1	20	1425	610
30	18	5	0	7	3	10	410	540
30	19	1	0	7	3	14	805	1320
30	20	2	0	0	0	23	1305	0
30	21	0	0	0	0	25	700	0
30	22	4	0	0	0	21	750	0

30	23	5	0	0	5	15	830	675
30	24	5	0	3	10	7	300	755
30	25	0	0	4	11	10	290	780
30	26	0	0	0	4	21	225	1500
30	27	0	0	1	0	24	1005	280
30	28	0	0	3	0	22	660	930
30	29	0	0	0	0	25	1690	0
30	30	0	0	0	0	25	1040	0
30	31	0	0	0	0	25	1030	0
30	32	0	0	0	0	25	660	0
31	1	0	0	25	0	0	0	0
31	2	0	0	25	0	0	0	0
31	3	0	0	25	0	0	0	0
31	4	0	0	5	3	17	395	1300
31	5	0	0	3	4	18	660	725
31	6	0	0	0	0	25	500	0
31	7	0	0	0	0	25	660	0
31	8	2	0	0	0	23	1770	0
31	9	0	0	0	0	25	0	0
31	10	0	0	0	0	25	660	0
31	11	0	0	0	0	25	0	0
31	12	4	0	0	0	21	1070	0
31	13	5	0	0	0	20	695	0
31	14	5	0	0	0	20	1110	0
31	15	5	0	0	0	20	1350	0
31	16	5	0	0	9	11	160	1315
31	17	5	0	5	5	10	0	670
31	18	5	0	3	2	15	555	895
31	19	5	0	0	2	18	1440	370
31	20	5	0	0	10	10	560	780
31	21	5	0	0	3	17	0	1085
31	22	1	0	0	0	24	750	0
31	23	0	0	2	9	14	0	925
31	24	0	0	6	19	0	0	460
31	25	0	0	6	19	0	0	0
31	26	0	0	1	2	22	0	755
31	27	0	0	2	0	23	1305	1005
31	28	0	0	0	0	25	0	0
31	29	0	0	0	0	25	660	0
31	30	0	0	0	0	25	0	0
31	31	0	0	0	0	25	0	0
31	32	0	0	0	0	25	0	0
32	1	0	4	9	12	0	0	0
32	2	0	0	19	6	0	0	0
32	3	0	0	25	0	0	0	0
32	4	0	0	10	1	14	420	1355
32	5	0	0	4	7	14	460	1115
32	6	0	0	2	2	21	660	685
32	7	0	0	0	0	25	660	0
32	8	2	0	0	0	23	1780	0

32	9	3	0	0	5	17	0	875
32	10	5	0	0	5	15	0	0
32	11	5	0	0	0	20	0	0
32	12	3	0	0	0	22	1060	0
32	13	0	0	0	0	25	395	0
32	14	0	0	0	0	25	925	0
32	15	0	0	0	10	15	0	925
32	16	0	0	11	12	2	0	460
32	17	0	1	8	8	8	0	765
32	18	0	0	1	2	22	1360	1095
32	19	1	4	0	3	17	1650	855
32	20	0	0	0	20	5	0	1235
32	21	0	0	4	5	16	135	910
32	22	0	0	0	0	25	660	0
32	23	0	0	2	7	16	160	995
32	24	0	0	0	25	0	0	0
32	25	0	0	0	25	0	0	660
32	26	0	0	0	0	25	0	0
32	27	0	0	0	0	25	900	0
32	28	0	0	0	0	25	1395	0
32	29	0	0	0	0	25	1215	0
32	30	0	0	0	0	25	0	0
32	31	0	0	0	0	25	0	0
32	32	0	0	0	0	25	0	0
33	1	0	0	9	16	0	0	0
33	2	0	8	12	5	0	530	0
33	3	0	0	0	0	25	320	0
33	4	0	0	0	11	14	0	1225
33	5	0	0	8	0	17	1180	395
33	6	0	0	1	9	15	330	2265
33	7	0	0	1	0	24	435	440
33	8	5	0	0	0	20	1515	0
33	9	2	0	6	0	17	640	845
33	10	0	0	0	4	21	0	911
33	11	1	0	0	0	24	0	0
33	12	2	1	6	0	16	660	1122
33	13	0	0	2	0	23	0	575
33	14	0	0	1	0	24	0	565
33	15	0	0	0	17	8	0	757
33	16	0	0	17	5	3	0	860
33	17	0	2	8	0	15	700	1110
33	18	0	0	0	0	25	660	0
33	19	0	0	2	0	23	725	990
33	20	0	0	0	0	25	1255	0
33	21	0	0	4	0	21	0	1170
33	22	0	0	2	0	23	600	265
33	23	0	0	4	4	17	0	1035
33	24	0	0	0	25	0	0	0
33	25	0	0	0	25	0	0	355
33	26	0	0	0	10	15	0	660

33	27	0	0	6	5	14	0	750
33	28	1	0	3	5	16	690	1625
33	29	0	0	0	0	25	1440	0
33	30	0	0	0	0	25	0	0
33	31	0	0	0	0	25	0	0
33	32	0	0	0	0	25	0	0

APPENDIX D

FIELD MAPS

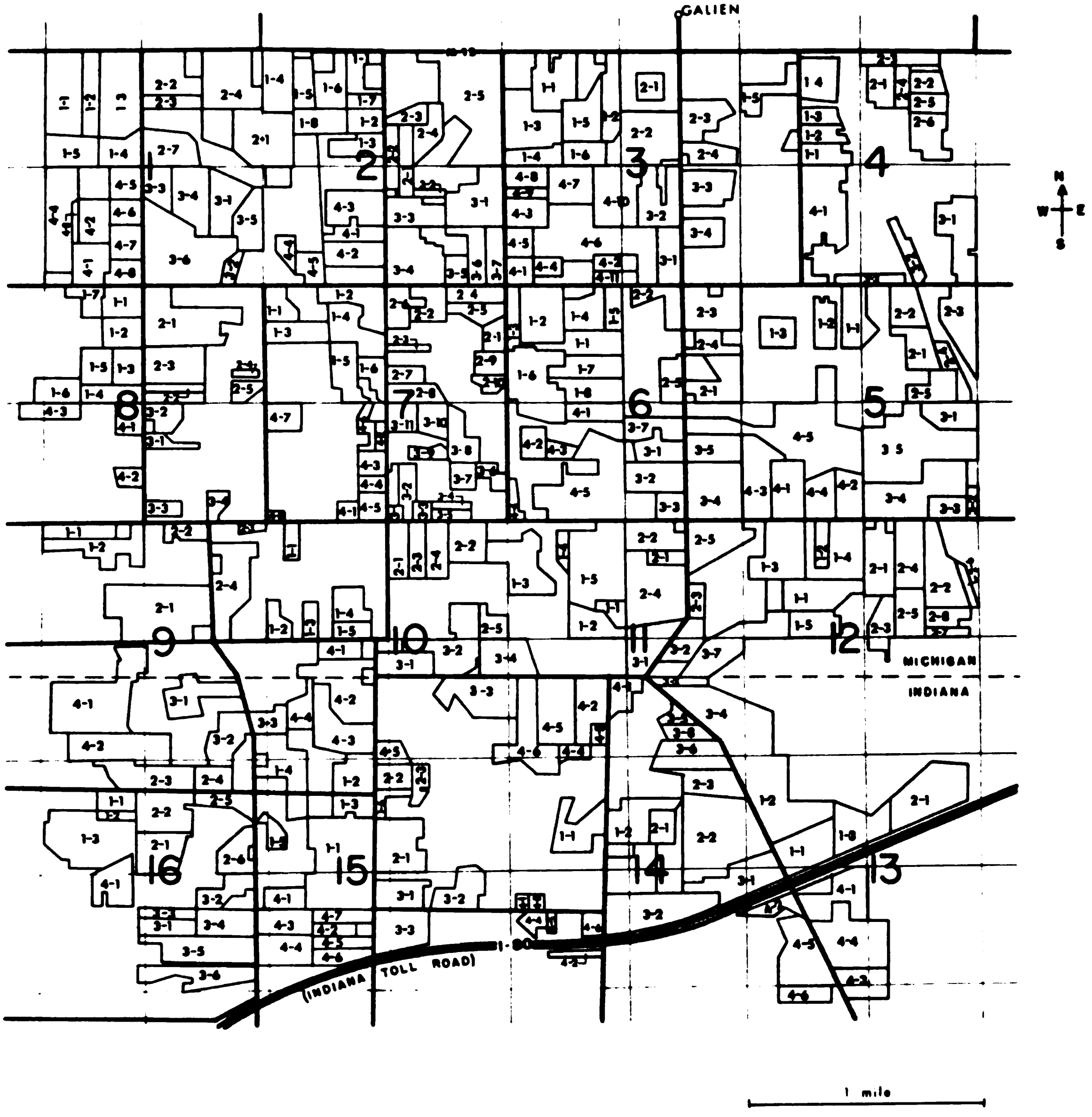


Fig. D1.--The Galien study area (from Logan 1977, p. A4-1).

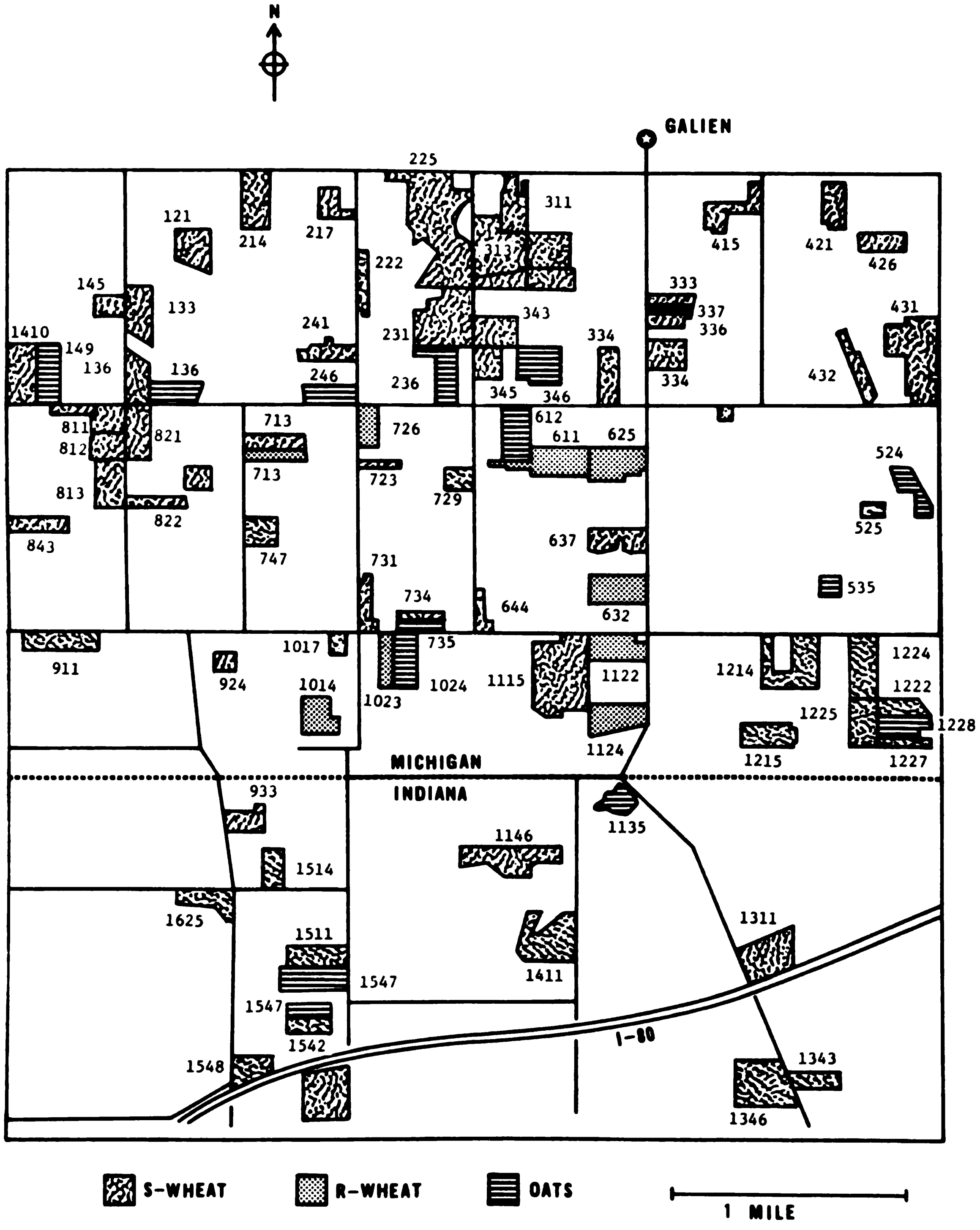


Fig. D2.--Small grain fields in 1976.

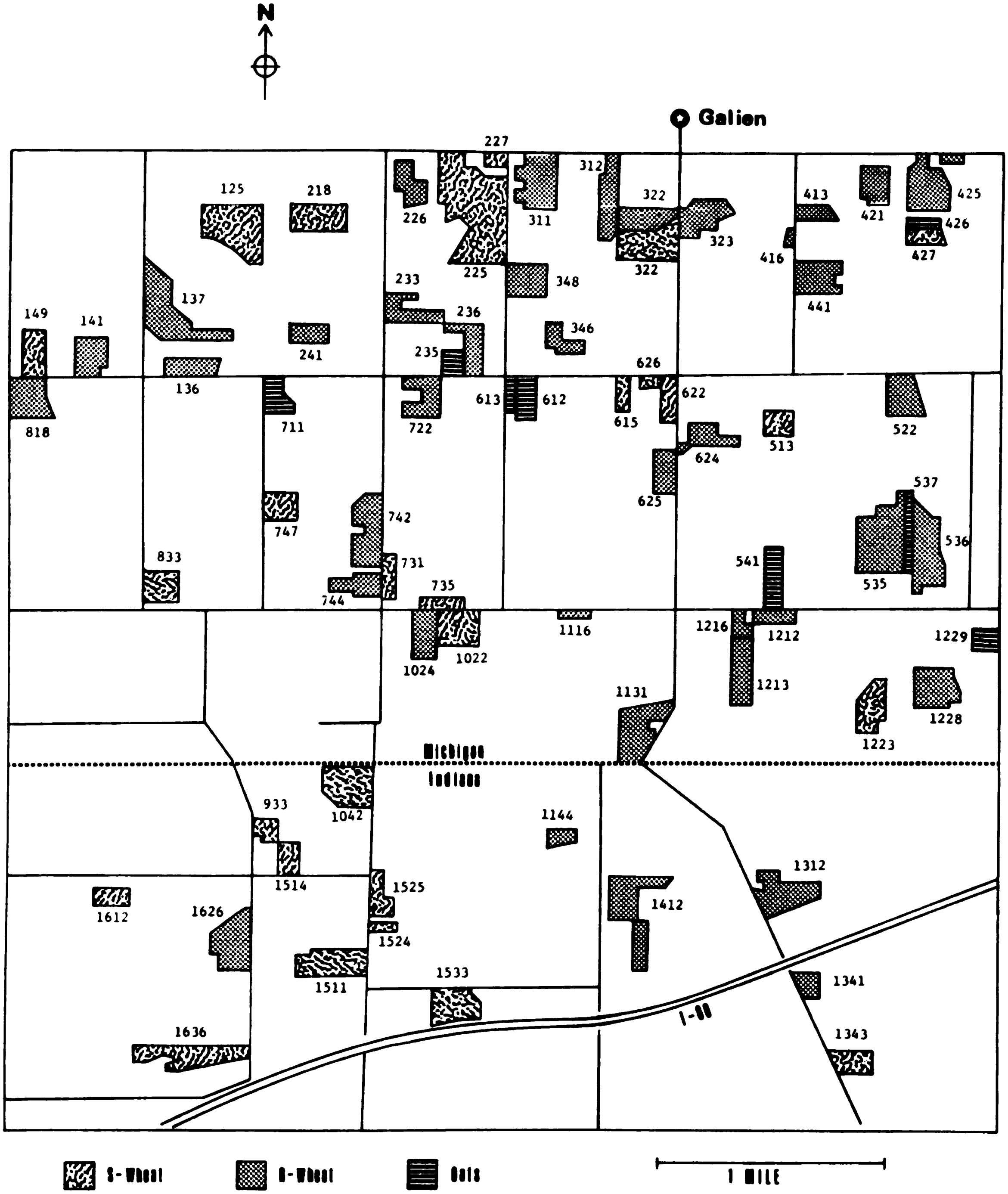


Fig. D3.--Small grain fields in 1977.

```
XXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXX
X        1     1  1              X
X        1  1  1111      1   1   X
X      1       11111           1 X
X            1  1111             X
X   11          1      1         X
X    1         111     3        1X
X1   1      1   3133   1      1 1X
X13  13     3   3               1X
X  111       2    3              X
X  111   11       32222          X
X   1  1        1                X
X   11                        1 3X
X 1      1           11          X
X                                X
X                    22          X
X            1 1 1               X
X  1    1   1 3    1122     1 1  X
X             3    11      11 1  X
X          2       1122       11 X
X          2               1  13 X
X                                X
X                                X
X       1             3          X
X                11              X
X        1                       X
X      1          1              X
X                 11       1     X
X         11              11     X
X         33                     X
X          3                     X
X                                X
X       11                       X
XXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXX
```

Fig. D4.--Digitized field map for 1976. Each numeral is a 10-acre cell. 1 = S-wheat, 2 = R-wheat, 3 = oats.

```
XXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXX
X              11 2 2          2 X
X            2 11 2 2        2 2 X
X      11 11   11    2122  2   3 X
X       1       1    11   2    1 X
X                22        22    X
X    2       23                  X
X    22   2       2              X
X1 2  23       32                X
X2       3    2  3   11       2  X
X                         1   2  X
X                      2         X
X                     2          X
X        1  2                 2  X
X           2                232 X
X                            222 X
X    1      21 1          3      X
X             21   2     22      X
X              1         2       X
X                        2     2 X
X                    2       1 2 X
X                    2           X
X          1                     X
X          1                     X
X        1         2             X
X        1                       X
X  1                 2    2      X
X           1        2    2      X
X      22   1        2           X
X         11                     X
X                          2     X
X              1                 X
X     11                    1    X
XXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXX
```

Fig. D5.—Digitized field map for 1977. Each numeral is a 10-acre cell. 1 = S-wheat, 2 = R-wheat, 3 = oats.

```
XXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXX
X                                X
X                         5 5    X
X                        56  65 5X
X      6  6   7     6    6   66  X
X  5    6 5    6         55  6666X
X        65             566  666 X
X                        66  5 6 X
X       6          6      6    5 X
X 5                              X
X 6        5  66                 X
X       7     55         5    6  X
X              6                 X
X  7    5  6    5           66   X
X 66   55 66 6  5          6     X
X 66  55 55   6  6               X
X     55  5     5                X
X    6            5             6X
X 66 6555         5             5X
X  6   5     6666 5              X
X  6   56    66   6         6    X
X    66566        666    56 56666X
X    65555   6          6666666 6X
X   56       66      6    666666 X
X     5      6666         666666 X
X         6   666556       6757  X
X         6   666555        7    X
X6     6      5655               X
X6    6  6    655556  6          X
X66           6   5              X
X555            6       66       X
X555                    66       X
X655            6   6   66       X
XXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXX
```

Fig. D6.--Digitized map of woodlots and water at Galien. 5 = sparse woods, 6 = dense woods, 7 = water.

APPENDIX E

PROGRAM SEARCH

```
      PROGRAM SEARCH(TAPE1,TAPE2,TAPE3,TAPE4,OUTPUT)
C
C PROGRAM SEARCH SEARCHES AROUND FIELDS IN A CIRCULAR PATTERN
C AT 4 FIXED RADII AND REPORTS THE ACRES OF EACH OF 8 CATEGORIES
C OF HABITAT FOR EACH QUADRANT OF THESE CIRCLES.  TAPE1 CONTAINS
C THE ROW BY COLUMN GRID-CODED ACREAGES FOR 5 HABITATS (GRID
C CELLS ARE 10 ACRES TOTAL) OBTAINED FROM INTERPRETTING AN AERIAL
C PHOTO OF THE 4.125 (N-S) BY 4 (E-W) MILE PUBESCENT WHEAT STUDY AREA IN
C BERRIEN COUNTY SOUTH OF GALIEN.  TAPE2 CONTAINS INFO IDENTIFYING
C THE SHAPE, SIZE AND LOCATION OF FIELDS TO BE SEARCHED AROUND.
C TAPE3 CONTAINS ACRES OF SMALL GRAINS IN CELLS WITH GRAIN FIELDS
C SMALL GRAIN ACREAGE MAY EXCEED 10 ACRES PER CELL, SINCE GRAIN
C FIELDS WERE ASSIGNED EVENLY TO N/10 CELLS, WHERE N IS THE
C FIELD ACREAGE ROUNDED TO THE NEAREST 10 ACRES.  THUS A 14
C ACRE FIELD WOULD BE ASSIGNED TO ONE 10-ACRE CELL, AND THAT CELL
C WOULD HAVE 14 ACRES OF GRAIN RECORDED FOR IT.
C TAPE4 IS OUTPUT, GIVING THE ACREAGE OF EACH HABITAT IN EACH QUADRANT
C OF 4 "CIRCLES" OF RADII .125, .250, .375 AND .500 MILE FROM
C FIELD BOUNDARY.
C CATEGORY (HABITAT) CODES:
C 1= EDGE OF WOODS (20 FT INTO WOODS)
C 2= SPARSE WOODS (75 PCT OR LESS CANOPY CLOSURE), SHRUBBY AREAS
C 3= TREE LINES, FENCE ROWS
C 4= CROPLAND (INCLUDING SMALL GRAINS)
C 5= DENSE WOODS
C 6= SUSCEPTIBLE WHEAT
C 7= RESISTANT WHEAT
C 8= OATS
C
      DIMENSION A(33,32,8),FACTOR(5,4),CAT(9),IXL(4),IXU(4),IYL(4),
     +IYU(4)
      INTEGER XMIN,XMAX,YMIN,YMAX,CODE
      LOGICAL IPART
C NOTES WHETHER OR NOT QUASDRANT IS ONLY PARTIALLY
C WITHIN GRID BOUNDARIES.
      DATA FACTOR/1.0,.938,.950,.917,.920,
     +            1.0,.938,.947,.909,.933,
     +            1.0,.967,.971,.947,.961,
     +            1.0,.966,.969,.944,.963/
C FACTOR TO CORRECT TOTAL ACREAGE FOR ODD CORNERS WHICH MUST BE
C REMOVED TO ACCOUNT FOR FIELD SHAPE (WITHOUT REGARD TO SPECIFIC
C LOCATION OF THESE CELLS).  FACTOR(CODE,IR) IS REDUCTION FACTOR
C FOR FIELD WITH SHAPE GIVEN BY CODE AND SEARCH RADIUS IR.
C CODES:  1=RECTANGULAR (ANY NO. CELLS)
C         2=L-SHAPED, 3 CELLS
C         3=SHAPE OF FIELD 5-3-5 IN 1977
C         4=SHAPE OF FIELD 2-2-5 IN 1977
C         5=SHAPE OF FIELD 3-1-3 IN 1976
C SHAPES 2,3,4 REQUIRE DROPPING ADDITIONAL CELLS FROM SEARCH PATTERN
      READ(1,101)(((A(I,J,K),K=1,5),J=1,32),I=1,33)
```

```
C STORE GRID
      DO 60 I=1,33
      DO 60 J=1,32
      DO 60 K=6,8
60    A(I,J,K)=0.0
      NGC=0
61    READ(3,105)ICROP,IROW,ICOL,ACRES
      IF(EOF(3))63,62
62    ICAT=ICROP+5
      NGC=NGC+1
      A(IROW,ICOL,ICAT)=ACRES
      GO TO 61
63    PRINT 106,NGC
      NR=0
1     READ(2,102)IC,IF,ACRES,CODE,XMIN,XMAX,YMIN,YMAX
C READ DATA FOR ONE FIELD TO BE SEARCHED AROUND
      IF(EOF(2))50,2
2     IF(CODE.NE.0)GO TO 3
      CODE=1
      YMIN=XMAX
      YMAX=XMAX
      XMAX=XMIN
C FOR SINGLE-CELLED FIELD, READ ONLY X,Y
3     CFACT=1
      NR=NR+1
      XMID=FLOAT(XMIN+XMAX)/2.
      YMID=FLOAT(YMIN+YMAX)/2.
C LOCATE MIDDLE OF FIELD EXTREMES
      IXU(1)=XMID
      IXU(3)=XMID
      IXL(2)=XMID+.5001
      IXL(4)=XMID+.5001
      IYU(1)=YMID
      IYU(2)=YMID
      IYL(3)=YMID+.5001
      IYL(4)=YMID+.5001
C FIND INNER EXTREMES FOR EACH QUAD OF SEARCH PATTERN
      DO 4 IR=1,4
C LOOP OVER RADII
      IXU(2)=XMAX+IR
      IXU(4)=XMAX+IR
      IXL(1)=XMIN-IR
      IXL(3)=XMIN-IR
      IYU(3)=YMAX+IR
      IYU(4)=YMAX+IR
      IYL(1)=YMIN-IR
      IYL(2)=YMIN-IR
C FIND OUTER EXTREMES FOR EACH QUAD OF SEARCH PATTERN
      DO 45 IQ=1,4
C LOOP OVER QUADRANTS 1=NW, 2=NE, 3=SW, 4=SE
```

```
      WHOLE=FLOAT((XMAX-XMIN+1+2*IR)*(YMAX-YMIN+1+2*IR)*10)/4.
C CALCULATE ACREAGE OF WHOLE QUAD (INCLUDING CORNERS)
      IPART=.F.
      IF(IXL(IQ).GE.1)GO TO 5
      IXL(IQ)=1
      IPART=.T.
C PREVENT SEARCH FROM FALLING OUTSIDE GRID, AND NOTE PARTIAL QUAD
5     IF(IXU(IQ).LE.32)GO TO 6
      IXU(IQ)=32
      IPART=.T.
6     IF(IYL(IQ).GE.1)GO TO 7
      IYL(IQ)=1
      IPART=.T.
7     IF(IYU(IQ).LE.33)GO TO 8
      IYU(IQ)=33
      IPART=.T.
8     DO 9 ICAT=1,9
9     CAT(ICAT)=0.0
C ZERO TOTAL ACREAGE
      IRL=IYL(IQ)
      IRU=IYU(IQ)
      ICL=IXL(IQ)
      ICU=IXU(IQ)
C SET DO-LOOP PARAM FOR QUAD SEARCH
      DO 10 IROW=IRL,IRU
      R=1.0
      IF(ABS((FLOAT(IROW)-YMID)).LT.0.001)R=0.5
C IF CELL LIES ON MID-LINE, COUNT HALF IN EACH QUAD
      DO 11 ICOL=ICL,ICU
      C=1.0
      IF(ABS((FLOAT(ICOL)-XMID)).LT.0.001)C=0.5
      CAT(9)=CAT(9)+10.*R*C
C SUM UP TOTAL ACRES IN SEARCHED QUAD
      DO 12 ICAT=1,8
12    CAT(ICAT)=CAT(ICAT)+A(IROW,ICOL,ICAT)*R*C
C SUM UP CATEGORY TOTALS IN QUAD
11    CONTINUE
10    CONTINUE
      PART=1.
      IF(IPART)13,15
13    PART=CAT(9)/WHOLE
C CALCULATE PROPORTION OF QUAD LYING WITHIN GRID BOUNDARIES
      DO 14 ICAT=1,8
14    CAT(ICAT)=CAT(ICAT)/PART
C UPWARDLY ADJUST CAT TOTALS FOR PART OUSIDE GRID (ASSUME SAME
C HABITAT PROPORTIONS OUTSIDE AS IN).
15    GO TO (40,16,16,27)IR
C DIFFERENT RADII REQUIRE DIFFERENT CORNER ADJUSTMENTS
16    IF(IPART)22,17
17    CFACT=1.0
```

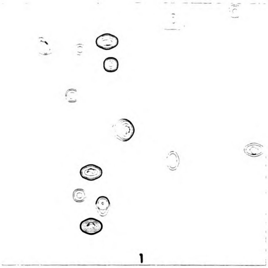
```
      GO TO (18,19,20,21)IQ
 18   IYO=IYL(IQ)
      IXO=IXL(IQ)
C LOCATE 1 CORNER CELL TO BE REMOVED (FOR .250 AND .375
C MILE RADII) TO CREATE ROUND (CIRCULAR) PATTERN
      GO TO 23
 19   IYO=IYL(IQ)
      IXO=IXU(IQ)
      GO TO 23
 20   IYO=IYU(IQ)
      IXO=IXL(IQ)
      GO TO 23
 21   IYO=IYU(IQ)
      IXO=IXU(IQ)
      GO TO 23
 22   CFACT=(WHOLE-10.)/WHOLE
C CFACT WILL REDUCE ACREAGE BY 1 CELL FOR QUAD WHOSE CORNER
C FALLS OUTSIDE GRID AND CANNOT THEREFORE BY SUBTRACTED DIRECTLY
 23   WHOLE=WHOLE-10.
      IF(IPART)40,24
 24   DO 25 ICAT=1,8
 25   CAT(ICAT)=CAT(ICAT)-A(IYO,IXO,ICAT)
C REMOVE CORNER
      GO TO 40
 27   IF(IPART)33,28
 28   CFACT=1.0
      GO TO (29,30,31,32)IQ
 29   IYO1=IYL(IQ)
      IYO2=IYL(IQ)
      IYO3=IYL(IQ)+1
      IXO1=IXL(IQ)
      IXO2=IXL(IQ)+1
      IXO3=IXL(IQ)
C FIND 3 CORNER CELLS TO REMOVE FOR .500 MILE RADIUS
      GO TO 34
 30   IYO1=IYL(IQ)
      IYO2=IYL(IQ)
      IYO3=IYL(IQ)+1
      IXO1=IXU(IQ)
      IXO2=IXU(IQ)-1
      IXO3=IXU(IQ)
      GO TO 34
 31   IYO1=IYU(IQ)
      IYO2=IYU(IQ)-1
      IYO3=IYU(IQ)
      IXO1=IXL(IQ)
      IXO2=IXL(IQ)
      IXO3=IXL(IQ)+1
      GO TO 34
 32   IYO1=IYU(IQ)
```

```
      IYO2=IYU(IQ)
      IYO3=IYU(IQ)-1
      IXO1=IXU(IQ)
      IXO2=IXU(IQ)-1
      IXO3=IXU(IQ)
      GO TO 34
33    CFACT=(WHOLE-30.)/WHOLE
C CFACT WILL REDUCE ACREAGE BY 3 CELLS FOR QUAD WHOSE CORNER
C FALLS OUTSIDE GRID
34    WHOLE=WHOLE-30.
      IF(IPART)40,37
37    DO 35 ICAT=1,8
35    CAT(ICAT)=CAT(ICAT)-A(IYO1,IXO1,ICAT)-A(IYO2,IXO2,ICAT)
     +-A(IYO3,IXO3,ICAT)
C REMOVE CORNER
40    SCAT=0.0
      DO 36 ICAT=1,8
      CAT(ICAT)=CAT(ICAT)*CFACT*FACTOR(CODE,IR)
C REDUCE ACREAGE BY CFACT FOR CORNER REMOVED (TO CREATE ROUND
C PATTERN) FOR THOSE QUADS WHOSE CORNERS WERE OUTSIDE GRID EDGES
C AND BY FACTOR FOR ODD-SHAPE OF SOME FIELDS WHICH
C REQUIRES DROPPING ADDITIONAL ACREAGE FROM SEARCH.
      IF(ICAT.GT.5)GO TO 36
      SCAT=SCAT+CAT(ICAT)
C SUM OF 5 CATEGORIES
36    CONTINUE
      AREA=WHOLE*FACTOR(CODE,IR)
C CALCULATE EXPECTED TOTAL ACREAGE TO COMPARE WITH SCAT
      WRITE(4,103)IC,IF,CODE,ACRES,IR,IQ,PART,(CAT(JJ),JJ=1,8),
     +SCAT,AREA
45    CONTINUE
4     CONTINUE
      GO TO 1
50    PRINT 104,NR
      STOP
101   FORMAT(9X,5F7.3)
102   FORMAT(2I5,F5.1,5I3)
103   FORMAT(I2,I5,I2,F5.1,2I2,F6.3,10F8.3)
104   FORMAT(I6* LINES READ FROM TAPE2*)
105   FORMAT(I5,5X,2I5,F7.3)
106   FORMAT(I6* LINES READ FROM TAPE3*)
      END
```

APPENDIX F

CONTOUR PLOTS

Adult densities at Galien
plotted daily from 11 April 1977



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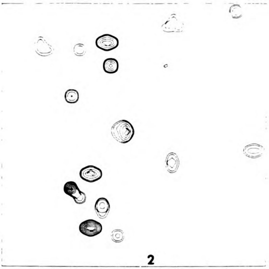

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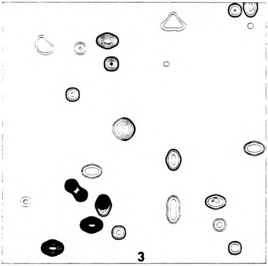

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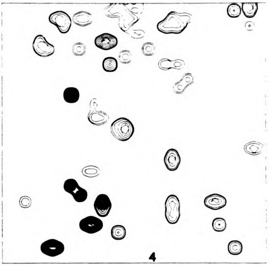

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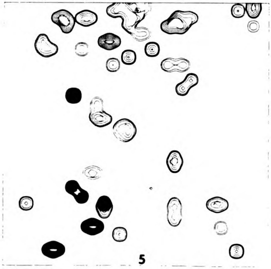

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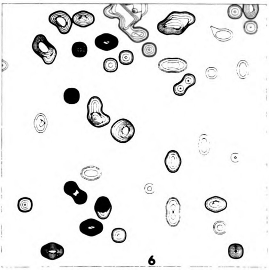

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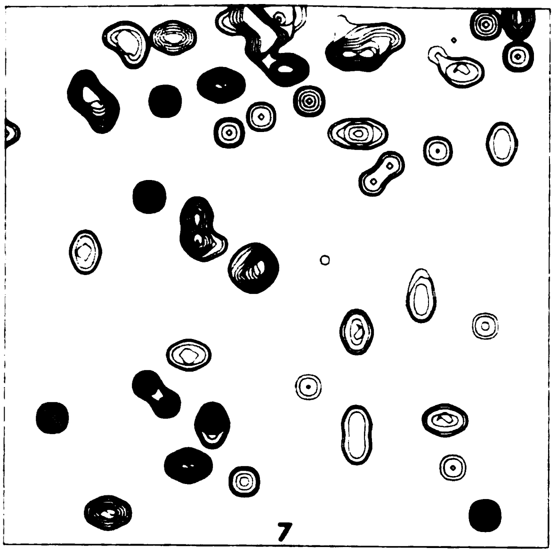
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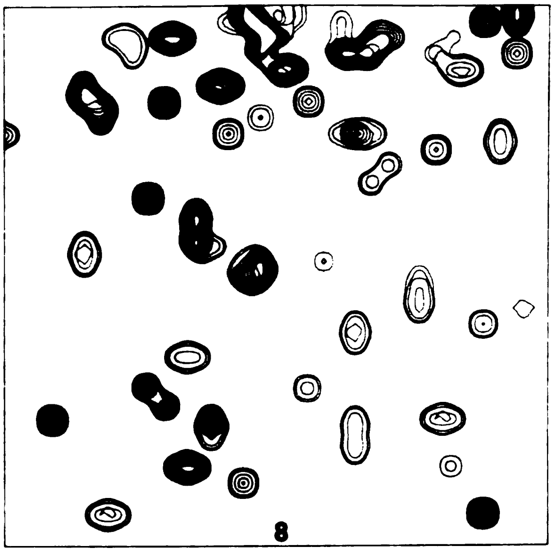
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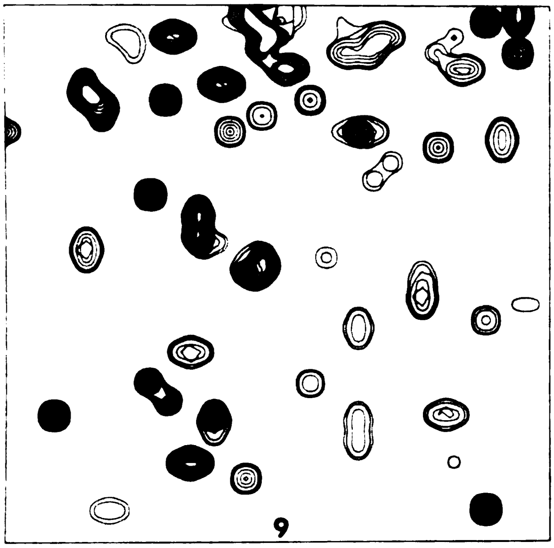
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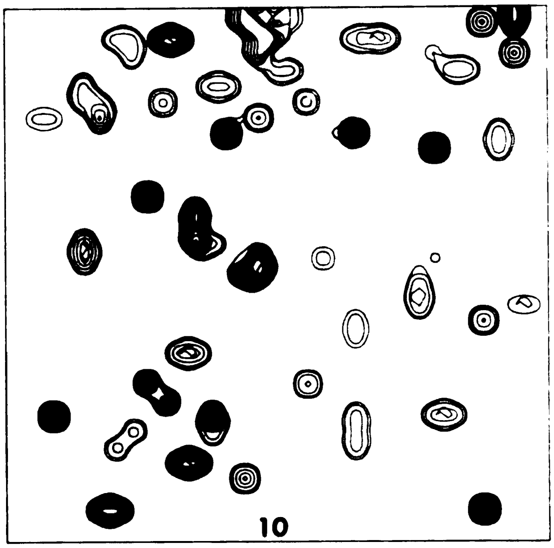
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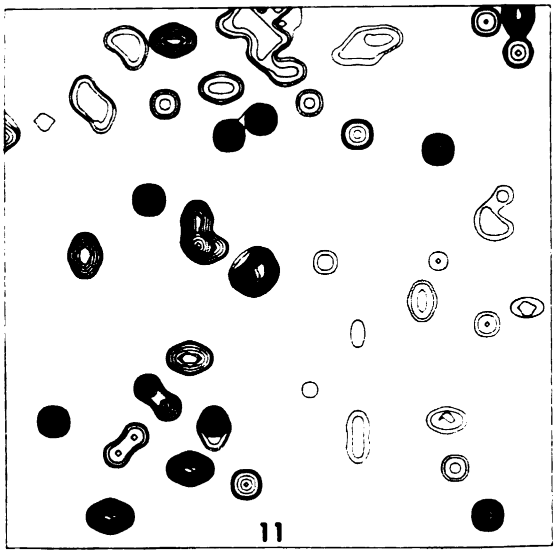
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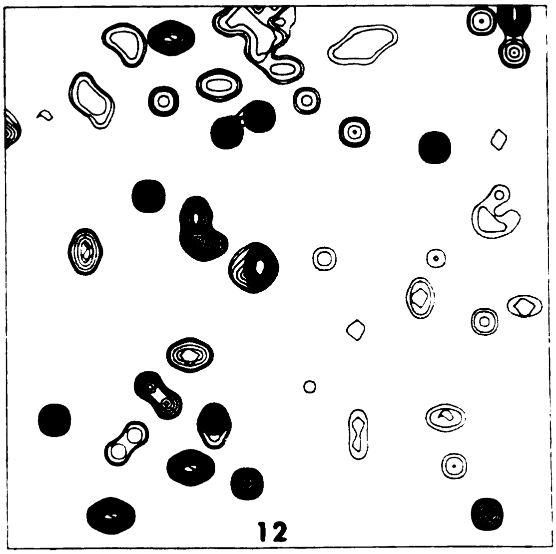
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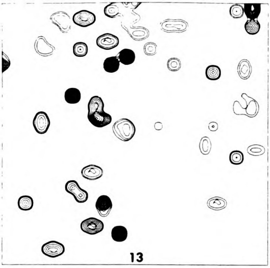
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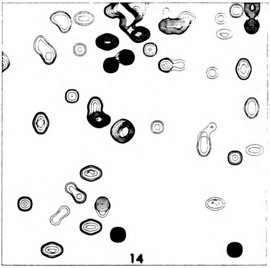
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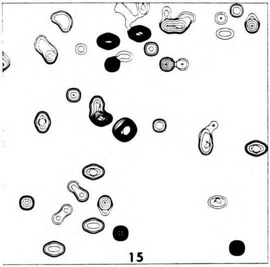
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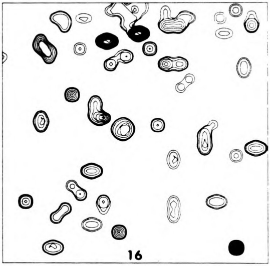
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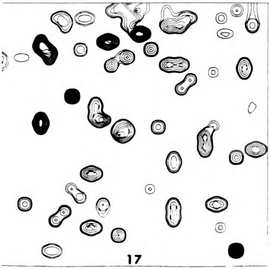
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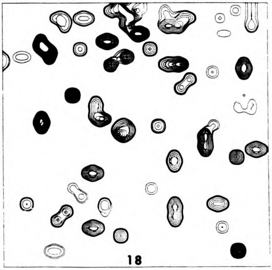
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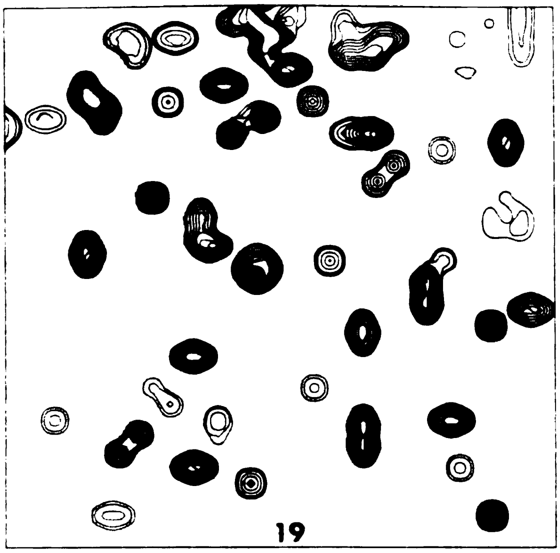
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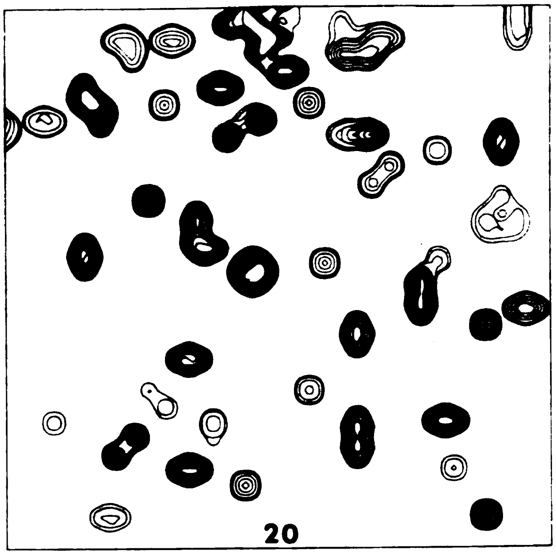
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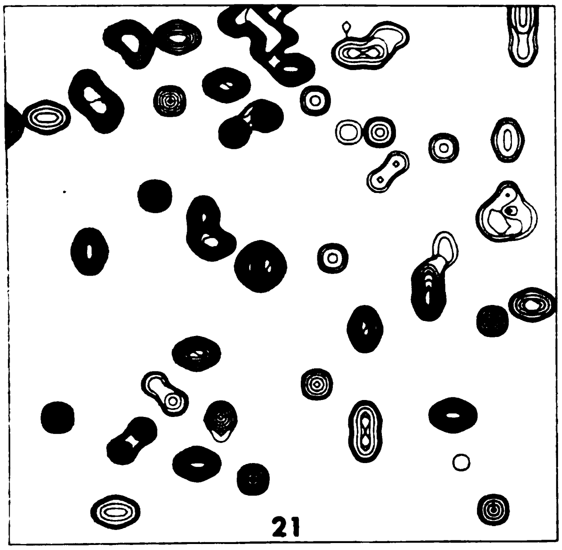
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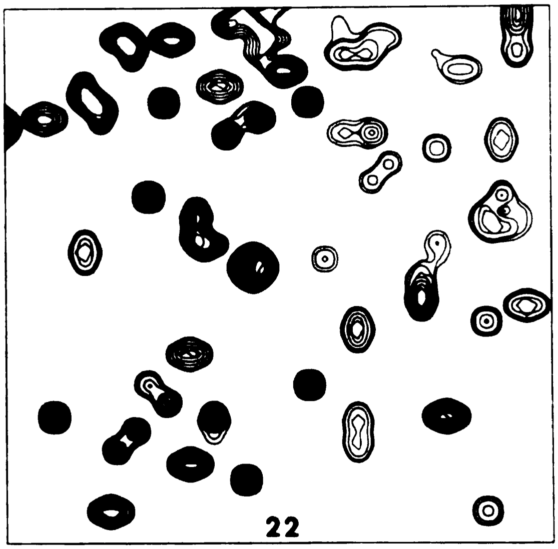
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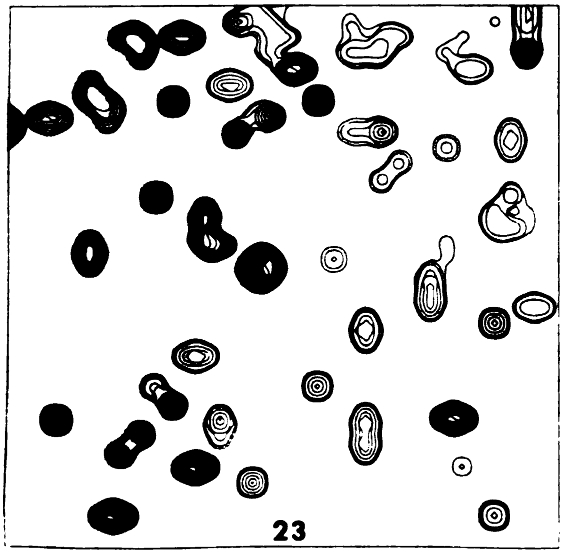
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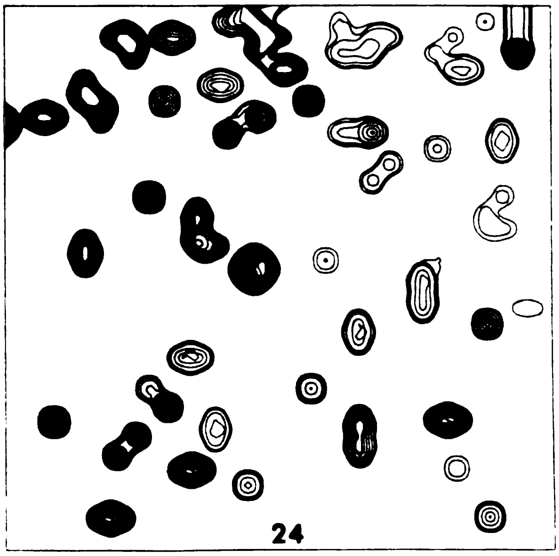
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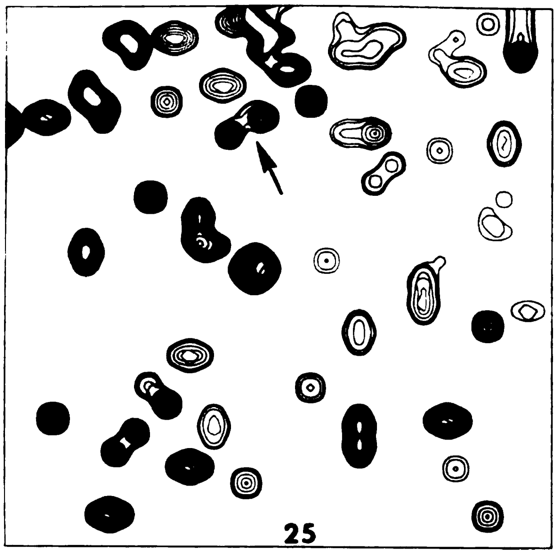

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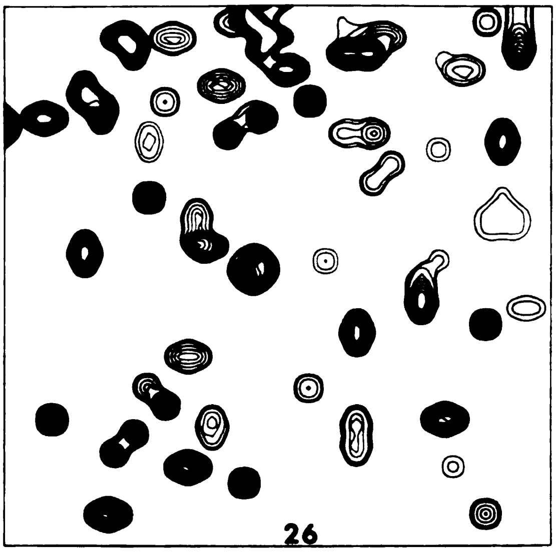

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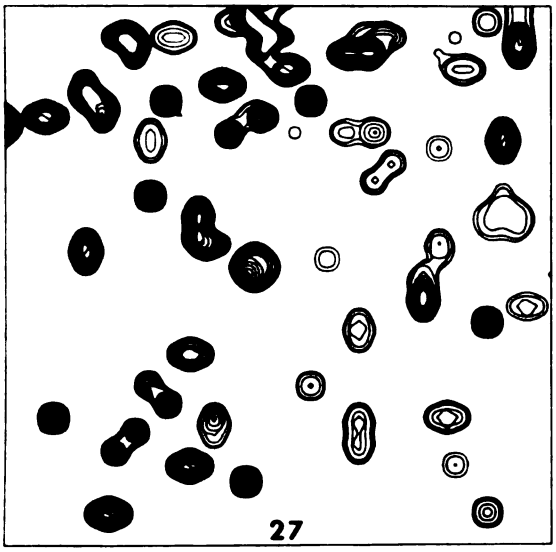

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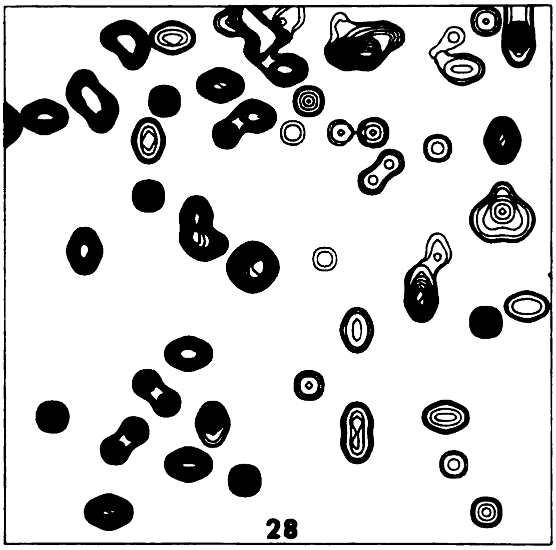

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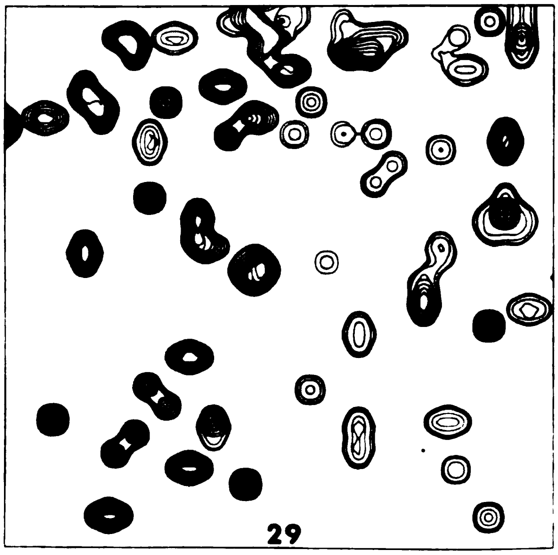

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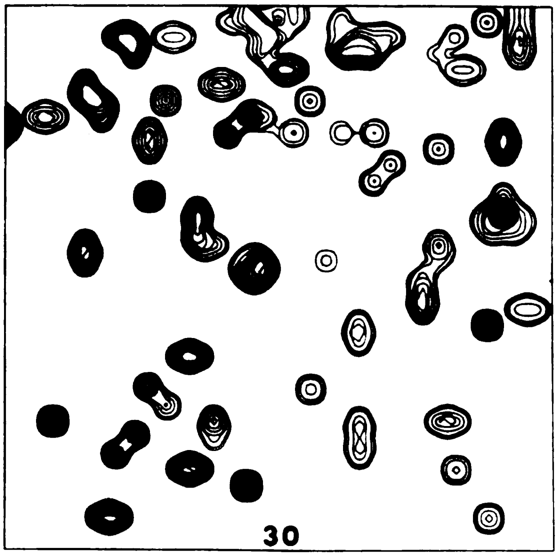

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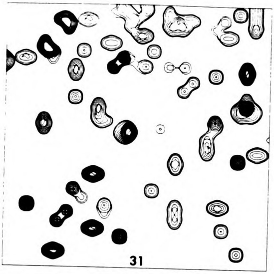
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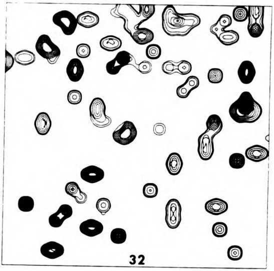
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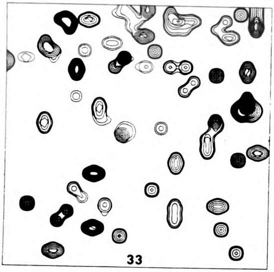
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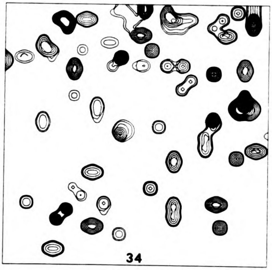
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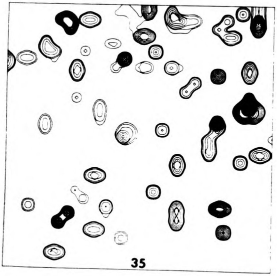
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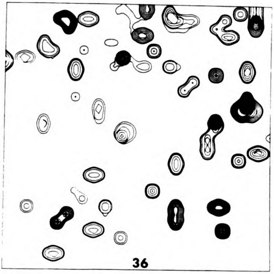
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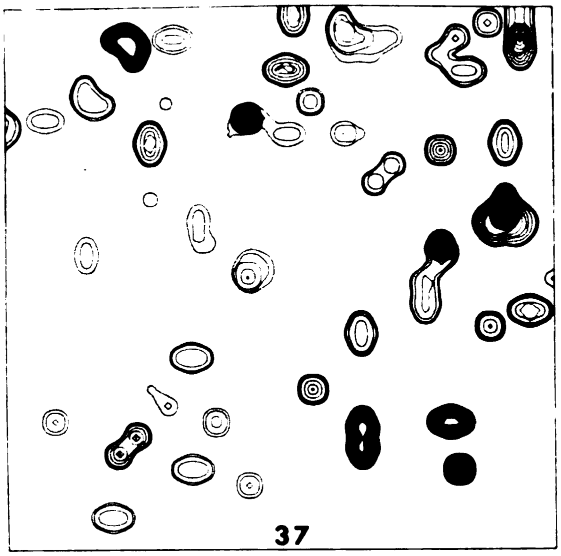
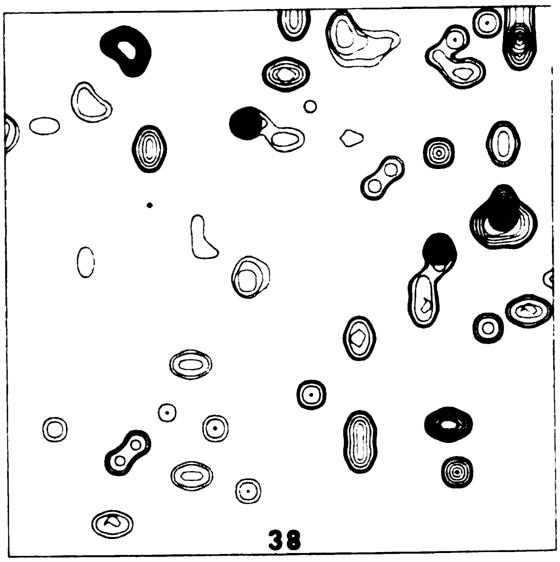


37



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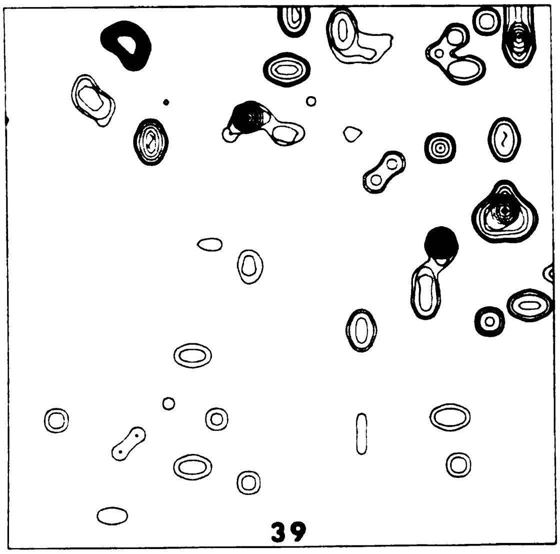

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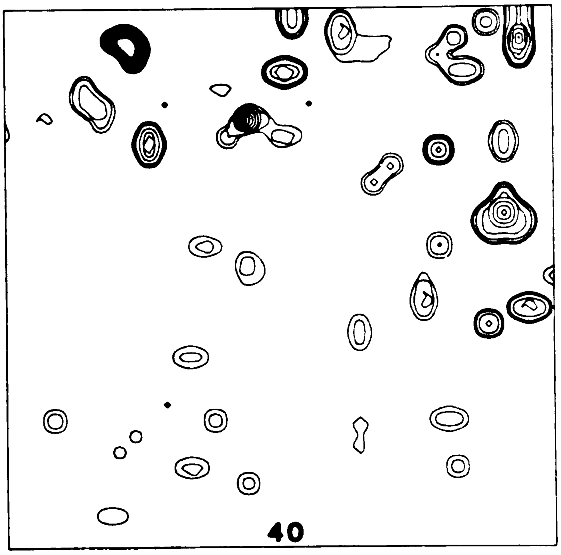

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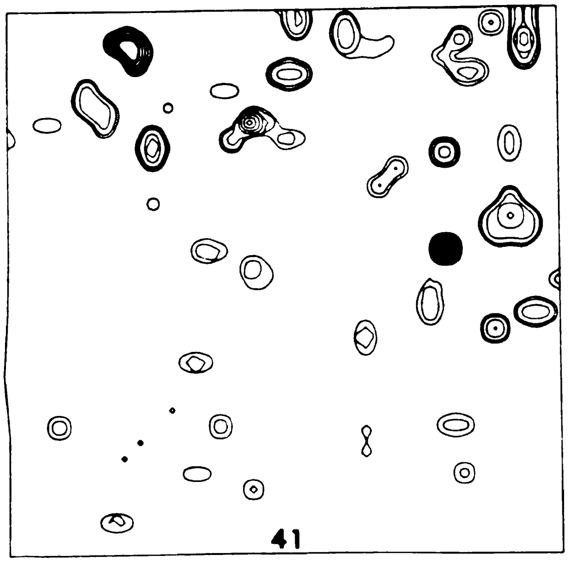

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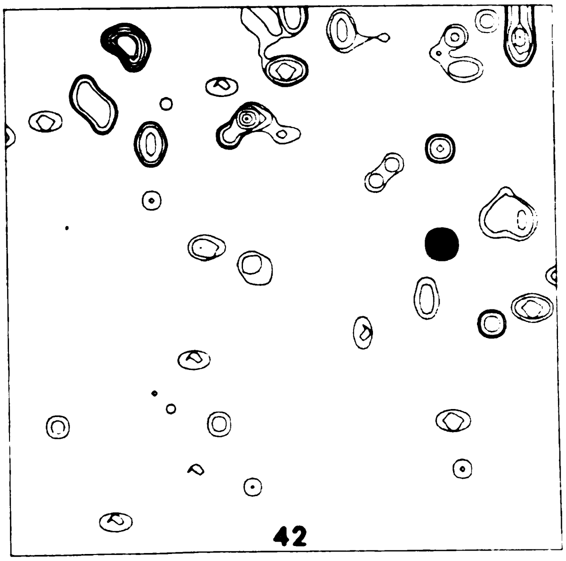

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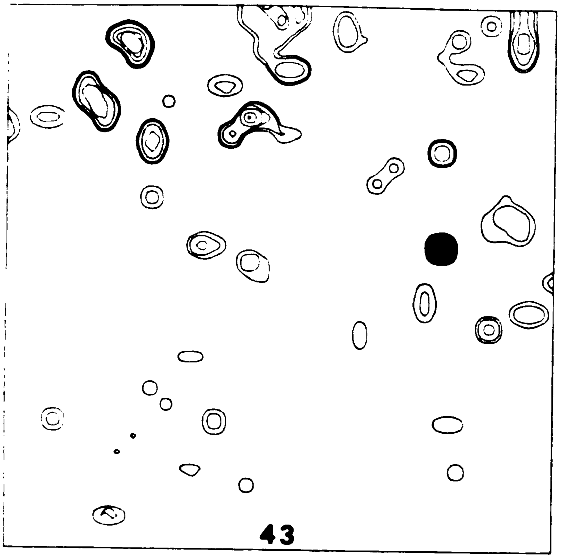
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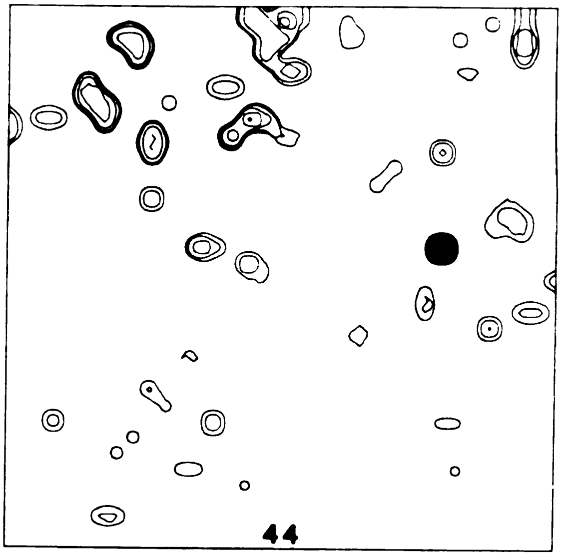
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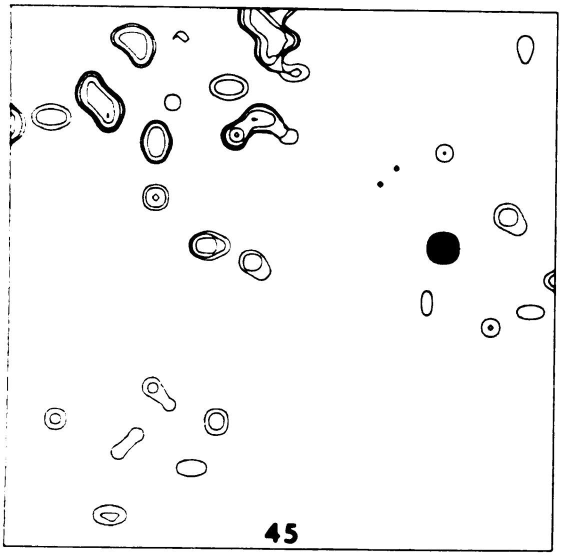
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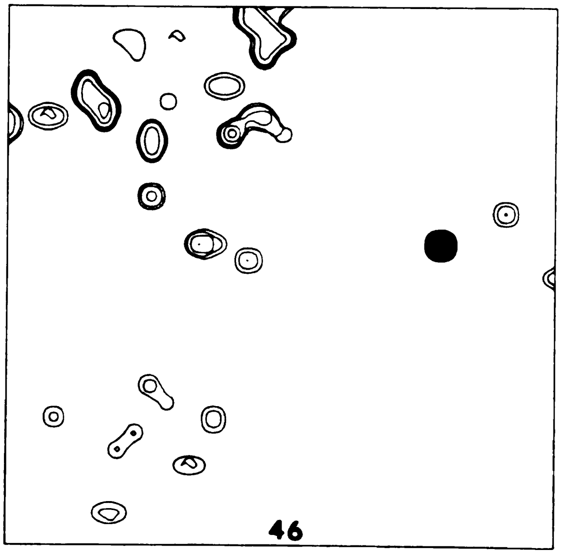
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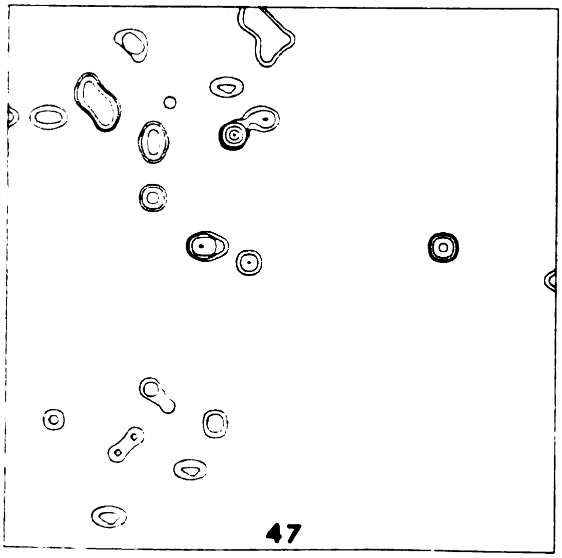
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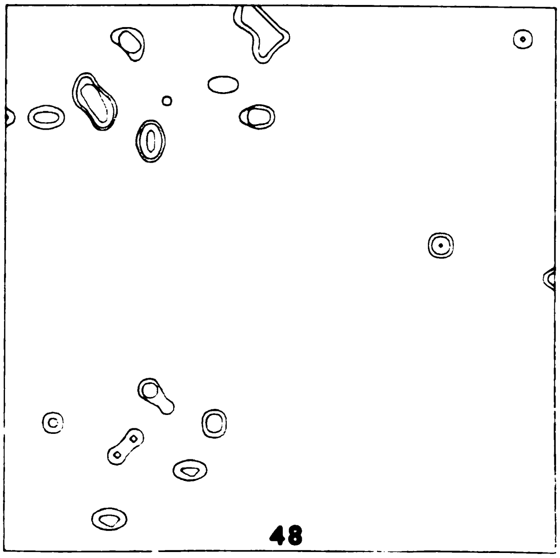
48

APPENDIX G

STICKY BOARD TRAP DATA

Table G1. Catch by date of incoming and outgoing cereal leaf beetles on sticky board traps placed along each border of six fields at Galien in 1977 (each entry is sum for 4 traps).

Date	North		East		South		West	
	In	Out	In	Out	In	Out	In	Out
S-wheat 1022								
4/20	0	0	0	0	0	0	0	0
4/21	11	9	0	0	0	0	0	0
4/22	3	9	0	0	0	0	0	0
4/26	2	1	0	0	0	0	0	0
4/27	2	1	0	0	0	0	0	0
4/29	0	0	0	0	0	0	0	0
5/03	1	1	1	0	0	0	0	0
5/05	1	1	0	3	0	0	0	0
5/09	4	14	11	3	0	0	0	1
5/12	3	21	3	8	13	13	0	0
5/18	197	127	59	37	31	39	7	15
5/20	19	77	19	40	21	34	0	1
5/24	23	20	20	16	3	15	9	24
5/27	15	8	1	0	0	0	0	0
6/01	9	1	3	0	4	8	0	0
6/08	5	6	3	3	1	4	0	1
6/13	9	1	0	5	0	2	0	0
6/14	0	3	0	1	0	1	0	0
6/16	101	323	10	52	10	38	6	41
6/21	302	485	9	29	56	129	6	27
6/24	243	365	5	44	101	165	62	122
7/01	60	43	2	7	31	54	26	73
S-wheat 322								
4/26	0	0	0	0	0	0	0	0
4/29	0	0	0	0	0	0	0	0
5/03	0	0	0	0	0	0	0	0
5/05	0	0	0	1	0	0	5	1
5/10	0	2	0	0	2	0	0	12
5/13	0	2	0	1	0	0	2	6
5/16	6	1	1	2	2	6	13	11
5/19	15	8	3	4	10	9	5	5
5/23	3	12	2	1	8	28	3	12
5/27	1	1	0	1	2	6	0	2
6/02	1	1	0	1	0	0	0	0

Table G1. Continued.

Date	North		East		South		West	
	In	Out	In	Out	In	Out	In	Out
				R-wheat 1024				
4/20	0	1	1	0	0	1	0	0
4/21	0	0	0	0	0	0	0	0
4/22	0	0	0	0	0	0	0	0
4/26	0	0	0	0	0	2	0	0
4/27	0	0	0	0	0	0	0	0
4/29	1	1	0	0	0	0	0	0
5/03	1	2	0	0	0	0	4	0
5/05	0	0	0	1	0	1	0	1
5/09	0	0	0	0	0	0	7	2
5/12	1	1	2	0	0	0	11	14
5/18	11	12	52	82	11	19	375	130
5/20	5	5	62	101	50	182	256	118
5/24	25	12	23	90	38	122	93	65
5/27	1	5	8	14	7	21	20	15
6/01	0	4	5	11	5	21	9	6
6/08	0	0	2	4	5	9	0	3
6/13	0	0	0	1	0	1	0	0
6/14	1	2	0	0	0	1	0	0
6/16	1	1	4	10	3	3	5	2
6/21	2	6	19	20	6	13	1	3
6/24	6	3	55	33	18	57	4	5
7/01	4	3	64	43	77	94	7	9
				R-wheat 323				
4/29	0	0	0	0	0	0	1	0
5/03	0	0	0	0	0	0	0	3
5/05	0	0	0	0	0	0	0	2
5/10	0	0	0	1	1	0	0	12
5/13	0	0	0	0	4	1	0	1
5/16	2	0	2	3	7	2	0	0
5/19	3	3	3	0	9	3	1	1
5/23	0	3	4	2	1	8	0	1
5/27	0	3	0	2	0	0	0	1
6/02	3	5	0	3	1	6	2	1

Table G1. Continued.

Date	North		East		South		West	
	In	Out	In	Out	In	Out	In	Out
Oats 541								
5/05	0	0	0	0	0	0	0	0
5/09	2	4	0	0	3	0	4	3
5/13	0	1	2	1	2	0	3	3
5/16	5	0	1	3	11	0	44	4
5/19	5	2	3	7	4	6	37	17
5/21	18	10	13	9	2	11	68	44
5/27	12	9	3	14	21	13	18	9
6/02	13	8	8	8	5	12	13	11
6/08	7	3	5	22	0	7	4	5
6/10	0	1	3	2	0	3	2	6
6/13	6	2	1	5	0	1	3	2
6/14	1	0	0	0	2	0	1	0
6/16	0	0	1	1	0	0	0	1
6/22	3	0	2	2	1	0	10	0
6/24	0	5	2	0	1	2	21	2
7/07	4	16	4	1	1	2	27	4
7/13	0	1	0	2	1	4	0	6
7/15	0	0	0	2	0	1	0	0
Oats 613								
5/13	3	19	4	1	0	1	2	5
5/16	2	6	10	3	1	1	2	1
5/19	2	4	4	1	0	2	1	7
5/24	2	4	3	4	0	0	2	1
5/27	4	0	0	1	1	2	2	2
6/02	0	6	0	0	0	0	0	0
6/08	1	4	1	2	2	2	0	3
6/13	0	2	0	0	0	0	0	0
6/14	0	1	0	0	0	0	0	1
6/16	0	0	1	0	0	0	0	1
6/22	4	6	1	3	0	1	3	4
6/24	3	4	2	0	0	0	3	5
7/07	14	8	5	0	0	0	5	3
7/13	0	1	0	2	0	0	1	2
7/15	0	1	1	1	0	1	1	1

APPENDIX H

SPATIAL DYNAMICS SIMULATION MODEL

```
      PROGRAM SPATIAL(OUTPUT=129,TAPE1=129,TAPE2=129,TAPE3=129,
     +TAPE4=129,TAPE61=OUTPUT)
      DIMENSION P(34,34),PL(7),OW(34,34),DEG48(22),DEG42(22),DOY(22),
     +A(7),D(7),EGGINR(3),CADDR(3),TAD(3),XMAT(4),YMAT(4),RMAT(15),
     +RP(34,34),AE(34,34),OVR(34,34),EGGIN(34,34),CADD(34,34),HT(3)
      INTEGER H(34,34),VARYA,VARYD
      REAL NB(34,34),MATUR
      LOGICAL ALTERD
      DATA XMAT/10.,15.6,21.1,26.7/
      DATA YMAT/32.,16.,10.,4./
      DATA DOY/91.,95.,100.,105.,110.,115.,120.,125.,130.,
     +135.,140.,145.,150.,156.,161.,166.,171.,176.,181.,186.,
     +191.,196./
      DATA DEG42/59.,88.,121.,160.,202.,246.,301.,366.,434.,
     +508.,600.,704.,825.,962.,1098.,1246.,1388.,1540.,1682.,
     +1836.,1988.,2152./
      DATA DEG48/27.,42.,58.,79.,103.,129.,160.,198.,242.,
     +286.,348.,416.,510.,620.,720.,832.,950.,1072.,1196.,
     +1320.,1448.,1576./
C****
C**** P = POPULATION IN CELL(I,J)
C**** PL = PROBABILITY OF LEAVING A CELL OF HABITAT TYPE H(I,J)
C**** H = HABITAT TYPE OF CELL(I,J)
C**** HABITATS ARE:
C****  1. SUSCEPTIBLE WHEAT
C****  2. RESISTANT WHEAT
C****  3. OATS
C****  4. NON-HOST CROPLAND
C****  5. SPARSE WOODS
C****  6. DENSE WOODS
C****  7. BORDER CELLS (1 TIER DEEP, ALL AROUND AREA)
C**** NB = NON-BARRIER PROPORTION OF CELL"S BOUNDARY
C****      (SUM OF A/4 FOR 4 NEIGHBORS)
C**** OW = WEIGHTED AMOUNT OF OVERWINTERING HABITAT IN CELL(I,J)/SQ. YD.
C****      (RANGES FROM 0.0 TO 0.2)
C****
      ALTERD=.F.
C**** SET FLAG INDICATING THAT ALTERATION IN WHEAT
C**** DIFFUSION RATE HAS NOT YET OCCURED.
      SEXR=0.5
C**** PROPORTION FEMALE, ADULTS
      IPRINT=1
      KM=15.
C**** ORDER OF DISTRIBUTED DELAY FOR MATURATION PROCESS
C****
C**** READ PARAMETERS
      READ(1,101)ISIZE,NDAYS,DT,NPRINT,IPF,(A(I),I=1,7),
     +(D(I),I=1,7),TOW,IOW,VARYA,VARYD,CHW,AWNEW,DWNEW,OVRED,DINCR,
     +DEM,DWX,DOX
101   FORMAT(I2/
```

```
     +I3/
     +F10.4/
     +I3/
     +A1/
     +7F3.0/
     +7F10.0/
     +F5.0/
     +A1/
     +A1/
     +A1/
     +F3.0/
     +F3.0/
     +F10.0/
     +F3.0/
     +F4.0/
     +F5.0/
     +F5.0/
     +F5.0)
C****
C**** ISIZE = NO. ROW AND COL IN GRID, INCLUDING BORDER CELLS
C**** NDAYS = DAYS TO SIMULATE
C**** DT = TIME STEP, FRACTION OF DAY
C**** NPRINT = DAYS BETWEEN PRINTING REGIONAL POPULATION TOTAL
C**** IPF (Y OR N) PRINT INDIVIDUAL FIELD POPS EVERY NPRINT DAYS?
C**** A = ABSORPTIVITY CONSTANT FOR HABITAT(I) (0 TO 1)
C**** 0 IS PERFECT BARRIER
C**** (0.LT.A.LT.1) IS PARTIAL BARRIER
C**** 1 IS NEUTRAL
C**** (A.GT.1) IS ATTRACTIVE
C**** D = DIFFUSION RATE FOR HABITAT(I) (1,2 AND 3 WILL LATER VARY)
C****     (IN*IN/MIN)
C**** TOW = SUM OF MEAN OVERWINTERING DENS (/SQ.YD.) IN 5 OW HABITATS
C**** IOW (Y OR N) WANT TO READ IN INDIVIDUAL OW FOR EACH CELL?
C****      (IF N, WILL READ FOR EACH HABITAT)
C**** VARYA (Y OR N) WANT TO ALTER ABSORPT OF WHEAT AFTER CHW?
C**** VARYD (Y OR N) WANT TO ALTER DIFFUSION IN WHEAT AFTER CHW?
C**** CHW = CRITICAL HEIGHT OF WHEAT (IN.) AT ALTERATION OF A OR D
C**** AWNEW = NEW A VALUE FOR WHEAT AFTER CHW
C**** DWNEW = NEW D VALUE FOR WHEAT AFTER CHW
C**** OVRED = FACTOR TO REDUCE OVIPOSITION IN RESISTANT WHEAT
C**** DINCR = FACTOR TO INCREASE DIFFUSION RATE IN RESISTANT WHEAT
C**** DEM = SHIFT MEDIAN EMERGENCE BY DEM DD48
C**** DWX = SHIFT WHEAT GROWTH CURVE BY DWX DD42
C**** DOX = SHIFT OAT GROWTH CURVE BY DOX DD42
C****
      AOAT=A(3)
      A(3)=A(4)
C**** ABSORPTIVITY OF OATS WILL BE SAME AS NON-HOST CROPLAND UNTIL
C**** OATS EMERGE
      ISM1=ISIZE-1
```

```
      READ(2,102)((H(I,J),J=1,ISIZE),I=1,ISIZE)
102   FORMAT(34I1)
C**** READ IN SPATIAL PATTERN
      IF(IOW.EQ.1HY)GO TO 3
      READ(2,103)(OW(I),I=1,7)
      GO TO 4
3     READ(2,103)((OW(I,J),J=1,34),I=1,34)
103   FORMAT(17F4.2)
C**** READ IN OW DISTRIBUTION
C****
C**** INITIALIZE CELL VARIABLES
C****
4     CONTINUE
      DO 10 I=2,ISM1
      DO 10 J=2,ISM1
C**** LOOP OVER CELLS (I = ROWS J = COLS)
      P(I,J)=0.
      RP(I,J)=0.
C**** POP LEVELS AND RATES FOR INNER CELLS
      CADD(I,J)=0.
      EGGIN(I,J)=0.
C**** CUMULATIVE ADULT DEGREE-DAYS (AREA UNDER CURVE) AND EGGS
      OVR(I,J)=0.
C**** OVIPOSITION RATE
10    NB(I,J)=(A(H(I,J+1))+A(H(I,J-1))+A(H(I+1,J))+A(H(I-1,J)))/4.
      DO 11 I=2,ISM1
      P(1,I)=0.
      P(ISIZE,I)=0.
      P(I,1)=0.
11    P(I,ISIZE)=0.
C**** FIX BOUNDARY CELLS AT ZERO POP. LEVEL
C****
C**** INITIALIZE STATE VARIABLES
C****
      T=91.
C**** TIME (DAYS) DAY 91 = APRIL 1
      CDD42=59.
      CDD48=27.
C**** CUMULATIVE DEG-DAYS (FAHRENHEIT) FOR EAU CLAIRE
      CEMERG=0.
      CMATUR=0.
      PMATUR=0.
C**** CUMULATIVE PROPORTION EMERGED AND SEXUALLY MATURE, AND PROPORTION
C**** OF EMERGED FEMALES WHICH ARE MATURE
      HTW=0.
      HTO=0.
C**** CROP HEIGHT (INCHES)
      ZAGW=27.
      ZAGO=27.
C**** BASE LINE (DD48) FOR AGE OF OVIPOSITING FEMALES
```

```
      DO 12 I=1,3
      CADDR(I)=0.
12    EGGINR(I)=0.
C**** REGIONAL CUMULATIVE TOTALS FOR HOST CROPS
C****
C**** INITIALIZE RATE VARIABLES
C****
      DD42=0.
      DD48=0.
C**** DEGREE-DAYS ACCUMULATED/DAY
      EMERG=0.
      MATUR=0.
C**** PROPORTION EMERGING AND MATURING PER DAY
      DELMP=32.
      DO 13 I=1,KM
13    RMAT(I)=0.
C**** DELAY TIME AND INTERNAL RATES FOR MATURATION PROCESS
      NPRINT=FLOAT(NPRINT)/DT+.5
      NIT=FLOAT(NDAYS)/DT+.5
C**** TOTAL NO. OF ITERATIONS, AND ITERATIONS BETWEEN PRINTING
C****
      DO 20 IT=1,NIT
C****
C**** LOOP OVER TIME
C****
C**** UPDATE STATES
C****
      T=T+DT
      CDD42=CDD42+DD42*DT
      CDD48=CDD48+DD48*DT
      CEMERG=CEMERG+EMERG*DT
      CMATUR=CMATUR+MATUR*DT
      IF(CEMERG.LE.0.)GO TO 21
      PMATUR=CMATUR/CEMERG
21    WX=CDD42+DWX
      OX=(CDD42-200.)+DOX
      HTW=AMAX1(HTW,(-3.948+0.0243*WX+0.0000908*WX*WX-0.0000000481
     +*WX**3)/2.54)
      HTO=AMIN1(HTW,AMAX1(0.0,-21.21+0.0563*OX-0.0000282*OX*OX+
     +0.818E-8*OX**3))
C**** LET MAX OAT HT = MAX WHEAT HT
      HT(1)=HTW
      HT(2)=HTW
      HT(3)=HTO
      IF(PMATUR.LT.0.05)ZAGW=CDD48
      OVAGW=(CDD48-ZAGW)*.55555
      IF(HTO.LE.0.)ZAGO=CDD48
      OVAGO=(CDD48-ZAGO)*.55555
C**** EFFECTIVE AGES (DD9 (C)) FOR OVIP BEETLE IN WHEAT AND OATS
      TAD(1)=0.
```

```
      TAD(2)=0.
      TAD(3)=0.
      DO 40 I=2,ISM1
      DO 40 J=2, ISM1
C**** LOOP OVER CELLS
      P(I,J)=P(I,J)+RP(I,J)*DT
C**** UPDATE POPUL. LEVELS
      GO TO(22,22,22,40,40,40,40)H(I,J)
C**** FOR HOST CROP CELLS, CALCULATE CUMULATIVE TOTALS
C**** (IF CROP HT GT 0.0)
22    IF(HT(H(I,J)).LE.0.0)GO TO 40
      CADD(I,J)=CADD(I,J)+P(I,J)*DD48*DT
      EGGIN(I,J)=EGGIN(I,J)+OVR(I,J)*DT
      CADDR(H(I,J))=CADDR(H(I,J))+P(I,J)*DD48*DT
      EGGINR(H(I,J))=EGGINR(H(I,J))+OVR(I,J)*DT
      TAD(H(I,J))=TAD(H(I,J))+P(I,J)
40    CONTINUE
C****
C**** UPDATE RATES
C****
      TP1=T+1.
      D1=TABLI(DEG48,DOY,T,22)
      D2=TABLI(DEG48,DOY,TP1,22)
      DD48=D2-D1
      DD9=DD48*.55555
      CDL48=ALOG10(CDD48)
C**** ACCUMULATION OF LOG10 DEGREE-DAYS (48 F)
      DL48=ALOG10(D2)-ALOG10(D1)
      DD42=TABLI(DEG42,DOY,TP1,22)-TABLI(DEG42,DOY,T,22)
      TEMP=DD42+42.
C**** MEAN TEMP (F) (APPROX)
      CTEMP=(TEMP-32.)*.55555
      DELM=TABLI(YMAT,XMAT,CTEMP,4)
C**** MATURATION DELAY (DAYS) AS FUNC. OF TEMP (C)
      MATUR=DELLVF(EMERG,RMAT,PIA,1.0,DELM,DELMP,DT,KM)
      EM=ALOG10(124.3+DEM)
      EMERG=DL48*2.4324*EXP(-18.5874*(CDL48-EM)**2)
C**** PROPORTION EMERGING/DAY
C**** MEAN = EM = 2.094, VAR = 0.0269 FOR LOG-NORMAL CURVE
C**** EM CAN BE SHIFTED WITH DEM
      OVW=0.93716*DD9*EXP(-1.830125E-5*(OVAGW-144.132)**2)
      OVO=DD9*0.92348*EXP(-1.02107E-5*(OVAGO-146.050)**2)
C**** DAILY OVIP RATE IN WHEAT AND OATS
      S=0.00194-0.00206*CTEMP
C**** INSTANTANEOUS SURVIVAL FOR ADULTS (1/DAY)
      DAS=EXP(S)
C**** DAILY ADULT SURVIVAL RATE (ALL CROPS)
      IF(HTW.LE.0.)GO TO 25
      IF(HTW.LT.CHW)GO TO 27
      IF(VARYA.EQ.1HN)GO TO 28
```

```
      A(1)=AWNEW
      A(2)=AWNEW
28    IF(VARYD.EQ.1HN)GO TO 27
      IF(ALTERD)GO TO 25
      D(1)=DWNEW
      D(2)=DWNEW
      ALTERD=.T.
      GO TO 25
27    D(1)=AMAX1(1.0,AMIN1(5000.,4230./HTW-148.3))
      D(2)=D(1)*DINCR
C**** CALCULATE DIFFUSION RATES IN HOST CROPS, BASED ON CROP HT
C**** INCORPORATES EFFECT OF CROP MATURATION ON BEETLE EXODUS
C**** FROM WHEAT.  MAY INCREASE RATE IN R-WHEAT
25    IF(HTO.LE.0.)GO TO 26
      D(3)=AMAX1(1.0,AMIN1(5000.,4230./HTO-148.3))
      A(3)=AOAT
C**** IF OATS ARE NOT YET EMERGED, TREAT AS NON-HOST CROPLAND
C**** WHEN OATS EMERGE, CALCULATE D(3) AND LET THEIR
C**** ABSORPTIVITY ASSUME ASSIGNED VALUE.
C**** D(1,2, AND 3) SHOULD INITIALLY BE SET TO D(4)
C**** A(3) AUTOMATICALLY SET TO A(4) INITIALLY
26    CONTINUE
      DO 30 I=1,7
30    PL(I)=10.**(-3.688+0.4958*ALOG10(2*D(I)*15.*60.))
C**** PROBABILITY OF LEAVING A 10 ACRE CELL IN ONE 15-HR DAY GIVEN D
      DO 50 I=2,ISM1
      DO 50 J=2,ISM1
      GO TO(51,52,53,54,54,54,54)H(I,J)
51    OVR(I,J)=P(I,J)*PMATUR*SEXR*OVW
      GO TO 54
52    OVR(I,J)=P(I,J)*PMATUR*SEXR*OVW*OVRED
      GO TO 54
53    OVR(I,J)=P(I,J)*PMATUR*SEXR*OVO
C**** OVIPOSTION INTO S-WHEAT, R-WHEAT AND OAT CELLS
54    CONTINUE
      OWS=OW(H(I,J))
      IF(IOW.EQ.1HY)OWS=OW(I,J)
      AE(I,J)=TOW*OWS*48400.*EMERG
C**** TOTAL ADULTS EMERGING/DAY INTO 10 ACRE CELL
      IF(HTW.LT.CHW)GO TO 60
      IF(VARYA.EQ.1HN)GO TO 60
      NB(I,J)=(A(H(I,J+1))+A(H(I,J-1))+A(H(I+1,J))+A(H(I-1,J)))/4.
      IF(I.GE.ISM1.AND.J.GE.ISM1)VARYA=1HN
60    CONTINUE
C**** RECALCULATE NON-BARRIER PROPORTION OF BOUNDARIES
C**** IF ABSORPTIVITY OF WHEAT HAS BEEN CHANGED
      RP(I,J)=AE(I,J)-((1.-DAS)+PL(H(I,J))*NB(I,J))*P(I,J)+
     +A(H(I,J))/4.*(PL(H(I,J+1))*P(I,J+1)+PL(H(I,J-1))*P(I,J-1)+
     +PL(H(I+1,J))*P(I+1,J)+PL(H(I-1,J))*P(I-1,J))
C**** RATE OF CHANGE OF POPULATION LEVEL IN CELL(I,J).
```

```
C**** INCORPORATES ADULT EMERGENCE, DEATH RATE, EMIGRATION, AND
C**** IMMIGRATION FROM 4 NEIGHBORING CELLS.
50    CONTINUE
      IF(IPRINT.NE.NPRINT)GO TO 70
      IPRINT=0
      IF(IPF.EQ.1HN)GO TO 57
      DO 55 I=2,ISM1
      DO 55 J=2,ISM1
      GO TO(56,56,56,55,55,55,55)H(I,J)
56    WRITE(3,104)T,I,J,H(I,J),P(I,J),CADD(I,J),EGGIN(I,J)
104   FORMAT(F10.2,3I5,3E15.5)
55    CONTINUE
57    WRITE(4,105)T,CDD48,(TAD(K),K=1,3)
105   FORMAT(2F10.2,3E15.5)
      WRITE(61,106)CDD42,CDD48,CEMERG,CMATUR,PMATUR,HTW,HTO,TEMP,
     +DELM,OVW,OVO,DAS,D(1),D(3),PL(1),PL(3)
106   FORMAT(*0*8E10.4/1X,8E10.4/1X,8E10.4)
70    IPRINT=IPRINT+1
C****
20    CONTINUE
C**** END TIME LOOP
C****
      DO 65 I=2,ISM1
      DO 65 J=2,ISM1
      GO TO(66,66,66,65,65,65,65)H(I,J)
66    IF(CADD(I,J).GT.0.)GO TO 67
      EPA=0.
      GO TO 68
67    EPA=EGGIN(I,J)/CADD(I,J)
68    WRITE(61,107)I,J,H(I,J),CADD(I,J),EGGIN(I,J),EPA
107   FORMAT(3I5,2E15.5,F10.4)
65    CONTINUE
      DO 80 I=1,3
      IF(CADDR(I).GT.0.)GO TO 81
      EPA=0.
      GO TO 82
81    EPA=EGGINR(I)/CADDR(I)
82    WRITE(61,108)I,CADDR(I),EGGINR(I),EPA
108   FORMAT(*0*I5,2E15.5,F10.4)
80    CONTINUE
      STOP
      END
```

```
      FUNCTION DELLVF(RIN,R,STRG,SURVR,DEL,DELP,DT,K)
      DIMENSION R(1)
C SURVR MUST BE COMPUTED ON A PER DT BASIS
      VIN=RIN
      FK=FLOAT(K)
      B=1.+(DEL-DELP)/(FK*DT)
      A=FK*DT/DEL
      DELP=DEL
      DO 10 I=1,K
      DR=R(I)
      R(I)=DR+A*(VIN-DR*B)
      VIN=DR
10    CONTINUE
      STRG=0.
      DO 30 I=1,K
      R(I)=R(I)*SURVR
      STRG=STRG+R(I)*DEL/FK
30    CONTINUE
      DELLVF=R(K)
      RETURN
      END
OK-
```

```
      FUNCTION TABLI(VAL,ARG,DUMMY,K)
      DIMENSION VAL(1),ARG(1)
      DUM=AMAX1(AMIN1(DUMMY,ARG(K)),ARG(1))
      DO 1 I=2,K
      IF(DUM.GT.ARG(I))GO TO 1
      TABLI=(DUM-ARG(I-1))*(VAL(I)-VAL(I-1))/
     +(ARG(I)-ARG(I-1))+VAL(I-1)
      RETURN
1     CONTINUE
      RETURN
      END
```

APPENDIX I

SPATIAL CONFIGURATIONS FOR SIMULATIONS

```
XXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXX
X  13         1111111          1 X
X           31 11 1 11       1 1 X
X      11 1111 11  1 1111  1   3 X
X    1  1       1    11   1    1 X
X   1            111       11    X
X    1       13 1  1             X
X  11111  11   3  11             X
X1 1  13        31 1     1    1   X
X1       3    1 13   11     1 11 X
X1                        1   111X
X     3    1          11         X
X   1               1 11    1   1X
X        1  1          1  1   1  X
X           1  1             1313X
X           1     1  11      111 X
X 1  1     111 1          3      X
X11        1  11   1     11      X
X           1 11 1       1       X
X     1    1             1   1 1 X
X3       11 1        1       1111X
X1            1      1           X
X1         1    131 1            X
X        131   1    1  1         X
X1       1 3      11  11         X
X1111    1                       X
X3 1                 1    1      X
X     1     11     1 11   1  1   X
X      11 1 1        1     1   1 X
X       1 11            1  1 1  1X
X      1       1     1     1     X
X   1     31  11     11         1X
X   1111  1  1              1   1X
XXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXX
```

Fig. I1.--Run 32: All grain acreage doubled.

```
XXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXX
X            3 11 1 1  1       1 X
X        1   1 11 1 1  3     1 11X
X      11 11   11 1  1111  11  3 X
X       1       1    11   1    1 X
X        1   1  111        11    X
X 1  1       13111         1     X
X   1111 11       1              X
X1 1  13     1 311            1  X
X1  1    3    1  3 1 11 1     1  X
X                1 1    1 1   1  X
X            1      1  1        1X
X1                    1          X
X        1  1 1          1    1  X
X           1           1    131 X
X                            111 X
X    1   1  1111          311    X
X   1         11 1 1  1  11 1    X
X             11         1       X
X          1             1 1   1 X
X         3          1     1 1 1 X
X 11      1     1    1           X
X  1       1         1           X
X        1 1     1 1             X
X  1     1         1 1 1 1       X
X        1            1          X
X  1                 1   11   1  X
X   11      1        1    11  1  X
X  1   11   1        1           X
X       1 11     1        1      X
X     1   1           1   11   1 X
X           1  1       1   1    1X
X   1 11          13 1 1    1  1 X
XXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXX
```

Fig. I2.--Run 33: All grain acreage doubled.

```
XXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXX
X         1    11 1 11         1 X
X111  1      1111 111        1 1 X
X      11 111  11    1111  1   3 X
X     1 1  31   1 1  11   1    1 X
X 1        1  1  111  1    11    X
X    1       13   1         3    X
X    11 1 11     11   1          X
X1 1 113       31       1     1  X
X1      13   11  3   11    1  1  X
X      1                  1   1  X
X                      1  13     X
X  1    11      33    1         1X
X       11 1 1  1            1  X
X           1      1    11   131 X
X1      1           11  1    111 X
X   11  1   11 1          31 1   X
X            11   1 1   111     X
X              1       111 1   1 X
X     1    1             11   11 X
X                    1       131 X
X1        1          1           X
X   1      11                  1 X
X 1     11 1                     X
X  1     1         1 1 3 1       X
X        1          1           1X
X  1       1         11   1      X
X  1        1        1  1 1     3X
X    1 11   1        1 11        X
X  1      111         11      1  X
X             1            1   1 X
X     1    1  11     1         1 X
X     11           1  1     11   X
XXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXX
```

Fig. I3.--Run 34: All grain acreage doubled.

```
XXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXX
X              1  1 1          1 X
X            1 1               1 X
X                      1         X
X       1       1     1          X
X                 1        1     X
X            13                  X
X     1           1              X
X1     3        1                X
X1       3       3   11          X
X                         1      X
X                      1         X
X                                X
X                             1  X
X                             31 X
X                            11  X
X    1      1                    X
X             11                 X
X              1         1       X
X                        1       X
X                              1 X
X                    1           X
X          1                     X
X                                X
X        1                       X
X        1                       X
X  1                             X
X           1        1           X
X      1                         X
X                                X
X                                X
X              1                 X
X      1                    1    X
XXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXX
```

Fig. I4.--Run 35: All grain acreage halved.

```
XXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXX
X              1  1            1 X
X            1               1 1 X
X      1  1     1    11          X
X       1       1    11   1      X
X                          11    X
X                                X
X    1                           X
X  1  13                         X
X                3    1          X
X                                X
X                                X
X                     1          X
X        1  1                    X
X                            131 X
X                            1 1 X
X    1      1  1          3      X
X             1          11      X
X                                X
X                        1     1 X
X                    1         1 X
X                    1           X
X          1                     X
X          1                     X
X                                X
X                                X
X  1                 1           X
X                         1      X
X           1        1           X
X          1                     X
X                                X
X              1                 X
X                                X
XXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXX
```

Fig. 15.—Run 36: All grain acreage halved.

```
XXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXX
X              1  1 1            X
X            1 1             1   X
X      1        1       1  1   3 X
X                    1         1 X
X                11              X
X             3                  X
X     1   1       1              X
X1    1         1                X
X             1  3   11       1  X
X                         1      X
X                                X
X                                X
X           1                 1  X
X                              1 X
X                                X
X    1                    3      X
X             1    1     11      X
X              1                 X
X                              1 X
X                    1       1   X
X                                X
X                                X
X                                X
X        1                       X
X        1                       X
X  1                             X
X                         1      X
X      11                        X
X         11                     X
X                          1     X
X              1                 X
X     11                    1    X
XXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXX
```

Fig. I6.--Run 37: All grain acreage halved.

```
XXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXX
X              11 1 1          1 X
X            1 11 1 1        1 1 X
X      11 11  311    1111  1   3 X
X       1       1    11   1    1 X
X                11        11    X
X    13      13                  X
X    11   1       1              X
X1 1  13       31                X
X1       3    1  3   11       1  X
X        3                1   1  X
X                    3 1         X
X                     1          X
X        1  1                 1  X
X           1                131 X
X                            111 X
X    1      11 1          3      X
X             11   1     11      X
X              1         1       X
X                        1     1 X
X                    1       1 1 X
X                    1           X
X          1                     X
X       3  1                     X
X        1         1             X
X        1                       X
X  1                 1    1      X
X           1        1    1      X
X      11   1        1           X
X         11                  3  X
X              3           1     X
X              1                 X
X     11                    1    X
XXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXX
```

Fig. I7.--Run 38: Oat acreage 2x.

```
XXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXX
X              11 1 1          1 X
X        3   1 11 1 1        1 1 X
X      11 11   11    1111  1   3 X
X       1       1    11   1    1 X
X3               11        11    X
X    1       13                  X
X    11   1       1              X
X1 1  13       31                X
X1       3    1  3   11       1  X
X                         1   1  X
X                      1         X
X                     1          X
X        1  1                 1  X
X           1                131 X
X                 3          111 X
X    1      11 1          3      X
X             11   1     11      X
X              1         1       X
X                        1     1 X
X                    1       1 1 X
X                    1           X
X          1                     X
X          1                     X
X        1         1             X
X        1                       X
X  1                 1    1      X
X           1        1    1      X
X      11   1        1           X
X         11          3          X
X                          1     X
X              1                 X
X     11               3    1    X
XXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXX
```

Fig. I8.--Run 39: Oat acreage 2x.

```
XXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXX
X              11 1 1          1 X
X            1311 1 1        1 1 X
X      11 11   11    1111  1   3 X
X       1       1    11   1    1 X
X                11        11    X
X    1       13                  X
X    11   1       1              X
X1 1  13       31                X
X1       3    1  3   11       1  X
X                         1   1  X
X                      1         X
X                     1          X
X        1  1                 1  X
X           1                131 X
X                            111 X
X    1      11 1     3    33     X
X             11   1     11      X
X          3   1         1       X
X                        1     1 X
X                    1       1 1 X
X          3         1           X
X          1                     X
X          1                     X
X  3     1         1             X
X        1                       X
X  1                 1    1      X
X           1        1    1      X
X      11   1        1           X
X         11                     X
X                  3       1     X
X    3         1                 X
X     11                    1    X
XXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXX
```

Fig. I9.--Run 40: Oat acreage 2x.

```
XXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXX
X3             11 131          1 X
X            1 11 1 1        1 1 X
X     311 11   11    1111  1   3 X
X       1       1    11   1    1 X
X    3   3       11        11    X
X    1       13                  X
X    11   1    3  1             3X
X1 1  13       31      3         X
X1       3    1  3   11       1  X
X                         1   1  X
X                      1         X
X                     1          X
X        1  1                 1  X
X           1                131 X
X3                           111 X
X    1      11 1          3      X
X     3       11   1    311      X
X              1         1       X
X                        1     1 X
X    3               1    3  1 1 X
X                    1           X
X          13          3         X
X          1                     X
X        1         1     3       X
X        1                       X
X  1                 13   1      X
X           1        1    1      X
X      11   1        1           X
X         11                     X
X                      3   1     X
X              1                 X
X    311  3                 1    X
XXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXX
```

Fig. 110.--Run 41: Oat acreage 4x.

```
XXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXX
X              11 1 1          1 X
X  3      3  1 11 1 1        1 1 X
X      11 11   11    1111  1   3 X
X    3  1       1    11   1    1 X
X           3    11        11    X
X    1       13      3           X
X    11   1       1              X
X1 1  13       31                X
X1       3    1  3  311       1  X
X                         1   1  X
X                      1         X
X                     1          X
X     3  1  1                 1  X
X           1                131 X
X                            111 X
X    1      11 1          3      X
X3            11   1     11      X
X              1   3     1       X
X                        1     1 X
X                    1       1 1 X
X            3       1           X
X          1                     X
X          13     3              X
X        1         1             X
X        1                       X
X  13                1    1      X
X           1        1    1      X
X      11   1        1      3    X
X         11                     X
X      3              3    1     X
X   3          1                 X
X     11         3          1    X
XXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXX
```

Fig. 111.--Run 42: Oat acreage 4x.

```
XXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXX
X              11 1 1          1 X
X  3         1 11 1 1        1 1 X
X      11 11   11    1111  1   3 X
X       1       1    11   1    1 X
X     3    3     11        11    X
X    1       13                  X
X    11   1       1              X
X1 1  13       31                X
X1       3    1  33  11       1  X
X                         1   1  X
X                      1   3     X
X                     1          X
X        1  1                 1  X
X           1 3              131 X
X           3               3111 X
X    1      11 1          3 3    X
X             11   13    11      X
X              1         1       X
X                        1     1 X
X                    1       1 1 X
X         3          1     3     X
X 3        1     3               X
X          1                     X
X        1         1             X
X        1                       X
X  1         3       1    1      X
X           1        1    1 3    X
X      11   1        1           X
X         11    3                X
X                         31     X
X    3         1                 X
X     113             3     1    X
XXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXX
```

Fig. I12.--Run 43: Oat acreage 4x.

```
XXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXX
X              1131 1  3       1 X
X3           1 11 1 1  3     1 1 X
X3     11 11   11    1111  1   3 X
X       1  3   31    11   1    1 X
X    3           11        11    X
X    1       13                  X
X    113  1 3    31     3        X
X1 1  13    3 331    3           X
X1      33    1  3   11 3     1  X
X         3            3 31   1  X
X                    3 1         X
X 33 3                1          X
X        1  13   3     3      1  X
X           1                131 X
X                        3   111 X
X    1      11 1          3      X
X        3    11   1     11   3  X
X          3   1     3   1       X
X        3          3    1     1 X
X               3    1       1 1 X
X                    1           X
X          1  3                  X
X 3        1        3            X
X        1         1             X
X       31                       X
X3 1                 1    1      X
X    3      1        1    1 33   X
X  3   11   1        1   3 3     X
X         11   3                 X
X                          1     X
X     3       31 3 3           3 X
X     11      3            31 3  X
XXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXX
```

Fig. I13.--Run 44: Oat acreage 8x.

```
XXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXX
X            3 11 1 1          1 X
X  33        1 11 1 1        1 1 X
X 3    11 11   11    1111  1   3 X
X 33    1       1    11   1    1 X
X                11        11    X
X    1       13  3  3 3          X
X    113  1     3 1             3X
X1 1  13    3  31        3  33   X
X1       33   13 3   11       13 X
X   3    3         3      1  31  X
X                 3    1    3    X
X            3        1          X
X        1  1          3      1  X
X           1       3    33 3131 X
X                     3     3111 X
X    1      11 1         33 3    X
X             11   1     11      X
X   3      3   1         1       X
X         3              1     1 X
X     3    3         1       1 1 X
X   3                1     3     X
X          1         3 3         X
X          13                    X
X3   3   13        1             X
X        1                       X
X  1        3        1  3 1     3X
X        3 31        1    1      X
X 3    11   1        1 3  3      X
X         11                     X
X              3           1  3  X
X        3     1            3    X
X     11                    1    X
XXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXX
```

Fig. I14.--Run 45: Oat acreage 8x.

```
XXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXX
X              11 1 1          1 X
X     33     1 11 1 1        1 1 X
X 3 3  11 11   11    1111  1   3 X
X       1  33   1    11   1    1 X
X                11  3     11    X
X    1       13    3        3    X
X    11   1       1   3          X
X1 1  13       31            3   X
X1    3  3    1  3   11       1  X
X   3                     1   1  X
X                3     1         X
X 3     3         3   1          X
X        13 1      33         1  X
X3          1  3       3     131 X
X                 3   33    3111 X
X    1      11 1   3 3    3      X
X             11   1  3  11    3 X
X              1       3 1       X
X                       31     1 X
X                3   1       1 1 X
X                    1           X
X          1                     X
X          13    3               X
X   33   1         1 3           X
X        1                       X
X3 1  3              1    1      X
X    3      1        1    1      X
X    3 11 3 1        1  3        X
X  33     11                     X
X    3       3             1     X
X              1   3             X
X     11                    1    X
XXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXX
```

Fig. I15.--Run 46: Oat acreage 8x.

```
XXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXX
X                                X
X                                X
X                                X
X                                X
X                                X
X                                X
X                                X
X                    WWWW        X
X                    WWWW        X
X                    WWWW        X
X                    WWWW        X
X                                X
X                  WWWW          X
X                  WWWW          X
X                  WWWW          X
X                  WWWW WWWW     X
X                       WWWW     X
X                       WWWW     X
X                       WWWW     X
X                                X
X                                X
X                                X
X                                X
X WWWW              WWWW         X
X WWWW              WWWW         X
X WWWW              WWWW         X
X WWWW              WWWW         X
X                                X
X   WWWW                         X
X   WWWW                         X
X   WWWW                         X
X   WWWW                         X
XXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXX
```

Fig. I16.--Run 47: Six 160-acre wheat fields.

```
XXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXX
X                                X
X                                X
X                                X
X                                X
X                                X
X          WWWW                  X
X          WWWW                  X
X          WWWW      WWWW        X
X          WWWW      WWWW        X
X   WWWW             WWWW        X
X   WWWW             WWWW        X
X   WWWW                         X
X   WWWW                         X
X                                X
X                                X
X                                X
X        WWWW                    X
X        WWWW                    X
X        WWWW                    X
X        WWWW                    X
X                                X
X                                X
X                                X
X WWWW                           X
X WWWW                           X
X WWWW                  WWWW     X
X WWWW                  WWWW     X
X                       WWWW     X
X                       WWWW     X
X                                X
X                                X
X                                X
XXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXX
```

Fig. I17.--Run 48: Six 160-acre wheat fields.

```
XXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXX
X     WWW                        X
X     WWW                        X
X     WWW             WWW        X
X                     WWW        X
X                     WWW        X
X                                X
X              WWW               X
X  WWW         WWW               X
X  WWW         WWW               X
X  WWW                           X
X                                X
X                                X
X                       WWW      X
X                       WWW      X
X                       WWW      X
X                        WWW     X
X                        WWW WWW X
X                        WWW WWW X
X                            WWW X
X                                X
X                                X
X                                X
X                     WWW        X
X                     WWW        X
X                     WWW        X
X  WWW                       WWW X
X  WWW                       WWW X
X  WWW                       WWW X
X                  WWW           X
X                  WWW           X
X                  WWW           X
X                                X
XXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXX
```

Fig. 118.--Run 49: Eleven 90-acre wheat fields.

```
XXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXX
X                                X
X                                X
X                                X
X                                X
X          WWW                   X
X          WWW                   X
X          WWW                   X
X                                X
X                                X
X                WWW             X
X                WWW          WWWX
X                WWW          WWWX
X                             WWWX
X                                X
X                    WWW WWW     X
X                    WWW WWW WWW X
X        WWW         WWW WWW WWW X
X        WWW                 WWW X
X        WWW                     X
X                                X
X                                X
X                     WWW        X
X                     WWW        X
X                     WWW        X
X                        WWW     X
X                        WWW     X
X                        WWW     X
X                                X
X         WWW               WWW  X
X         WWW               WWW  X
X         WWW               WWW  X
XXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXX
```

Fig. I19.--Run 50: Eleven 90-acre wheat fields.

```
XXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXX
X                       WW       X
X                  WW   WW       X
X                  WW            X
X                          WW    X
X                WW        WW    X
X                WW              X
X                                X
X                            WW  X
X           WW               WW  X
X           WW                   X
X                                X
X                WW      WW      X
X                WW      WW      X
X                                X
X                              WWX
X             WW             WWWWX
X             WW             WW  X
X                                X
X                       WWWW     X
X                       WWWW     X
X                                X
X                                X
X         WW     WW              X
X         WW     WW              X
X     WW                         X
X WW  WW                         X
X WW                           WWX
X          WW                  WWX
X          WW        WW       WW X
X          WW        WW       WW X
X          WW             WW WW  X
X                         WW WW  X
XXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXX
```

Fig. I20.--Run 51: Twenty-four 40-acre wheat fields.

```
XXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXX
X                      WW        X
X                    WWWW        X
X                    WW          X
X                                X
X                     WW         X
X                     WW         X
X     WW                         X
X     WW        WW               X
X               WW          WW WWX
X                           WW WWX
X WW             WW              X
X WW             WW WW           X
X                 WWWW           X
X                 WW             X
X                 WW             X
X                 WW          WW X
X               WW            WW X
X               WW               X
X          WW                    X
X          WW                    X
X                    WW          X
X                WW  WW          X
X                WW              X
X WW                             X
X WW  WW                         X
X     WW            WW           X
X           WW      WW           X
X           WW                   X
X          WW                    X
X          WW                 WW X
X        WW                   WW X
X        WW                      X
XXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXX
```

Fig. I21.--Run 52: Twenty-four 40-acre wheat fields.

```
XXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXX
X          W      W              X
X    W W           W          W  X
X           W        WW          X
X W  WW                          X
X     W                          X
X           W  W                 X
X                    WWW         X
X     WW                      W  X
XW       W  W         W          X
X    W      WW         W W       X
X                           WW   X
XW                     W         X
XW     W     WW       W    W  W  X
X   W         W                  X
X               W                X
X W      W     W                 X
X      W         W         W     X
XW        W                      X
X   W               W      W W   X
X           W              W W   X
X            W W           W     X
X                      W       W X
X     WW  W      WW              X
X W              W    WW         X
X      WW                        X
X      W             W         W X
X   W               W    WW  W   X
X W          W         W         X
X                    W  W   W    X
X     WW                     W   X
X             WW               W X
X                            W   X
XXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXX
```

Fig. I22.—Run 53: Ninety-six 10-acre wheat fields.

```
XXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXX
X     W      WWW                WX
X                W  WW  WW   W   X
X                   W  W         X
X               W         W     WX
X            W   W               X
X       W          W W           X
X              W   W  W          X
X W                    W         X
X     W     W             WW  W  X
X     W                        W X
XW                    W    W     X
X W                              X
X        W   W            W      X
X                        W    W  X
X           W                W W X
X          W  W                  X
X                    W  WW    W  X
X          W          W          X
X           W               W W  X
XW  WW      W           W       WX
X                    W W         X
X           W  W                 X
X  W           W W               X
X    W  W                       WX
X    W                   W     W X
X           W          WWWW  W   X
X    W                 W      W  X
X   W   W                      W X
X     W         W         W      X
X                         W      X
X             W                  X
X    W       W     W  W          X
XXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXX
```

Fig. I23.--Run 54: Ninety-six 10-acre wheat fields.

```
XXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXX
X     W                          X
X     W                          X
X     W         WWWWWWWWW        X
X     W         W                X
X     W         W                X
X     W         W                X
X     W         W                X
X     W         W                X
X     W         W                X
X               W                X
X               W         W      X
XWWWWWWWWW      W         W   W  X
X                         W   W  X
X                WWWWWWWWWW   W  X
X                         W   W  X
X                         W   W  X
X                         W   W  X
X                         W   W  X
X                         W   W  X
X                      W      W  X
X                      W         X
X                      W         X
X                   W  W         X
X                   W  W         X
X                   W  W         X
XWWWWWWWWW          W  W         X
X                   W  WWWWWWWWWWX
X                   W  W         X
X                   W            X
X                   W            X
X                   W            X
X                                X
XXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXX
```

Fig. I24.--Run 55: Eleven elongate 90-acre wheat fields.

```
XXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXX
X                                X
X                                X
X                                X
X                                X
X                                X
X                               WX
X                               WX
X        WWWWWWWWW              WX
X                               WX
X                               WX
X                               WX
X               WWWWWWWWW W   W WX
X                       W W   W WX
X                       W W   W WX
X                       W W   W  X
X          W            W W   W  X
X          W            W W   W  X
X          W            W W   W  X
X          W            W W   W  X
X          W            W W   W  X
X          W            W        X
X          W        W            X
X          W        W            X
X          W        W            X
X                   W            X
X                   W            X
X                   W WWWWWWWWW  X
X                   W            X
X                   W   WWWWWWWWWX
X                   W            X
X       WWWWWWWWW                X
X                                X
XXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXX
```

Fig. I25.--Run 56: Eleven elongate 90-acre wheat fields.

```
XXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXX
X              3           3     X
X   13                     1     X
X       3          31          1 X
X       1                        X
X                                X
X                                X
X   3        1                1  X
X                                X
X              1                 X
X                                X
X                   1            X
X                   3   31       X
X        3       1               X
X        1                       X
X       1                       3X
X          1           1        1X
X   3      3                     X
X   1        1     13      3     X
X       1                        X
X              1                 X
X              3                 X
X                              1 X
X       1                        X
X                                X
X                                X
X                                X
X 13              13             X
X      1                      1  X
X                                X
X        3                1      X
X   1    1                       X
X                                X
XXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXX
```

Fig. 126.—Run 57: Configuration for simulating the effect of specific field locations.

APPENDIX J

DEGREE-DAY ACCUMULATIONS NEAR GALIEN

Table J1. Degree-days > 48 (F) accumulated at Glendora, Michigan (Berrien County) during 1976 and 1977. Source: PMEX DEGREEDAYS.

Day	April	May	June	July
		1976		
1	99[a]	309	573	1172
2	100	309	586	1187
3	109	309	598	1201
4	109	315	615	1217
5	112	335	636	1236
6	115	335	652	1256
7	117	335	669	1278
8	117	338	690	1299
9	117	349	714	1321
10	123	361	739	1356
11	123	363	765	1389
12	123	367	797	1404
13	129	381	826	1417
14	142	394	855	1446
15	167	409	885	1473
16	191	424	897	1491
17	215	426	914	1505
18	236	429	937	1524
19	244	437	950	1548
20	255	453	962	1579
21	268	461	978	1606
22	279	465	994	1626
23	285	468	1013	1655
24	294	473	1030	1683
25	294	479	1049	1704
26	294	486	1072	1730
27	294	498	1100	1756
28	295	512	1124	1780
29	298	525	1143	1802
30	304	542	1156	1824
31		558		1843

Table J1. Continued.

Day	April	May	June	July
		1977		
1	112[b]	401	973	1478
2	124	414	977	1495
3	125	426	987	1518
4	126	437	1011	1553
5	126	458	1033	1587
6	126	474	1042	1621
7	128	481	1048	1652
8	128	485	1056	1675
9	130	486	1061	1698
10	145	488	1070	1722
11	166	496	1086	1747
12	185	507	1095	1776
13	205	524	1107	1797
14	214	539	1123	1826
15	230	562	1140	1861
16	249	587	1163	1888
17	272	613	1190	1917
18	297	636	1215	1946
19	315	660	1234	1980
20	337	688	1252	2012
21	353	715	1264	2041
22	356	745	1281	2064
23	364	772	1299	2082
24	364	798	1327	2102
25	364	823	1349	2125
26	365	846	1369	2137
27	377	865	1393	2150
28	378	889	1419	2168
29	381	913	1441	2190
30	388	939	1459	2213
31		959		2241

[a] 99 °D > 48 accumulated during March 1976 at Eau Claire, Michigan (Berrien County) (Michigan Climatological Data, NOAA).

[b] 110 °D > 48 accumulated during March 1977 at Dowagiac, Michigan (Cass County) (Michigan Climatological Data, NOAA).