

EVALUATION OF MODELS OF SPRUCE BUDWORM - FOREST DYNAMICS:  
COMPARISON OF PREDICTIONS TO REGIONAL FIELD DATA

Richard A. Fleming  
Forest Pest Management Institute  
Canadian Forestry Service  
P.O. Box 490  
Sault Ste. Marie, Ontario  
Canada  
P6A 5M7

and

Christine A. Shoemaker  
Department of Environmental Engineering  
Cornell University  
Ithaca, N.Y.  
U.S.A.  
14853

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## ABSTRACT

The two large scale spruce budworm-forest simulation models were evaluated by comparing their output with Maine Forest Service survey data collected annually at 1000 sites from 1975 to 1980. Analysis of the models' output showed how the models' site conditions (defoliation and budworm density) one year were related to those in the next. Comparing these relationships, derived from model output, with the corresponding relationships derived from the survey data showed that neither model produced output which consistently mimicked the survey data.

Inconsistencies were most prevalent at low budworm densities, especially after spraying, when modeled budworm populations increased more slowly than the survey data suggests they ought to. Questions were posed concerning the models' representation of the Maine Forest Service spray policy, budworm population growth at low densities, and the effectiveness of spraying (especially at low budworm densities).

As a consequence of these uncertainties, the models' recommendation of early outbreak suppression as a superior alternative to the forest protection strategy currently used by the Maine Forest Service, should be regarded with some reservation.

## INTRODUCTION

The spruce budworm-balsam fir ecosystem has been the focus of some of the most intensive and innovative studies in the history of ecological modelling. These studies have included simulation (Jones 1979, Stedinger 1985), optimization (Winkler 1975) analytical (Fleming et al. 1987, Ludwig et al. 1978, 1979) topological (Jones 1977) and economic (Bell 1977) models. In addition, a number of models of specific components of the budworm-balsam fir ecosystem have also been developed (Blais and Archambeault 1982, Clark 1979, Fleming 1984, Osawa et al. 1983, Seymour et al. 1985, Gage and Sawyer 1979, Baskerville and Kleinschmidt 1981, MacLean 1982, Régnière 1983).

The results of these varied models have influenced forest management policy over much of Canada and the United States (Holling et al. 1979, Seymour 1985). The most widely applied of the ecosystem models is the one developed by Jones (Cuff and Baskerville 1982). Because of the interest in these models for establishing regional policy, government supported groups have been formed to adapt the Jones model, or parts of it, for local conditions (e.g., Baskerville 1976, Hall 1978).

The parameter values and functional relationships used in the simulation models were based upon data available to the authors when their studies were published. The primary source was data taken at some 45 scattered plots in the Green River area of northwestern New Brunswick from 1945 to 1959 (Morris 1963). From these and other limited sources the models attempt to describe the dynamics of the spruce budworm-forest ecosystem over large regions for long periods of time. None of the

models have been validated by detailed comparison of model output to regional field observations. It is the purpose of this study to make these comparisons. We have chosen for analysis the simulation models by Jones and by Stedinger because they represent the most thorough attempts to mimic the biological complexity of the system.

The spruce budworm *Choristoneura fumiferana* (Clem.) is economically the most important defoliator of North America's spruce/fir forests. This native insect has killed millions of hectares of trees during its 5-15 year population outbreaks; between outbreaks it remains rare for periods of 25-70 years. Since 1952 aerial insecticide applications have reduced the mortality in Maine and New Brunswick, but consequently, the particularly vulnerable older stands dominated by balsam fir, *Abies balsamea* (L.) Mill., now occupy much of this area.

Figure 1 illustrates the budworm life cycle. Moths emerge from their pupae in late June-early July and mated females lay about 10 masses of 15-20 eggs each on suitable foliage. Females lay almost all of their eggs close to their site of emergence and mating unless the local budworm population is large and the trees heavily defoliated. In that case, females may lay over half of their eggs after dispersing on the prevailing winds for an average of about 40 km (Greenbank et al. 1980) and sometimes much further (Dobesberger et al. 1983). The Maine Forest Service conducts its surveys of egg mass densities and tree damage shortly after egg laying is completed. The tiny first instar larvae hatch from the eggs by mid-August and crawl to suitable overwintering sites on the trees. Second instar larvae emerge from hibernation in early May and seek staminate flowers or mine unopened vegetative buds

and old needles as feeding sites in early May. By late May the larvae are developed enough to attack new foliage when the buds flush. The Maine Forest Service tries to time insecticide applications to coincide with the peak of the fourth larval instar population (Triall and Thurston 1980) which usually occurs between the last week of May and the first week of June. By mid-June the sixth instar larvae are 20-30 mm long and feeding heavily on new shoots. They will attack older needles once the new ones have been eaten. The larvae pupate in late June and the moths emerge in July, renewing the annual cycle.

#### SIMULATION MODELS OF THE SPRUCE BUDWORM ECOSYSTEM

The need to design and evaluate alternative policies for insect control and forest management motivated the development of the spruce budworm simulation models by Jones (1979) and Stedinger (1984). These authors attempted to comprehensively synthesize current scientific understanding and thus capture the essential qualitative behavior of the ecosystem. The models were to provide "laboratory worlds" in which the consequences of various alternative management strategies could be investigated.

Following Watt (1964), Jones and Stedinger divided the study area into rectangular grids or "sites" covering 173 km<sup>2</sup> and 93.3 km<sup>2</sup>, respectively. At each site the models compute the budworm population in any year  $t$  as a function of the budworm population density in year  $t-1$ , the age structure, foliage condition, and species composition of the trees, and the immigration and age specific survival rates of the insect (Fig. 2). Insecticide applications are assumed to kill 90% of the

budworm in the targeted area. The models treat defoliation and tree mortality as functions of budworm feeding, and after accounting for mortality, update the density, age structure, and species composition of the trees in the site. Because the models allow migration to occur from one site to another, decisions to spray or not spray one site eventually affect surrounding sites in the models.

The qualitative behavior of the models is conveniently described by the use of recruitment ratios (Ricker 1954). If  $EGG(t)$  is the density of budworm eggs in a site in year  $t$ , then the recruitment ratio,  $EGG(t+1)/EGG(t)$ , is greater than, less than, or equal to 1.0 when the budworm population is increasing, decreasing, or at equilibrium, respectively. Figure 3(a) shows recruitment ratios for the Jones model plotted against budworm population size for sites with forest conditions ranging from very poor for budworm (VP) to very good for budworm (VG). These forest conditions depend on the species composition, age structure, and foliage condition of the trees at the site.

To follow the qualitative behavior of the models let us first consider the recruitment curve for good (G) forest conditions for budworm in Figure 3(a). This curve shows budworm equilibria at  $L^*$ ,  $U$ , and  $H^*$ ; the three budworm densities where the recruitment curve crosses the  $EGG(t+1)/EGG(t) = 1.0$  line. It can be seen from the curve that the equilibrium at  $U$  is unstable since slightly larger budworm densities lead to continued increase and slightly smaller densities to continued decrease. By an analogous argument, the high and low density equilibria,  $H^*$  and  $L^*$ , are stable to small changes in budworm density.

The shape of the recruitment curves in Figure 3(a) reflects hypotheses regarding the relative impact of the various ecological processes (Figure 2) considered in the model (Holling et al. 1979). Competition among budworm for food causes the drop in the recruitment rate at high densities. Bird predation on budworm is largely responsible for the "pit" in the curve at budworm densities slightly above  $.5 \text{ masses/m}^2$  while parasitism limits survival at very low densities.

To understand the dynamics of the Jones (1979) model, consider recruitment curve G of Figure 3(a) which applies to a relatively mature forest. Suppose budworm densities are initially at their low equilibrium,  $L^*$ . The recruitment curve rises in response to forest aging because budworm have higher survival and reproductivity in older forests. As a result, the lower and middle equilibria,  $L^*$  and  $U$ , come together, coalesce, and then disappear as the bottom of the "pit" rises above the equilibrium line:  $\text{EGG}(t+1)/\text{EGG}(t) = 1$ . As the forest grows older still, it provides progressively better environments for budworm so the recruitment curve continues to rise, finally arriving at position VG in Fig. 3(a). The now overmature forest represented by position VG presents a very good environment for the budworm so its population increases quickly in response. During the outbreak the forest is assumed to suffer considerable defoliation and many of the older trees are killed (Blais 1985). Consequently, budworm population growth becomes food-limited and the forest age structure changes to one dominated by immature trees. This sudden deterioration of forest conditions, which results in declining budworm survival and reproductivity, is represented by a drop of the recruitment curve from position VG, through

positions G and then P, and ending with the recruitment curve at position VP in Figure 3(a). Here  $EGG(t+1)/EGG(t)$  is substantially less than 1 so the budworm population quickly collapses. The recruitment curve subsequently rises (to position P, for example) as maturation of the regenerated forest slowly improves the environment for budworm. Although another outbreak could theoretically develop in this situation (because the recruitment curve in position P crosses above the equilibrium line:  $EGG(t+1)/EGG(t) = 1.0$  when  $EGG(t)$  is large), the population collapse has carried the local budworm densities well below the 13 egg masses/m<sup>2</sup> needed to initiate an outbreak. (To trigger a local outbreak, moth immigration must increase the local budworm density to this level.) Further aging of the forest entails a slow rise in the recruitment curve, eventually returning it to position G in Figure 3(a).

Thus, in the Jones model the budworm responds very quickly to particular forest conditions (as represented by a particular position of the recruitment curve). Forest aging is represented by a slow rise in the recruitment curve (from position VP to position VG); the destruction of the mature forest and its replacement by an immature one are represented by a fast drop in the recruitment curve [from position VG to position VP in Figure 3(a)].

Jones (1977) and Casti (1982) have analyzed this phenomenon in terms of catastrophe theory, pointing out that as the forest ages it causes the budworm recruitment curve to rise from position G to position VG and thus transforms an inherently stable ecosystem with relatively low budworm densities into a highly unstable one which will only be restabilized by the destruction of the tree population serving as the



budworm's food source. Ludwig et al. (1978) demonstrated the ecosystem dynamics associated with these mathematical assumptions in an ecosystem with no migration, spraying or spatial heterogeneity.

Stedinger (1984) based his model on the general structure of the Jones model but used a different approach in deriving functional relationships. Whereas Stedinger relied almost exclusively on what detailed quantitative data was available in the literature, Jones and co-workers frequently gave substantial weight to the intuition of experienced entomologists and foresters due to a concern that much of this data (i.e. Morris 1963) was collected from an area unrepresentative of most of New Brunswick. As a result, some of the functional relationships in Stedinger's model differ markedly from those in Jones' model. Of particular importance, Stedinger excluded the avian predator "pit" and reduced small larval survivorship in his model. These changes had a substantial effect on the recruitment curve (Figure 3[b]): no lower stable equilibrium (corresponding to  $L^*$ ) exists and the distance between the unstable and upper stable equilibrium is less than for Jones' model. Outbreaks occur in Stedinger's model only when moth immigration raises the local population density above the current density of the unstable equilibrium; local populations below that density decline rapidly. As with Jones' model, the shape and position of the recruitment curve depends upon forest conditions.

#### METHODS

Our goal in this paper is to compare output from the Jones (1979) and Stedinger (1984) simulation models with field observations.

For this we used the field data collected by the Maine Forest Service in surveys of balsam fir defoliation and budworm egg mass densities from 1975 to 1980. Data were collected at approximately 1000 sampling sites each year shortly after egg laying was finished. At each sampling site, egg mass density was calculated as the mean number of new healthy egg masses per  $m^2$  of foliated branch surface, and defoliation as the percentage of balsam fir foliage produced in the current year which has been destroyed by budworm. Trial and Thurston (1980) and Morris (1955) describe the data collection methods in detail.

The ranges of defoliation and egg mass density were divided into the classes listed in Table 1 to provide a basis for making comparisons with model output. The six egg mass density classes correspond to those of the Maine Forest Service sequential sampling procedure. This procedure identified the discrete class in which a sampling site's egg mass density lay with a pre-determined degree of confidence.

Unfortunately, the Maine Forest Service rarely collected data in precisely the same sampling site in consecutive years. Therefore, to estimate how forest conditions one year affected those in the next, we enlarged the spatial scale beyond individual sampling sites, and for convenience, adopted the grid of 6.4 km x 8.0 km "blocks" of forest used by the Maine Forest Service in mapping their surveys. Blocks containing both sprayed and unsprayed sampling sites were excluded from the analysis for that year. The mean egg mass density and defoliation of a block were then estimated by averaging over all sampled sites in the block. By comparing block conditions in successive years, we estimated how

conditions one year were related to those in the previous year (Fleming et al. 1983, 1984).

To properly appraise the biological aspects of the models, initial conditions and the nonbiological components (e.g., spray and harvest policy submodels) must be reasonably representative of Maine conditions. Otherwise, one can't tell whether the biological aspects or these other aspects of the models, or both, are responsible for any discrepancies between model output and field observations. Where model structure (e.g., the limited spatial resolution) or information gaps (e.g., the lack of field data for stand foliage levels) preclude precise representation of Maine conditions, we adopted assumptions made by Stedinger (1984) in using his model as a "laboratory world" for Maine. (To our knowledge Jones never specifically adapted his model to Maine conditions.) Hence, in the simulations, stands were even-aged as observed (Baskerville 1976, Seymour 1980) and all trees were cut at age 60 as directed by Stedinger's representation of the harvest policy used in Maine. The models were relatively insensitive to realistic alternatives to this cutting age.

Since model output was sensitive to spray policy and since the historical data differed with parts of Stedinger's representation of Maine's spray policy, we ran simulations for each of five different spray policies. These five different spray policies are discussed in detail below.

Transient effects due to the choice of initial conditions possibly unrepresentative of Maine in the simulations could also distort our testing of model accuracy. We allowed time for such distortions to

damp out by running the simulations for 110 years and deleting output for the first 10 years from the statistical records. We found no evidence of transient effects after these first 10 years.

Thus, during each simulation, the egg mass density and percent current defoliation for each of the 80 modeled sites of forest were recorded for each of the last 100 years. These records were subsequently analyzed to determine the relationships between site conditions one year and site conditions the next. These relationships, derived from model output, are compared with the corresponding relationships derived from Maine Forest Service observations below. Since modeled sites are assumed to be either totally sprayed or totally unsprayed in any given year, field observations were ignored from blocks of forest in which part of the sampled sites were sprayed.

#### COMPARISON OF FIELD DATA AND MODEL RESULTS

It would be instructive to isolate the biological component of the budworm models by comparing field data to the curves given in Figure 3. However, while Figure 3 represents the dynamics of an area which is unsprayed and which is unaffected by migration, the MFS field data is necessarily collected in areas where both migration and spraying are important. Hence, as Jones and Stedinger found while validating their models, for purposes of comparison with historical data, it is necessary to deal with the complete simulation models which include three interacting and mutually dependent components: a spruce budworm submodel, a forest submodel, and a management policy submodel. We begin by consid-

ering observations which largely reflect the influence of just one of these three components.

### *Spray policy submodel*

Initially we consider the submodel concerned with management policy. As an approximation of the forest-protection policies used in Maine and New Brunswick, Stedinger (1984) developed what he termed the "forest-protection" policy for his management submodel. According to this policy, insecticide is applied to all modeled sites likely to suffer excessive tree mortality in the absence of spraying. Such sites are identified when their lack of foliage and their budworm egg densities fall in a previously defined danger zone. This policy is deterministic in the sense that whenever a site's forest conditions deteriorate sufficiently, the site is sprayed in the next year; otherwise it is not. Hence, we will refer to this as the deterministic spray policy and denote it by DSP.

To appraise the spray policy submodel we compare the observed frequency with which blocks of forest in a particular condition were sprayed with the corresponding frequency resulting from the use of the spray policy submodel on modeled sites. Since the variables common to both the models and the survey data were egg mass density and current defoliation, these variables were used to classify forest conditions as shown in Table 1. Table 1's six egg mass density classes correspond to those used in the Maine Forest Service (MFS) sampling procedure; because of the sequential aspect of this sampling procedure, the discrete egg

mass density classes are used where possible rather than the mean egg mass densities themselves.

Table 2 gives the spray frequencies observed as a function of estimated block conditions in the previous year. For instance, observations showed that current defoliation was in Class 4 and egg mass density was in Class 3 for 199 blocks from 1975-1979. Of these 199 blocks, 19% were sprayed in the following year. As indicated by the confidence limits (estimated from Pearson and Hartley, 1968, Table 41), we can be 95% confident that the true mean spray frequency for such blocks lies in the range 0.14-0.25. Tables 3 and 4 give the corresponding spray frequencies in modeled sites over 100 years when the Stedinger and Jones models, respectively, were run with the DSP.

Tables 2, 3 and 4 suggest that both models overestimated spray frequencies for sites in poor condition [i.e., with large values of DEF(t) and EGG(t)] and underestimated spray frequencies for sites in good condition [i.e., with small values of DEF(t) and EGG(t)]. For example, the 95% confidence interval for the proportion of forest blocks in current defoliation class 5 and egg mass density class 5 which was sprayed in the following year was 0.17-0.34 (Table 2). For sites with the same defoliation and egg mass density classifications, the Stedinger and Jones models produced spray frequencies of 0.60-0.77 (Table 3) and 0.90-0.99 (Table 4), respectively, when run with the deterministic spray policy (DSP).

One possible explanation for these discrepancies is that, because of its deterministic values, the DSP does not entirely represent the 1976-1980 Maine Forest Service spray policy. According to the DSP

all sites whose condition has deteriorated beyond the pre-determined danger thresholds, and no others, are sprayed. Actually, the MFS spray policy has a stochastic quality to it: a threshold is used to determine those blocks to be considered for spraying but many of them are subsequently withdrawn from the spray program for environmental, political, or financial reasons (Trial and Thurston 1980). We incorporated this stochastic element into the DSP by spraying only part of the sites with poor forest conditions. Three different stochastic versions of the DSP were incorporated in the Stedinger and Jones models, but none produced output that resembled that of Table 2.

As a fourth alternative for the spray policy submodel, we also developed a "stochastic spray policy", denoted as SSP, which is not derived from the deterministic spray policy (DSP). Two constraints were placed on possible SSP's: First that they empirically mimic the observations given in Table 2, and second, that the spray frequency be a monotonically increasing function of both egg density and defoliation. Table 5 presents the SSP used in this analysis (the results were insensitive to small variations in the SSP). Although Table 5 empirically approximates aspects of the actual spray policy, it is an incomplete description because it excludes some factors (e.g., previous damage suffered by the stand) considered by the Maine Forest Service when deciding where to spray.

### *Biological submodels*

So far we have concentrated on the spray policy components of the simulation models. We now consider the biological components and

try to isolate their effects as much as possible from the immediate influences of the spray policies. We do this by examining the relationships between indicators of the biological condition of unsprayed forest blocks at successive times and comparing these relationships with corresponding ones determined from model output.

Figure 4 illustrates such relationships between the current defoliation sustained by an average unsprayed block of forest and its budworm egg mass density later in the same summer. The model output for this figure derives from simulations for a region of 8 x 10 sites in which the sites were classified in terms of their current defoliation each year according to Table 1; the vertical axis gives the mean egg mass density and 95% confidence interval, assuming 20 eggs per mass (Morris 1963), for sites in each defoliation class. In this and the following figures the deterministic (DSP) and stochastic (SSP) spray policies were used in parts a and b, respectively. Although the areas providing the data for Fig. 4 are unsprayed, spraying still has some impact on the results: the rates of budworm migration into these unsprayed areas are affected by spray policies in neighboring areas and current forest conditions in the area are affected by the area's spray history.

Underrating of the smoothing effect of dispersal could account for the models' apparent underestimation of budworm egg densities at low levels of defoliation and the overestimation of budworm egg densities at high levels of defoliation (Fig. 4). A greater tendency for moths to lay eggs after dispersing in the models would cause a net transference



of eggs (due to the net flux of moth dispersal) from sites suffering much current defoliation to blocks suffering little.

Figure 4 also shows that discrepancies between field data and model output are more marked for the deterministic (DSP) than for the stochastic (SSP) spray policy. This supports the contention that the SSP better approximates the spray policy in effect during the period of data collection. However, even with the stochastic spray policy, in only four of 12 cases does model output produce a confidence interval which overlaps the corresponding interval for the Maine Forest Service survey data (Fig. 4b). The trends represented by the model output with the SSP are also qualitatively different from those represented by the survey data. The egg mass densities from the model output increase steadily with increasing current defoliation but decrease at very high levels of current defoliation. The survey data, on the other hand, show a more gradual increase but one which is sustained throughout the range of current defoliation.

A notable feature of Fig. 4 is that unsprayed sites sustaining high current defoliation tend to receive higher egg mass deposits under the deterministic (DSP) spray policy than under the stochastic (SSP) one. This occurs because, in contrast to the SSP, all sites with little remaining foliage and high egg mass densities are sprayed in the following year under the DSP, thus preventing a site from sustaining high defoliation in successive years. Hence, unsprayed sites suffering high defoliation in the current year generally sustained less defoliation of new shoots in the previous year, and therefore have better foliage conditions overall under the deterministic spray policy (DSP) than under

the stochastic (SSP) one. Since poor overall foliage condition of a site can substantially restrict budworm numbers in the models (Fig. 3), it follows that an unsprayed site sustaining much current defoliation will generally have lower egg mass densities under the stochastic spray policy (SSP) than under its deterministic counterpart. This effect is more pronounced with the Jones model than with Stedinger's because the former generally provides the budworm with greater capacity for immediate increase under a given set of forest conditions (Fig. 3).

Figure 5 describes field and model observations concerning the relationship between the egg density in an unsprayed block of forest and the defoliation sustained by that block in the next summer. Since moth dispersal does not occur between the time eggs have been laid and the time at which the resulting larvae have completed their attack on host tree foliage (Fig. 1), underestimation of the smoothing effect of dispersal cannot be invoked to account for the models' apparent underestimation of defoliation at low egg mass densities.

Figures 6 and 7 show the corresponding relationships between successive egg densities and between successive percentages of current defoliation, respectively. For large values of the abscissa in Figures 5 and 6, model output provides slightly better approximations to observation for the stochastic (SSP) than for the deterministic (DSP) spray policy. However, the same cannot be said for Figure 7 so, on the whole, Figs. 5-7 provide only weak evidence, at best, that the SSP better approximates Maine Forest Service practice than the DSP.

Differences between the output of the models in Figures 5-7 are generally the result of differences in each model's dynamic structure

(Fig. 3) operating in concert with different spray policies (Tables 3, 4, and 5). For instance, in Fig. 6, Jones' model gives larger egg mass densities than Stedinger's model for sites with 60 masses/m<sup>2</sup> in the previous year (i.e. for sites with EGG(t) = 60) because Jones' model tends to have greater recruitment ratios (Fig. 3) than Stedinger's model at these densities. Furthermore, both models tend to give larger mean values of EGG(t+1) with the deterministic (DSP) than with the stochastic (SSP) spray policy in unsprayed sites (Fig. 6). This occurs because sites with bad conditions for budworm are more likely to be sprayed (and therefore excluded from consideration in Fig. 6) under the DSP than under the SSP; hence, the average rate of recruitment for budworm tends to be higher with the DSP than with the SSP (Fig. 3).

Sampling error explains at least part of the consistent discrepancy between model output and observation at the abscissa's lower extreme in Figures 5-7. Because defoliation and egg mass density are measured together at each sampling point, the MFS survey provides a record of the relationship between the current defoliation sustained by a stand and the egg density that resulted from egg laying by local and immigrating moths later that summer (e.g., Figure 4). Unfortunately, data were rarely collected in the same stand in consecutive years. Therefore, to determine how forest conditions one year influenced those in the following year for Figures 5-7, the spatial scale of the analysis was enlarged beyond individual sampling points. Because the MFS uses 6.4 km x 8.0 km 'blocks' of forest to map their survey, we adopted this scale and the MFS mapping system to delineate block boundaries. Enlarging the spatial scale can lead to sampling error, especially when only

one, possibly unrepresentative, site is measured within the block (as happened in 60% of the cases examined). Thus, a number of blocks whose actual condition is average could fall within the extreme classes of the abscissa variable of Figures 5-7. Since observations in average blocks in the subsequent year are expected to indicate average conditions, some bias towards the overall mean is expected for the indicator of block conditions plotted along the ordinate in Figures 5-7. This provides a partial explanation for the apparent underestimation by the models at the lower end of the abscissa in these figures.

There is a way to quantify the sampling error. This error arises because, with only one or two forest sites sampled within most blocks in any year, the averages may be little more precise than one observation from a randomly selected site within a block. Figure 8 shows the variability of reported egg mass densities in both sprayed (letter 's') and unsprayed (letter 'u') forest blocks in which measurements at four or more sites were taken. Because the Maine Forest Service increased the sampling density in areas where variability was expected (Trial and Thurston 1980), Figure 8 also represents a likely upper limit to the sampling error due to estimating conditions throughout a forest block from a single sample site.

However, sampling error alone cannot account for all of the differences between observations and model output. If the error introduced by sampling only a few sites within a block is substantial, it should also consistently produce apparent overestimation by the models for large classes of the abscissa variables in Figures 5-7. Such consistent overestimation is not evident. Moreover, the discrepancies between

model output and observation in Figure 4 cannot be explained by such sampling error because here both the ordinate variable and the abscissa variable were measured at the same sampling site.

### *Insecticide application*

We now examine the short term effects of insecticide application on the survey observations and model predictions. Figures 9-11 describe the same relationships as Figures 5-7, respectively, except that Figures 9-11 apply to blocks which were sprayed in year  $t+1$ . Differences between the deterministic (DSP), and stochastic (SSP) spray policies seem relatively small in comparison with the differences between observations and model output; the models overestimate the effectiveness of spraying (i.e., underestimate the variable plotted on the ordinate).

The value of 90% used for the per capita spray mortality rate in the models is typical for small scale insecticide trials. But there are at least three reasons to suspect that these reported mortality rates are not appropriate for the models. First, the rates were estimated by measuring the change in larval population densities per 18 inch branch tip on balsam fir. Since the branch tips are the parts of the foliage most exposed to spray, the estimated mortality rates on the branch tips should be viewed as upper bounds to the actual rates for the foliage as a whole. But since larvae prefer to feed near the branch tips, the average spray mortality rate for all budworm on a tree may not be far below this upper bound.

Second and more serious, although balsam fir is the dominant tree species in Maine's forest protection area, it comprises only about

35% of the trees. The spruces, which contribute about 25% of the trees, are the only other species group comprising over 10% of the forest (Mott 1980). While insecticide-caused budworm mortality rates of 80-95% are common in efficacy trials on balsam fir, effective spray application on spruce is harder to achieve. For instance, in controlled tests in eight different areas, Trial and Devine (1982, p. 21) report a median spray mortality rate of just 45% on spruce. This difference in spray mortality rates would not be important if balsam fir was always heavily favored by budworm as its principal host species. This was widely believed to be the case when the models were first constructed, but later work (e.g., Seymour 1980, Webb and Irving 1983) has brought this view into question. If spruce does support an important part of the budworm population, then the average spray mortality rate for Maine's forest protection region probably lies somewhere between 45 and 90%.

There is a third reason for suspecting that operational spray mortality rates lie below the 90% value used in the models. Insecticide applications are generally well timed in the small scale trials producing 90% mortality, but operationally, good timing is difficult to achieve. Asynchrony in larval development and foliage expansion, logistical difficulties, and poor weather conditions have all posed problems. Ideally, insecticide is applied when foliage expansion provides an adequate spray target and when the larval population is in its vulnerable fourth instar stage. When these two events do not coincide, the Maine Forest Service uses bud development as the primary criterion for spray timing. Difficulties can arise where applications are mistimed. For instance, where carbaryl applications were delayed in 1979, 89%

current defoliation occurred and 2.8 larvae survived per 45 cm branch tip compared to 33% defoliation and 0.9 larvae with proper timing (Trial and Thurston, 1980, pp. 40-41).

On the other hand, shortcomings in the survey methodology could lead to an underestimation of the effectiveness of spraying from the field data in Figures 9-11. For example, when sampling occurs near roads over which pilots stop spraying (for environmental reasons), suppression in spray blocks may appear less effective than it really is.

Comparing model output in Figs. 5-7 with that of Figs. 9-11, it can be seen that the patterns displayed are quite different depending on whether insecticide was applied, or not. With spraying, monotonically (almost linearly) increasing curves (Figures 9-11) can describe model results. In the absence of spraying, plots of the corresponding model output often show non-monotonic (humped) curves (Figures 5-7). The assumption common to both models that budworm recruitment rates decline during conditions of resource limitation (Fig. 3) contributes to the 'humped' shape of these curves.

The model output also differs from the survey data with respect to the effectiveness of spraying under various forest conditions. For instance, model output suggests that the largest relative 'improvements' in forest conditions associated with spraying occur at egg densities of 20-60 masses/m<sup>2</sup> (compare Figure 5 with 9 and 6 with 10) and at 20-60% current defoliation (compare Figure 7 with 11). By contrast, the field data suggest that spraying is most effective at high egg densities and high defoliation levels.

Another factor, besides the difficulties in estimating budworm mortality caused by operational sprays, could also contribute to these discrepancies between model output and observation. Both models use an unstable equilibrium at low densities in their representation of budworm population dynamics (Fig. 3) and it may contribute to differences between the shapes of curves describing model output and those describing field observations. Whenever spraying lowers budworm densities just below this unstable equilibrium, the models predict further population decline because of the assumption that per capita mortality due to natural factors increases as budworm density decreases in this range. Hence, if spraying reduces the budworm numbers below this threshold in the models, natural factors can delay subsequent recovery of the population. In effect, the budworm population in a modeled block becomes 'trapped' at low densities and external factors (e.g., weather, moth invasion rates, forest conditions) must change before an outbreak can occur. In contrast, if budworm densities remain much larger than this threshold, the contribution of natural mortality factors is assumed to be relatively small until the population becomes resource limited. Therefore, if this low density 'trapping effect' in the models were reduced, (by assuming, for instance, higher budworm survival or reproductive at low densities), modeled populations would recover from spraying more quickly and thus bring model predictions into better agreement with the survey observations in Figures 9-11.

In fact, some workers dispute the very existence of a low density unstable equilibrium and its associated 'trapping effect'. To a large extent, the budworm dynamics of the models are based on Morris'



(1963) analysis of the data from the Green River project in New Brunswick. Dissatisfied with Morris' analysis, Royama (1984) has re-analyzed the Green River data along with information on the budworm-forest ecosystem in New Brunswick acquired since the models were constructed. While acknowledging a number of limitations of his data set, Royama argues against the models' concept of low density and epidemic states separated by an unstable equilibrium which serves as a "release" density (Fig. 3). Rather, contradicting the model's implication that low density populations can be 'trapped', Royama suggests that such populations increase smoothly with time.

Alternatively, a constant net influx of dispersing moths could dampen a real low density 'trapping effect' in the budworm population dynamics. The models employ reflecting boundaries to represent moth dispersal at the edge of the modeled region. Accordingly, the number of egg-laying moths leaving the set of blocks described by the models are exactly compensated by an equal number of immigrants traveling the same distance in the opposite direction. A consistently high level of net immigration would violate the reflecting boundary assumption and could provide a partial explanation for the differences between survey observations and model output noted above. However, there's neither evidence that areas bordering on Maine had the consistently higher budworm densities likely to produce such influx (Kettela 1983, Trial 1980), nor that such influx consistently occurred (Weed 1977, Trial and Thurston 1980).

*Overall model behavior*

Thus far we have tried to study particular components of the models in relative isolation. By comparing model predictions with observations, we have made inferences about the reliability of the models' representations of management spray policy, of spruce budworm-forest dynamics, and of the effect of spraying on these dynamics. However, the main purpose of these models has been to predict the average long-term behavior of the budworm-forest ecosystem as a whole when different management policies are followed. Hence, to test the suitability of the models for this objective, we examine model output which reflects on overall model behavior. We attempt this in Tables 6-11.

Table 6 shows the mean annual frequency of spraying in the model output for various spray policies and in the Maine Forest Service survey data. The models' tend to underestimate the mean spray frequency of .226 observed in the survey data. This tendency is consistent with the suggestion made earlier when discussing Figs. 9-11 that the models may be overestimating spray mortality and/or underestimating low density budworm recruitment rates. Either of these potential miscalculations would unrealistically prolong the time taken by modeled budworm populations to recover their pre-spray densities. Such prolonged recovery times would, in turn, slow the rate of forest damage in the models and ultimately delay the time when the budworm-forest system had deteriorated enough to warrant spraying again. Thus the time between spray applications would be unrealistically long, and hence, the frequency of spraying would be unrealistically small.

Table 6 also adds support to the suggestion made above that the models may be overestimating spray mortality rates. When Stedinger (1977) reduced the spray mortality rate for budworm larvae from 90% to 80% with the deterministic spray policy (DSP2), he computed a mean annual spray frequency of  $.222 \pm .014$  per site in his model. This is remarkably close to the estimated true mean of  $.226 \pm .046$ .

Table 7 gives the frequencies observed in the survey data with which the conditions in blocks of forest fell in the different egg mass density and current defoliation classes defined in Table 1. Thus, the frequencies reported for each of the 36 possible EGG(t) x DEF(t) states sum to 1.0. The range of the 95% confidence intervals is given in parentheses underneath the mean frequency corresponding to each DEF(t) x EGG(t) combination.

Tables 8-11 give the corresponding frequencies observed in model output. In these tables the presence of an asterisk distinguishes those DEF(t) x EGG(t) combinations for which the 95% confidence interval about the models' mean does not overlap the corresponding interval about the survey data's mean. For instance, the lack of an asterisk for the [DEF(t) = 1] x [EGG(t) = 1] combination in Table 8 shows that the 95% confidence interval (.02-.04) about the mean predicted by the Stedinger DSP model overlaps with the corresponding interval (.02-.03, Table 7) for the survey data.

The large sample sizes (6325 survey sites, 8000 model sites) cause the confidence intervals to be quite small in Tables 7-11. Hence, overlap of confidence intervals represents a severe test of model accuracy: small errors in the models are unlikely to be hidden by small

sample sizes. The results reflect the severity of the test: the 95% confidence intervals overlap for only 22% (Table 11) to 42% (Table 10) of the 36 different DEF(t) x EGG(t) combinations possible in each of Tables 8-11.

A shortcoming of this approach is that the frequency of overlap of confidence intervals does not reflect the magnitude of differences between the relevant means. While many differences may be statistically significant (due to the large sample sizes), the magnitude of the differences may be so small as to be considered trivial. To account for this, the difference between the means calculated from the survey data and the model output is provided in Tables 8-11 for each class of block conditions. This difference, denoted by the letter 'e' in the keys of Tables 8-11, is given in parentheses after the mean corresponding to each defoliation x egg density combination. For instance, the value of -.69 for the combination [DEF(t) = 1] x [EGG(t) = 1] in Table 11 indicates that the mean frequency calculated from model output (.71) exceeded that from the survey data by 0.69.

Two general patterns emerge from examining these differences in Tables 8-11. First, with each model x policy combination, the model's frequency vastly exceeds the reported frequency with which the budworm-forest-management system resides in certain [DEF(t) = 1] x [EGG(t) = 1 or 2] states. The maximum model-survey differences between the mean frequencies of occurrence for each model x policy combination are: 0.21 (Stedinger x DSP, DEF(t) = 1 x EGG(t) = 2), 0.32 (Stedinger x SSP, DEF(t) = 1 x EGG(t) = 2), 0.43 (Jones x DSP, DEF(t) = 1 x EGG(t) = 1), and 0.69 (Jones x SSP, DEF(t) = 1 x EGG(t) = 1).

There is also a tendency for the models to underestimate the observed frequency with which 90% to 100% of new foliage was consumed (defoliation class 6). Summing over EGG classes 1-6 for DEF = 6 in Table 7, between 90% and 100% current defoliation occurred in an average of 37% of the blocks per year in Maine's forest protection area from 1975 to 1980. The corresponding model predictions are 13% (Stedinger x DSP), 11% (Stedinger x SSP), and 0% (Jones x both spray policies).

Taken together, these two patterns indicate that the models tend to predict the occurrence of "good"/"bad" conditions more/less often than they were observed to occur in the survey data. This supports the conjecture made above when discussing Table 6, that the models unrealistically prolong the time taken by their budworm populations to recover after spraying. There are a number of possible reasons for this, some of which have been discussed above. These include: (1) overestimation of operational spray efficacy in the models, (2) underestimation of operational spray efficacy in our analysis of the survey data, (3) underestimation of the growth of budworm populations at low density in the models, (4) sampling error in the analysis of the survey results, and (5) inaccurate representation of the relevant spray policies in the models. Of these five possible explanations, the first and third are most appealing because, besides providing a possible mechanism to explain the discrepancies between model output and observation in Tables 6-11, they may also apply to some of the figures and the other tables as discussed above. Inaccurate representation of the spray policy is less appealing as a universal explanation: it is unclear how

such misrepresentation could produce the pattern of discrepancies reported for unsprayed blocks (Figures 4-7). Likewise, underestimation of operational spray efficacy in analyzing the survey data, while probably a factor in Figs. 9-11, is unlikely to play a role elsewhere in our analysis. Similarly, sampling error cannot explain the discrepancies between model output and the survey data where analysis of the latter have used the sampling site as the unit of spatial resolution (Fig. 4, Tables 8-11).

However, questions about the survey data remain. The Maine Forest Service surveys are arguably the most appropriate independent data set currently available for testing the models. Nonetheless, the surveys were not designed for this purpose and are not perfectly suited to it for a number of reasons. First, the spatial resolution of the data is quite different from the spatial resolution on which the models operate. The data are often collected at sites within forest stands and these data are pooled and manipulated, as described earlier, to infer how the condition of average 6.4 km x 8.0 km (51 km<sup>2</sup>) 'blocks' of forest change from year-to-year. In contrast the Jones model uses approximately 11 km x 16 km (190 km<sup>2</sup>) blocks (Holling 1978, Figure 11.5) and Stedinger's model uses approximately 9.7 km x 9.7 km (93 km<sup>2</sup>) blocks. Both models assume spatial homogeneity within a block: budworms, host trees, host foliage, predators, parasites, and insecticide (if applied) are all uniformly distributed. But it is unclear how the models' limited representation of spatial variability could cause the observed discrepancies between the survey data and model output.

A second weakness in using the Maine Forest Service survey data to test the models, is that the surveys have been conducted on a large scale only since 1975, while the models were studied using runs of 100 years. Comparing this survey data with model output therefore implicitly invokes the assumption that, since 1975, the Maine budworm-forest-management system was in a state corresponding to 100 year averages of model conditions. But because Maine's forest was going through an outbreak during this period (Kettela 1983) Table 7 includes the larger frequencies of occurrence of heavy defoliation and the smaller frequencies of low egg counts and low defoliation associated with an outbreak, and not 100 year averages. Similarly, the mean spray frequencies for the survey data in Table 6 apply to situations of frequent spraying. Hence, the fact that observations were recorded during an outbreak provides a possible explanation for some of the discrepancies between model output and the survey data in Tables 6-11. However, this does not readily explain the discrepancies evident in Figures 4-7 and 9-11 and evident in comparing Table 2 with Tables 3 and 4. The particular relationships illustrated in these tables and figures are relatively independent of the phase of the outbreak cycle.

The third possible weakness in the data applies only to the Jones model. This model was developed for New Brunswick which is slightly different from Maine in terms of its forest structure, climate, and various other ecological factors. It is only natural to expect such ecological differences to show themselves in comparisons of the output of a model designed for New Brunswick and field observations from Maine. However, it is not clear which, if any, of these ecological dif-

ferences could account for the sizes and particular patterns of the discrepancies between observation and output of the Jones model in Tables 6-11. Moreover, with only small adjustments, the developers of this model have applied it as far away as northwestern Ontario (Holling 1978).

#### CONCLUSIONS

Generally output from Stedinger's (1984) model provided a closer match to the 1975-1980 Maine Forest Service survey data than that of Jones' (1979) model, although neither model produced output which consistently mimicked the survey data. Inconsistencies were most prevalent at low densities, especially after spraying, when budworm populations increased more slowly in the models than in the survey data.

Causes for these inconsistencies could lie in our treatment of the survey data, in the biological aspects of the models, and in the management aspects of the models. The relatively short observation record (6 consecutive years) and the sampling errors associated with data collection and analysis limit the degree to which this survey data reflects long term budworm-forest dynamics in Maine.

Questions concerning the biological and management aspects of the models are more serious. Royama (1984) argued that the statistical analysis of Morris' (1963) Green River data, upon which the models are based, is flawed. After reanalyzing this data, Royama concluded that the Green River budworm populations increased smoothly from low densities without enduring the 'trapping effect' of a low density unstable equilibrium inherent in the models. Our results for Maine (Figs. 5-7, 9-11; Tables 6-11) are not inconsistent with Royama's claim.



The suitability of the biological aspects of the models for Maine conditions is also open to question. Both models base their biology on the Green River data from northwestern New Brunswick where the forest ecosystem is slightly different from that in much of Maine with respect to weather, species composition, phenology, etc. Furthermore, Jones specifically developed his model for New Brunswick, not Maine, although it has been freely adapted to a wide range of budworm habitat in Canada (Holling, 1978).

Questions concerning the management submodels centre on how accurately they reflect Maine Forest Service policy (Tables 3-4) and on whether they accurately represent the effectiveness of operational insecticide applications (Figs. 9-11, Tables 6-11). Because of the complex interaction of the management submodels with the biological submodels, and because of the form of the survey data, we cannot provide conclusive answers to these questions. For instance, the tendency of the models to overestimate spray frequencies for sites suffering much current defoliation in the previous year (Tables 3-4) could be due to inaccuracies of the deterministic spray policy (DSP). On the other hand, possible biological problems with the models which too often associated heavy current defoliation with large egg mass densities (Fig. 4) could also contribute. Such problems would cause sites suffering heavy current defoliation in the previous year to warrant spraying too often.

Moreover, both the stochastic (SSP) and the deterministic (DSP) spray policies have flaws: the SSP considers only forest damage inflicted in the previous year in selecting sites for spraying, the DSP

also ignores all the stochastic elements (e.g., weather, logistical difficulties, environmental and financial concerns) which can prevent the spraying of a selected block of forest. In addition, the models' value of 90% spray mortality is probably overestimated.

A key question is what effect correcting the inconsistencies noted above could have on the best strategies developed on the models. Would the implementation of faster budworm population growth at low densities or reduced spray mortality rates in the models alter their jointly recommended strategy of spraying low density budworm populations?

Both of these implementations would likely work against the cost/benefit ratio of the low density spray threshold: modeled budworm populations would now be higher and growing at a faster per capita rate immediately after spraying than in earlier versions of the models. Hence, more frequent spraying would be needed to maintain low densities and this would result in higher costs.

Furthermore, Figs. 9-11 suggest the disturbing possibility for low density spraying that the operational per capita mortality rate decreases with budworm density. Fleming et al. (1984) suggest possible reasons for this. First, at high densities the heavy foliage depletion often causes increased larval movement over the branches in search of feeding sites. Second, high density populations 'thin' the foliage. As a result, spray droplets may better penetrate to the normally less exposed foliage within the enclosure of a tree's branches and thus give better spray coverage. Both these factors tend to increase the proportion of larvae contacting spray residue and thus increase spray mortality. Third, if spraying interferes with those natural enemies which are

particularly effective at low budworm densities, then insecticide caused budworm mortality may be just replacing, rather than augmenting, natural mortality.

Given these uncertainties regarding the models' representation of spray mortality and of low density budworm population growth, the model results should be regarded with some reservation. Hence, although the low budworm density spray threshold may yet prove to be a good control strategy, an unequivocal statement to this effect is premature.

This raises questions about the process of model evaluation and points out that the term "validation" is a misnomer for testing model accuracy. Both the Jones model (Holling, 1978) and the Stedinger model (1984) were "validated" by the authors. Assuming reasonable accuracy of the spray and harvest policies in the models, they showed that the broad qualitative behavior of the models matched certain corresponding aspects of the system behavior "reasonably well". Our more detailed tests, based on information unavailable to the authors at the time, have established more restrictive limits to confidence in model accuracy. But this is to be expected: as new data arrive, established hypotheses are refined. In science, creative thinking is not always flawless, but it is almost always valuable.

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Table 1. Designation of classes by variable range.

Variable	Class	Class Description	Variable Range
EGG (masses per m <sup>2</sup> of foliage)	1	none	EGG < .05
	2	light	.05 ≤ EGG < 10.7
	3	moderate	10.7 ≤ EGG < 25.8
	4	high	25.8 ≤ EGG < 43.0
	5	very high	43.0 ≤ EGG < 107.6
	6	extreme	107.6 ≤ EGG
DEF (% of new foliage destroyed)	1	trace-light	⊕ DEF < 15
	2	light	15 ≤ DEF < 30
	3	moderate	30 ≤ DEF < 50
	4	heavy	50 ≤ DEF < 80
	5	severe	80 ≤ DEF < 90
	6	very severe	90 ≤ DEF < 100

Table 2. Spray frequencies as a function of block conditions in the previous year - field data. Table 1 defines the classifications.

DEF(t)	1	2	3	4	5	6
EGG(t)	1	2	3	4	5	6
1	.00(21)	.01(93)	.07(43)	.05(22)	.07(27)	.5(2)
2	(.00,.16)	(.00,.05)	(.01,.20)	(.00,.23)	(.01,.24)	
3	.00(10)	.09(80)	.06(66)	.14(28)	.04(26)	
4	(.00,.31)	(.04,.18)	(.02,.15)	(.04,.32)	(.00,.21)	
5	.00(4)	.09(94)	.14(95)	.09(50)	.21(42)	.5(2)
6	(.04,.17)	(.09,.23)	(.03,.21)	(.10,.37)		
1	.17(9)	.13(136)	.19(199)	.21(138)	.19(114)	.14(14)
2	(.01,.55)	(.08,.21)	(.14,.25)	(.14,.29)	(.12,.28)	(.02,.43)
3	.19(58)	.20(94)	.22(68)	.26(82)		.03(18)
4	(.10,.31)	(.13,.29)	(.13,.34)	(.17,.34)		(.00,.24)
5	.21(113)	.38(296)	.40(206)	.40(254)		.45(75)
6	(.14,.30)	(.32,.44)	(.33,.47)	(.34,.46)		(.33,.57)

KEY: m(n) where m = mean frequency, n = sample size, and U and L are the upper and lower 95% confidence limits, respectively.

Table 3. Spray frequencies as a function of block conditions in the previous year - Stedinger model with the DSP. Table 1 defines the classifications.

DEF(t)	EGG(t)					
	1	2	3	4	5	6
1	.00(229) (.00,.02)	.00(1957) (.00,.00)	.01(380) (.00,.02)	.24(17) (.07,.51)		
2	.00(13) (.00,.25)	.00(822) (.00,.01)	.01(684) (.00,.02)	.02(55) (.00,.11)	.5(4)	
3	.00(2) (.00,.01)	.00(350) (.00,.01)	.03(759) (.02,.04)	.07(309) (.04,.11)	.14(42) (.05,.29)	
4	.00(58) (.00,.06)*	.14(237) (.11,.19)	.26(457) (.22,.30)	.30(321) (.25,.35)		
5	.45(11) (.16,.73)	.60(40) (.47,.75)*	.69(124) (.60,.77)*	1.00(2)		
6	.5(6) (.85,.95)	.91(164) (.92,.97)*	.94(859) (.79,1.00)*			

KEY:  $m(n)$  where  $m$  = mean frequency,  $n$  = sample size, and  $U$  and  $L$  are the upper and lower (L,U) 95% confidence limits, respectively.

\* Indicates no overlap with the corresponding confidence interval for the field data (Table 2).

Table 4. Spray frequencies as a function of block conditions in the previous year - Jones model with DSP. Table 1 defines the classifications.

DEF(t)	1	2	3	EGG(t)		4	5	6
1	.00(3579) (.00,.00)	.00(1779) (.00,.00)	.00(38) (.00,.09)					
2		.00(307) (.00,.02)*	.00(384) (.00,.01)	.00(38) (.00.09)				
3		.00(261) (.00,.02)	.00(351) (.00,.01)	.00(240) (.00,.02)	.00(62) (.00,.06)*			
4			.00(44) (.00,.09)	.02(206) (.00,.05)	.39(479) (.34,.44)*	1.00(26) (.86,1.00)*		
5					.97(76) (.90,.99)*	1.00(25) (.86,1.00)*		
6						1.00(3)		

KEY: m(n) where m = mean frequency, n = sample size, and U and L are the upper and lower (L,U) 95% confidence limits, respectively.  
 \* indicates no overlap with the corresponding confidence interval for the field data (Table 2).

Table 5. The stochastic spray policy (SSP). Spray frequencies as a function of block conditions in the previous year. Table 1 defines the classifications.

DEF(t)	EGG(t)					
	1	2	3	4	5	6
1	0	0	.1	.1	.1	.1
2	0	.1	.1	.1	.1	.1
3	0	.1	.1	.1	.2	.2
4	.1	.1	.2	.2	.2	.2
5	.1	.2	.2	.2	.2	.2
6	.1	.2	.4	.4	.4	.4

Table 6. Proportion of sites sprayed per year  $\pm$  estimated standard error.

Source	Spray policy	Spray frequency
Stedinger model	DSP	.176 $\pm$ .009
	SSP	.107 $\pm$ .006
	DSP2 <sup>1</sup>	.222 $\pm$ .014
Jones model	DSP	.041 $\pm$ .006
	SSP	.027 $\pm$ .003
Survey data		.226 $\pm$ .046

<sup>1</sup>DSP with spray mortality reduced from 90% to 80% (Stedinger, 1977).



Table 7. Frequencies of block conditions recorded in the field.

DEF(t)	EGG(t)					
	1	2	3	4	5	6
1	.02 (.02, .03)	.04 (.03, .05)	.02 (.02, .03)	.01 (.01, .01)	.01 (.01, .01)	.00 (.00, .00)
2	.01 (.01, .01)	.04 (.03, .05)	.03 (.02, .04)	.01 (.01, .01)	.01 (.01, .01)	.00 (.00, .00)
3	.01 (.01, .01)	.04 (.03, .05)	.03 (.02, .04)	.02 (.02, .03)	.02 (.02, .03)	.00 (.00, .00)
4	.01 (.01, .01)	.05 (.04, .06)	.06 (.05, .07)	.04 (.03, .05)	.04 (.03, .05)	.01 (.01, .01)
5	.00 (.00, .00)	.03 (.02, .04)	.03 (.02, .04)	.03 (.02, .04)	.03 (.02, .04)	.01 (.01, .01)
6	.00 (.00, .00)	.06 (.05, .07)	.11 (.09, .13)	.07 (.06, .08)	.10 (.09, .12)	.03 (.02, .04)

KEY:  $m(n)$  where  $m$  = mean frequency,  $n$  = sample size, and  $U$  and  $L$  are the upper and lower 95% confidence limits, respectively.  
(L,U)

Table 8. Frequencies of block conditions - Stedinger model with the DSP.

DEF(t)	EGG(t)					
	1	2	3	4	5	6
1	.03(-.01) (.02, .04)	.25(-.21) (.24, .26)*	.05(-.03) (.04, .06)*	.00(.01) (.00, .01)	.00(.01) (.00, .00)*	.00(0) (.00, .00)
2	.00(.01) (.00, .00)*	.10(-.06) (.09, .11)*	.09(-.06) (.08, .10)*	.01(0) (.00, .01)	.00(.01) (.00, .00)*	.00(0) (.00, .00)
3	.00(.01) (.00, .00)*	.04(0) (.04, .05)	.10(-.07) (.09, .11)*	.04(-.02) (.03, .05)	.00(.02) (.00, .01)*	.00(0) (.00, .00)
4	.00(.01) (.00, .00)	.01(.04) (.00, .01)*	.03(.03) (.02, .04)*	.06(-.02) (.05, .07)	.04(0) (.03, .04)	.00(.01) (.00, .00)*
5	.00(0) (.00, .00)	.00(.03) (.00, .00)	.00(.03) (.00, .00)*	.00(.02) (.00, .01)*	.02(.01) (.01, .02)	.00(.01) (.00, .00)*
6	.00(0) (.00, .00)	.00(.06) (.00, .00)*	.00(.11) (.00, .00)*	.02(.05) (.02, .03)	.11(-.01) (.10, .12)	.00(.03) (.00, .01)

KEY:  $m(e)$  where  $m$  = mean frequency,  $e$  = survey mean -  $m$ , and  $U$  and  $L$  are the upper and lower

(L,U) } 95% confidence limits, respectively.

\* indicates no overlap with the corresponding confidence interval for the field data (Table 7).

Table 9. Frequencies of block conditions - Stedinger model with the SSP.

DEF(t)	EGG(t)					
	1	2	3	4	5	6
1	.22(-.19) (.21, .23)*	.36(-.32) (.35, .37)*	.06(-.04) (.06, .07)*	.00(.01) (.00, .01)	.00(.01) (.00, .00)*	.00(0) (.00, .00)
2	.00(.01) (.00, .00)*	.06(-.02) (.05, .07)	.05(-.02) (.04, .06)	.00(.01) (.00, .01)	.00(.01) (.00, .00)*	.00(0) (.00, .00)
3	.00(.01) (.00, .00)*	.02(.02) (.01, .05)	.04(-.01) (.03, .05)	.02(0) (.01, .03)	.00(.02) (.00, .01)*	.00(0) (.00, .00)
4	.00(.01) (.00, .00)*	.01(.04) (.00, .01)*	.02(.04) (.01, .02)*	.02(.02) (.02, .03)	.01(.03) (.01, .02)*	.00(.01) (.00, .00)
5	.00(0) (.00, .00)	.00(.03) (.00, .00)*	.00(.03) (.00, .00)*	.00(.03) (.00, .00)*	.01(.02) (.00, .01)*	.00(.01) (.00, .00)*
6	.00(.0) (.00, .00)	.00(.06) (.00, .00)*	.02(.09) (.01, .03)*	.04(.03) (.03, .04)*	.05(.05) (.04, .06)*	.00(.03) (.00, .00)*

KEY:  $m(e)$  where  $m$  = mean frequency,  $e$  = survey mean -  $m$ , and  $U$  and  $L$  are the upper and lower

(L,U) 95% confidence limits, respectively.

\* indicates no overlap with the corresponding confidence interval for the field data (Table 7).

Table 10. Frequencies of block conditions - Jones model with the DSP.

DEF(t)	EGG(t)					
	1	2	3	4	5	6
1	.45(-.43) (.43, .47)*	.23(-.19) (.21, .24)*	.00(.02) (.00, .01)*	.00(.01) (.00, .00)*	.00(.01) (.00, .00)*	.00(0) (.00, .00)
2	.00(.01) (.00, .00)*	.04(0) (.03, .05)	.05(-.02) (.04, .06)	.00(.01) (.00, .01)	.00(.01) (.00, .00)*	.00(0) (.00, .00)
3	.00(.01) (.00, .00)*	.03(.01) (.03, .04)	.04(-.01) (.04, .05)	.03(-.01) (.03, .04)	.01(-.01) (.00, .01)*	.00(0) (.00, .00)
4	.00(.01) (.00, .00)*	.00(.05) (.00, .00)*	.01(.05) (.00, .01)	.03(-.01) (.02, .03)	.06(-.02) (.05, .07)	.00(-.01) (.00, .01)
5	.00(0) (.00, .00)	.00(03) (.00, .00)*	.00(.03) (.00, .00)*	.00(.03) (.00, .00)*	.01(.02) (.01, .01)*	.00(.01) (.00, .01)
6	.00(0) (.00, .00)	.00(.06) (.00, .00)*	.00(.11) (.00, .00)*	.00(.07) (.00, .00)*	.00(.10) (.00, .00)*	.00(.03) (.00, .00)*

KEY:  $m(e)$  where  $m$  = mean frequency,  $e$  = survey mean -  $m$ , and  $U$  and  $L$  are the upper and lower

( $L, U$ ) 95% confidence limits, respectively.

\* indicates no overlap with the corresponding confidence interval for the field data (Table 7).

Table 11. Frequencies of block conditions - Jones model with the SSP.

DEF(t)	EGG(t)					
	1	2	3	4	5	6
1	.71(-.69) (.69, .73)*	.18(-.14) (.17, .19)*	.00(.02) (.00, .01)*	.00(.01) (.00, .00)*	.00(.01) (.00, .00)*	.00(0) (.00, .00)
2	.00(.01) (.00, .00)*	.02(.02) (.02, .03)	.02(.01) (.01, .02)	.00(.01) (.00, .00)*	.00(.01) (.00, .00)*	.00(0) (.00, .00)
3	.00(.01) (.00, .00)*	.01(.03) (.00, .01)*	.01(.02) (.01, .02)	.01(.01) (.00, .01)*	.00(.02) (.00, .01)*	.00(0) (.00, .00)
4	.00(.01) (.00, .00)*	.00(.04) (.00, .00)*	.00(.06) (.00, .01)*	.01(.02) (.00, .01)*	.01(.03) (.01, .02)*	.00(.01) (.00, .00)*
5	.00(0) (.00, .00)	.00(.03) (.00, .00)*	.00(.03) (.00, .00)*	.00(.03) (.00, .00)*	.00(.03) (.00, .01)*	.00(.01) (.00, .00)*
6	.00(0) (.00, .00)	.00(.06) (.00, .00)*	.00(.11) (.00, .00)*	.00(.07) (.00, .01)*	.00(.10) (.00, .01)*	.00(.03) (.00, .00)*

KEY:  $m(e)$  where  $m$  = mean frequency,  $e$  = survey mean -  $m$ , and  $U$  and  $L$  are the upper and lower

(L,U) 95% confidence limits, respectively.

\* indicates no overlap with the corresponding confidence interval for the field data (Table 7).

## FIGURES

Figure 1. Spruce budworm life cycle in Maine (see text).

Figure 2. Jones' (1979) representation of the budworm-forest system in his model. The outer circle represents the budworm life cycle, the inner circle the forest cycle. Ovals show budworm life stages; arrows indicate causal relationships among ecological processes and the budworm.

Figure 3. Recruitment ratios for the Jones (a) and the Stedinger (b) models plotted against budworm density (in new healthy egg masses/m<sup>2</sup> of foliated branch surface). The forest environment from the budworm's perspective is indicated as either very good (VG), good (G), poor (P), or very poor (VP). The budworm population is in equilibrium along the horizontal line,  $EGG(t+1)/EGG(t) = 1.0$ . The densities  $L^*$ ,  $U$ , and  $H^*$  represent the budworm population equilibria corresponding to curve G.  $L^*$  and  $H^*$  are the low and high stable equilibrium densities, respectively;  $U$  indicates the unstable equilibrium density (see text). (After Stedinger, 1984).

Figure 4. Relationships between the mean egg mass density  $E_{GG}(t)$ , and the average of the percent current defoliation class,  $DEF(t)$ , in unsprayed sites. Vertical bars encompass the larger  $E_{GG}(t)$  intervals of two SE about the mean. The survey data (boxes) are plotted along with output from Jones' (triangles) and Stedingers' (circles) models when run under the deterministic (a) and stochastic (b) spray policies. Sample sizes exceed 35 sites.

Figure 5. Relationships between the mean percent defoliation of new foliage in year  $t+1$ ,  $DEF(t+1)$ , and the egg-mass-density class in the previous year,  $E_{GG}(t)$ , for areas unsprayed in both years  $t$  and  $t+1$ . Vertical bars indicate the larger  $DEF(t+1)$  intervals of two SE about the mean. The influence of the deterministic (a) and stochastic (b) spray policies on output from Jones' (triangles) and Stedingers' (circles) models is shown along with the survey data (boxes). Sample sizes exceed 135 model sites and 40 survey blocks unless denoted in parentheses.

Figure 6. Relationships between the mean egg mass densities in successive years,  $EGG(t)$  and  $EGG(t+1)$ , for unsprayed areas. Vertical bars show the larger  $EGG(t+1)$  intervals of two SE about the mean. The effects of the deterministic (a) and stochastic (b) spray policies are indicated for Jones' (triangles) and Stedingers' (circles) models. Sample sizes exceed 40 forest blocks for the survey data (boxes) and 125 model sites unless denoted in parentheses.

Figure 7. Relationships between the mean percent current defoliation in successive years,  $DEF(t)$  and  $DEF(t+1)$ , for unsprayed areas. Vertical bars indicate the larger  $DEF(t+1)$  intervals of two SE about the mean. The influence of the deterministic (a) and stochastic (b) spray policies on Jones' (triangles) and Stedingers' (circles) models is shown. Sample sizes exceed 125 blocks for the survey data (boxes) and 25 model sites unless denoted in parentheses.

Figure 8. Relationship between the egg mass density at individual sampling sites within a forest block and the block mean. Only sprayed (S) and unsprayed (U) blocks with four or more sampling sites were considered. Sample sizes exceed 30 sites.



Figure 9. Relationships between the mean percent current defoliation,  $DEF(t+1)$ , and the egg-mass-density class' average in the previous year,  $EGG(t)$ , for areas unsprayed in year  $t$  and sprayed in year  $t+1$ . Vertical bars show the larger  $DEF(t+1)$  intervals of two SE about the mean. The influence of the deterministic (a) and stochastic (b) spray policies on output from Jones' (triangles) and Stedingers' (cricles) models is shown along with the survey data (boxes). Sample sizes exceed 15 model sites and 25 survey blocks unless denoted in parentheses.

Figure 10. Relationships between the mean egg mass densities in successive years,  $EGG(t)$  and  $EGG(t+1)$ , for areas unsprayed in year  $t$  and sprayed in year  $t+1$ . Vertical bars show the larger  $EGG(t+1)$  intervals of two SE about the mean. The effects of the deterministic (a) and stochastic (b) spray policies are indicated for Jones' (triangles) and Stedingers' (circles) models. Sample sizes exceed 25 forest blocks for the survey data (boxes) and 15 model sites unless denoted in parentheses.

Figure 11. Relationships between the mean percent current defoliation in successive years,  $DEF(t)$  and  $DEF(t+1)$ , for areas unsprayed in year  $t$  and sprayed in year  $t+1$ . Vertical bars encompass the larger  $DEF(t+1)$  intervals of two SE about the mean. The influence of the deterministic (a) and stochastic (b) spray policies on Jones' (triangles) and Stedingers' (circles) models is shown. Sample sizes exceed 10 blocks for the survey data (boxes) and 10 model sites unless denoted in parentheses.

Fig. 1

~~Fig. 1~~

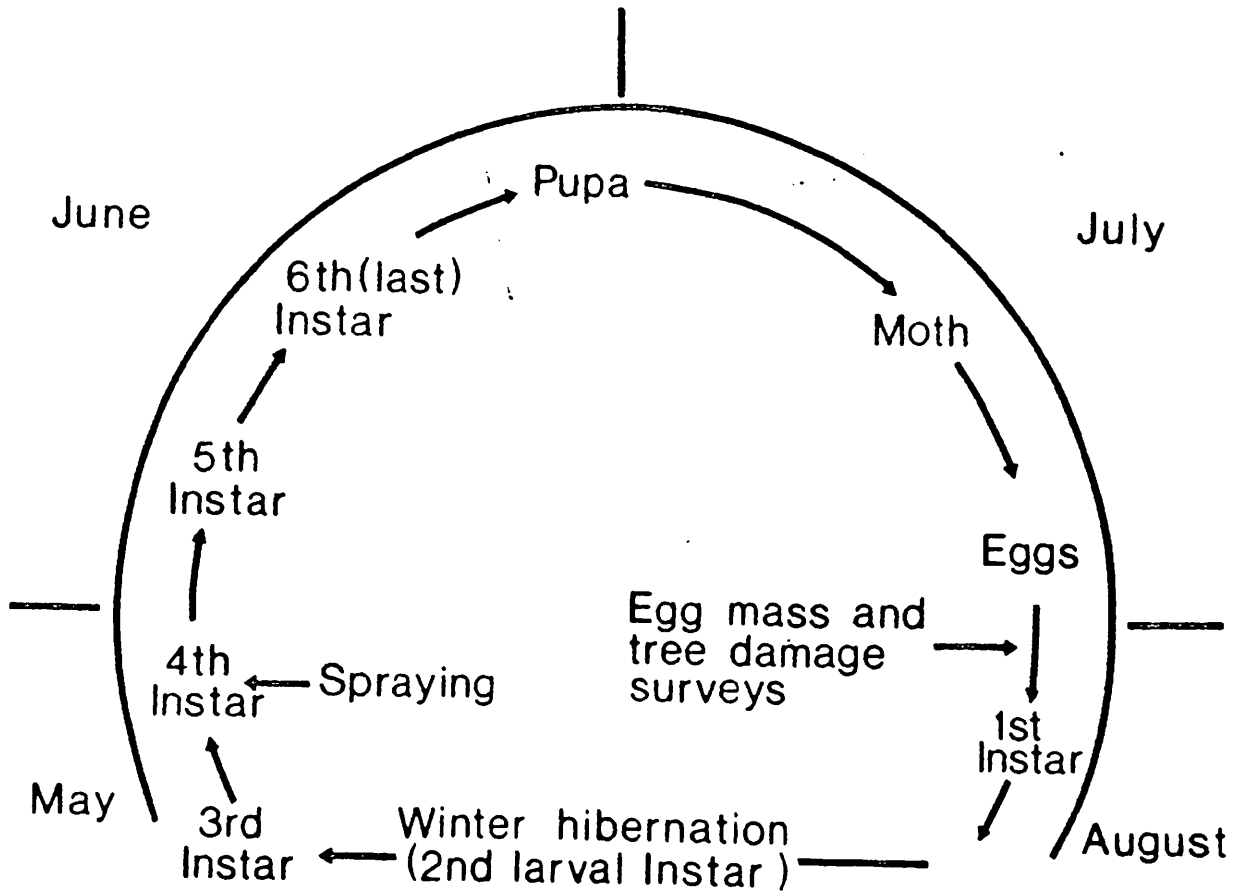


Fig. 2

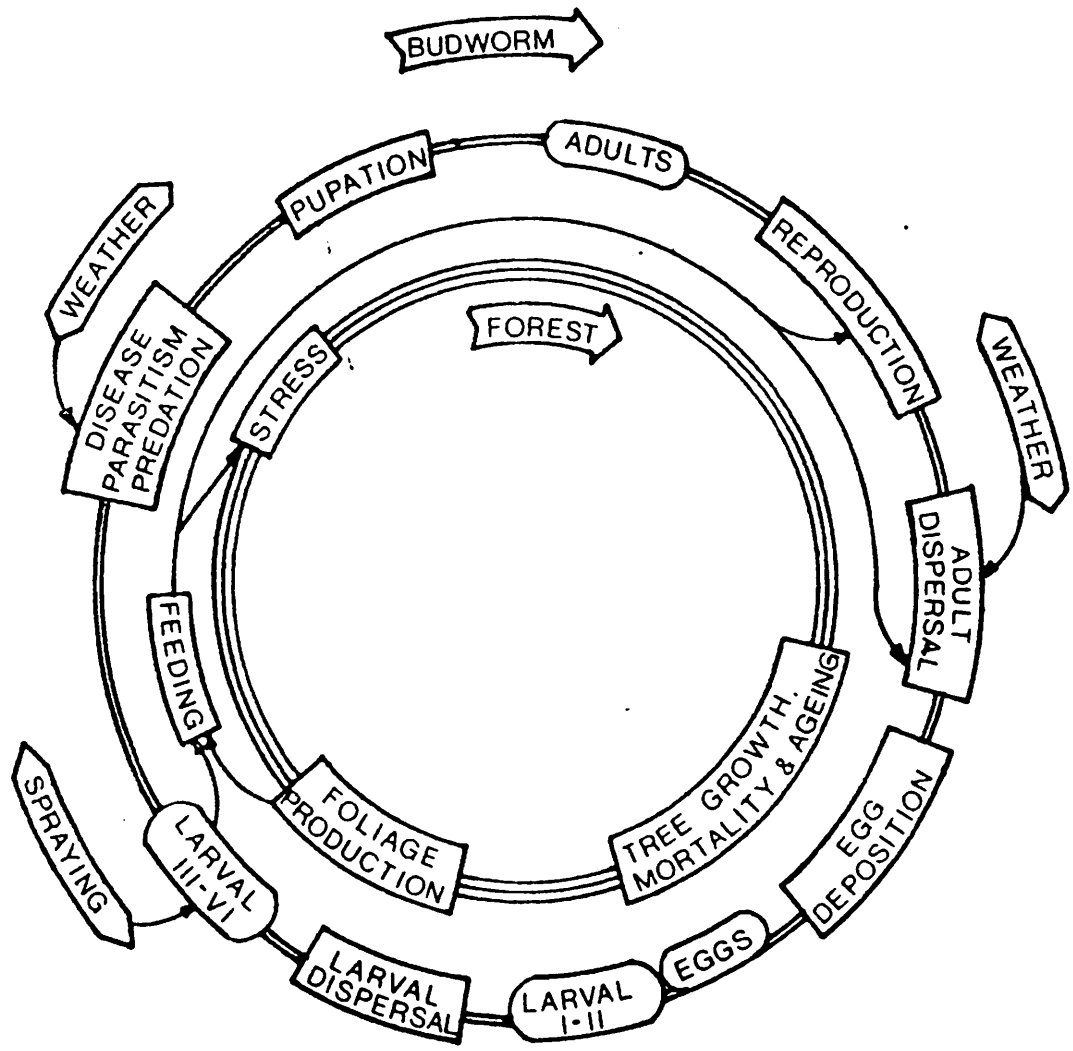


Fig. 3

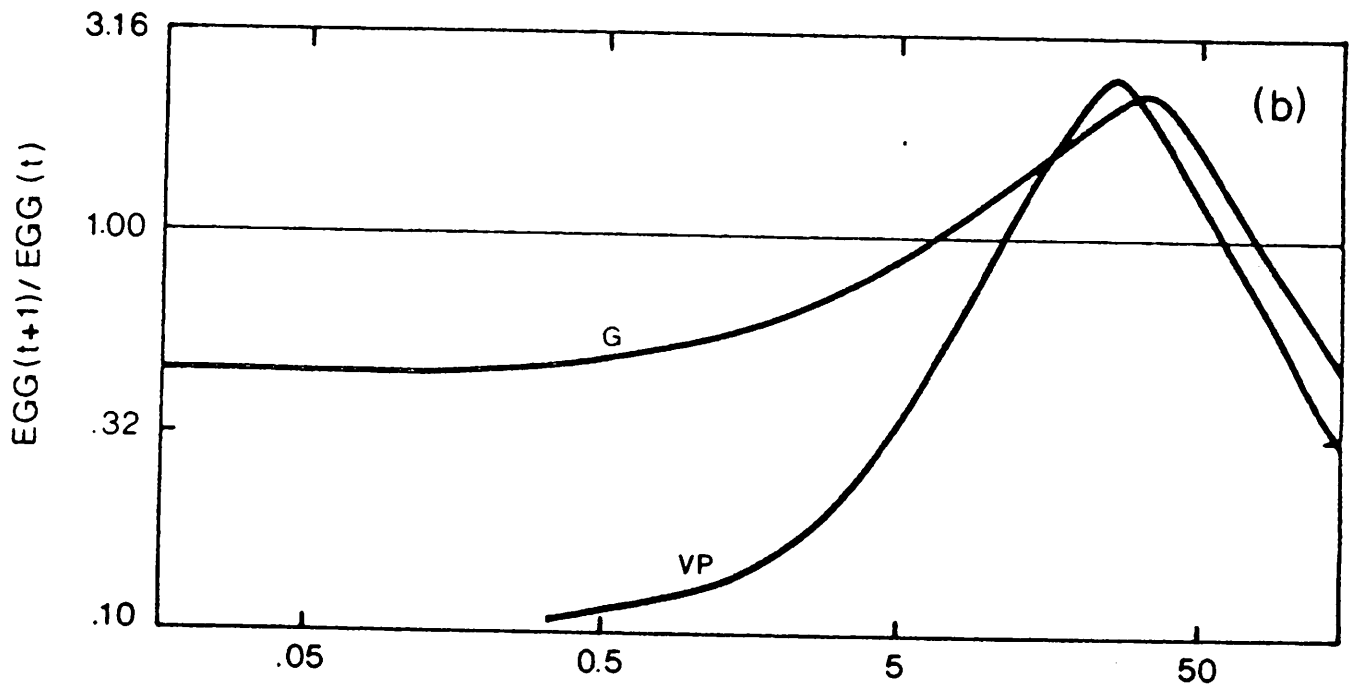
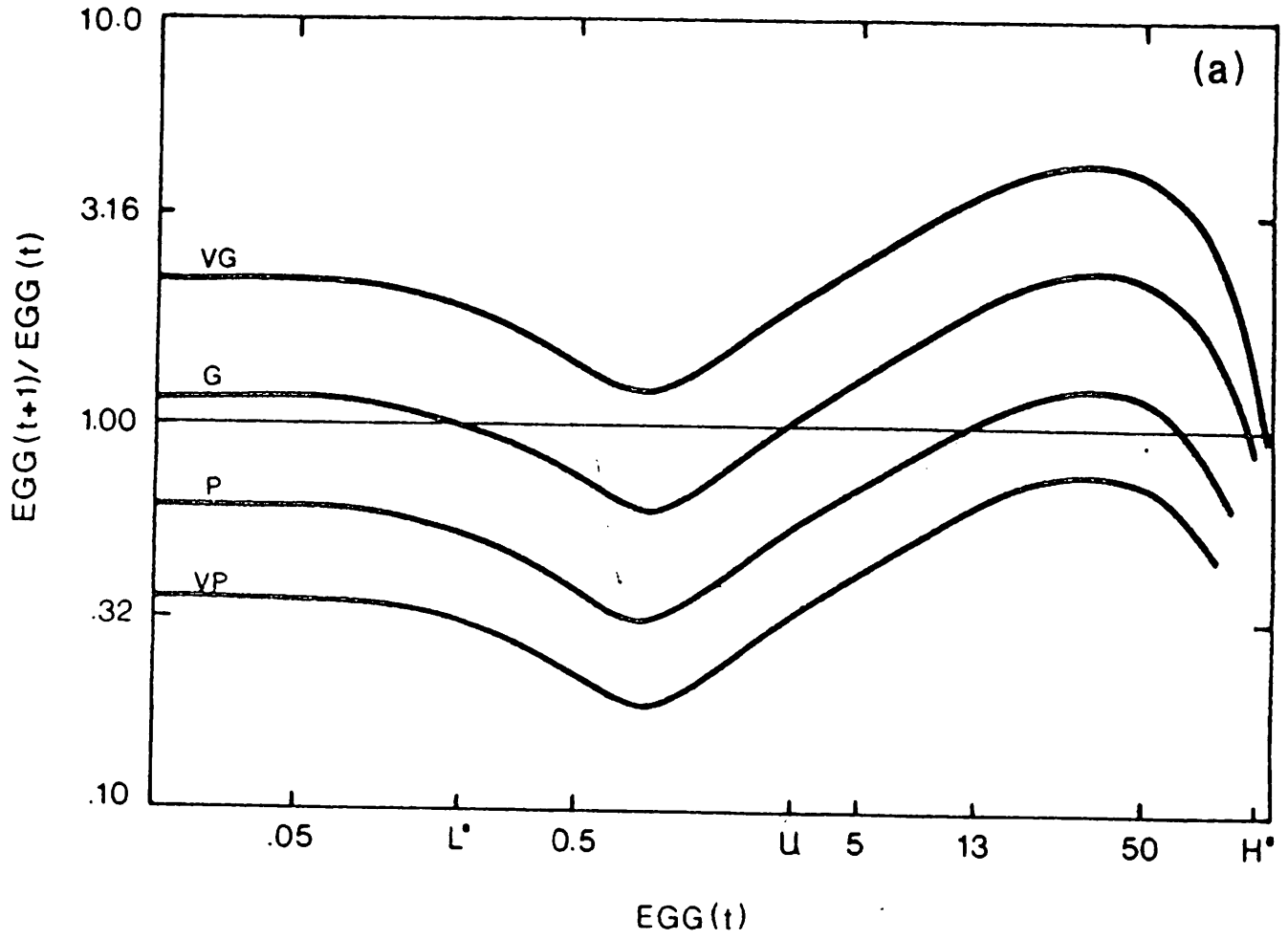


Fig. 4

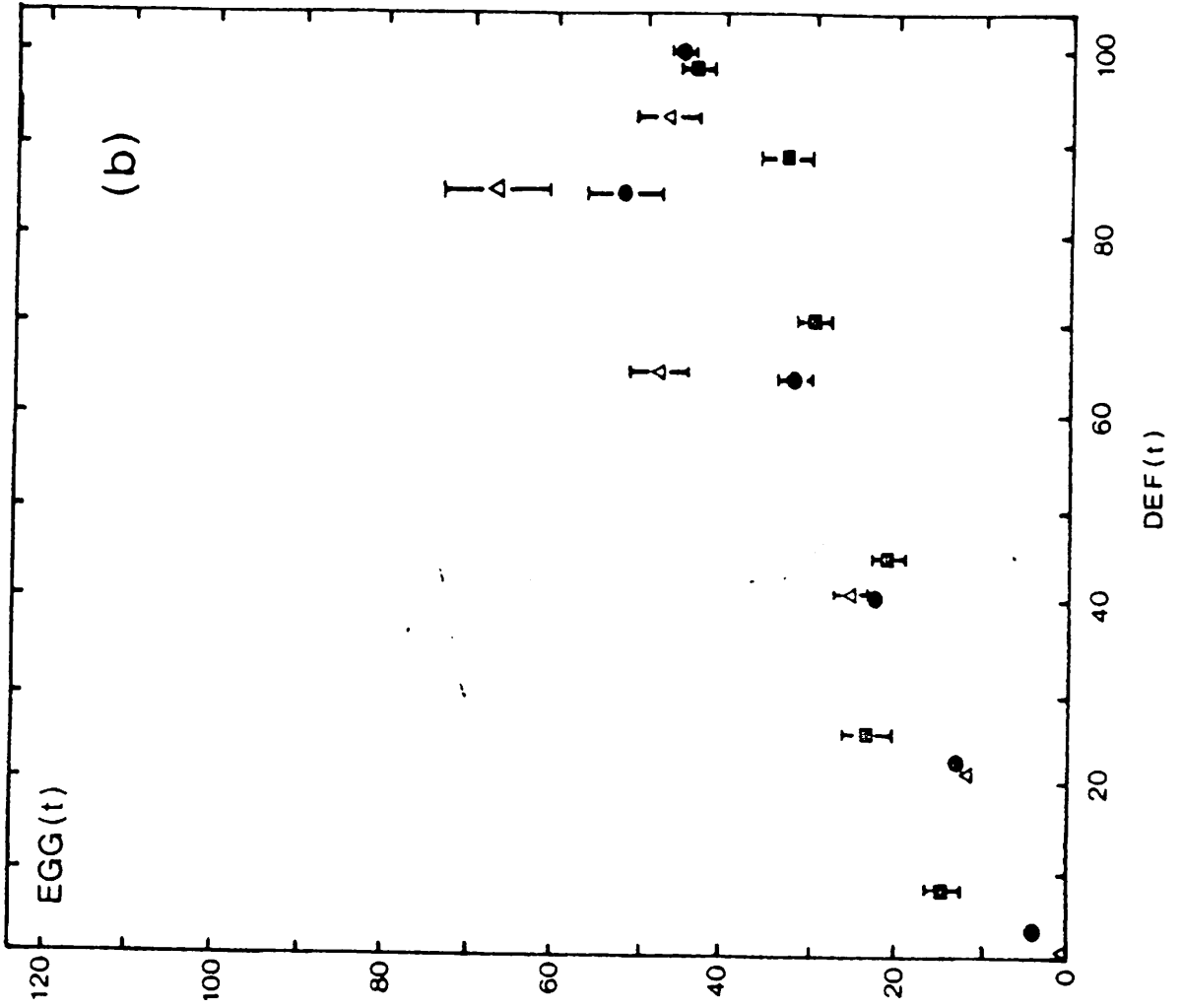
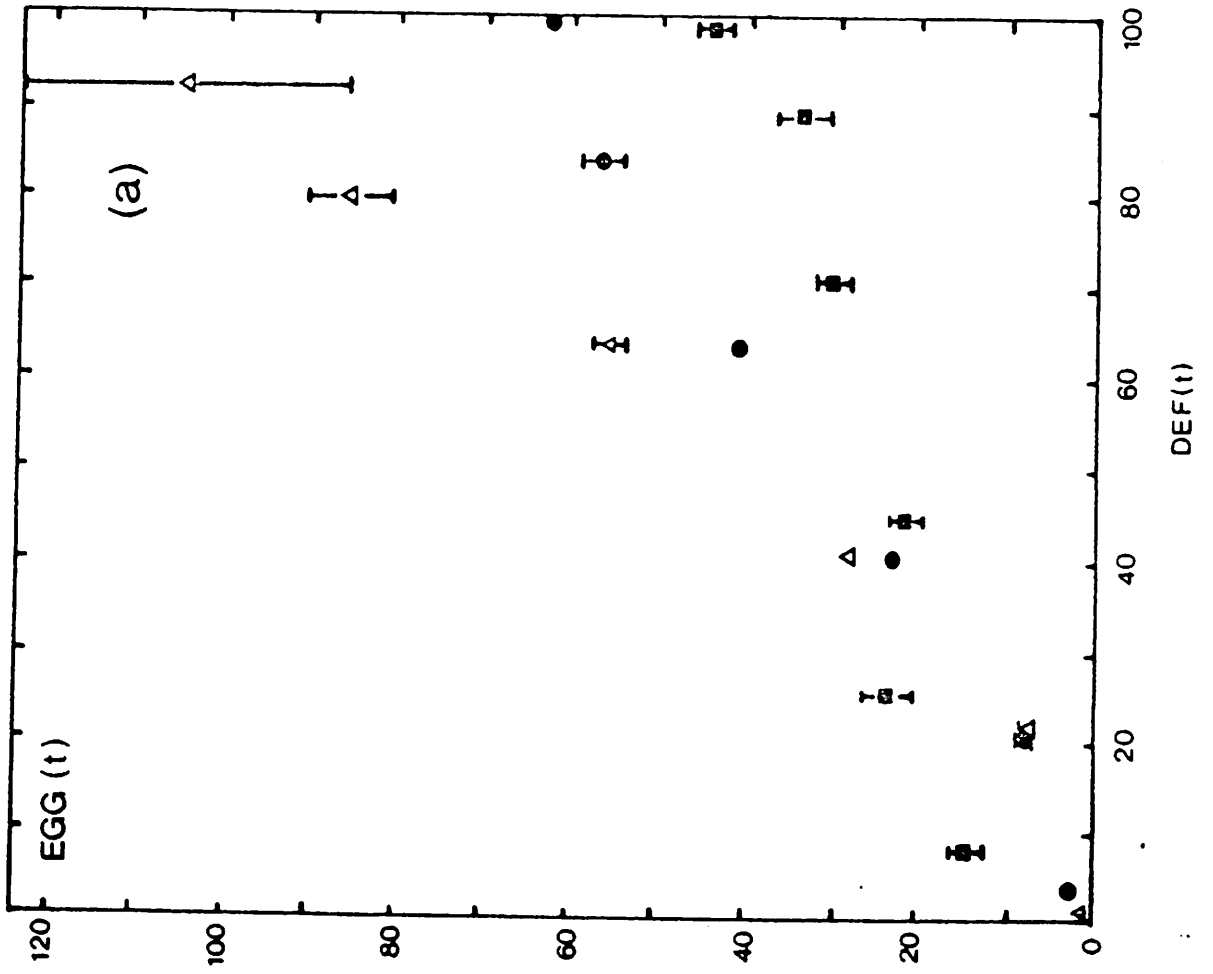


Fig. 5

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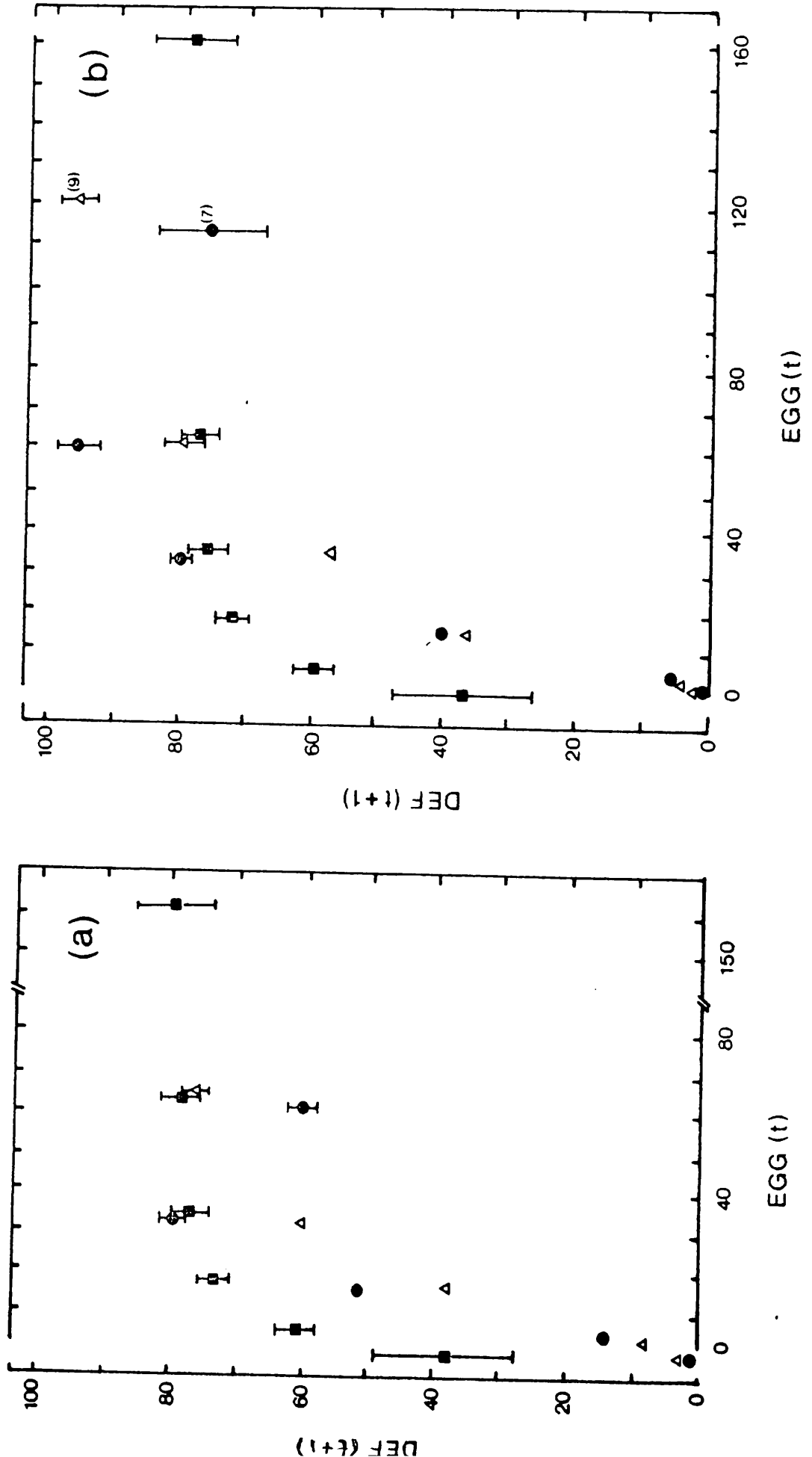


Fig 6

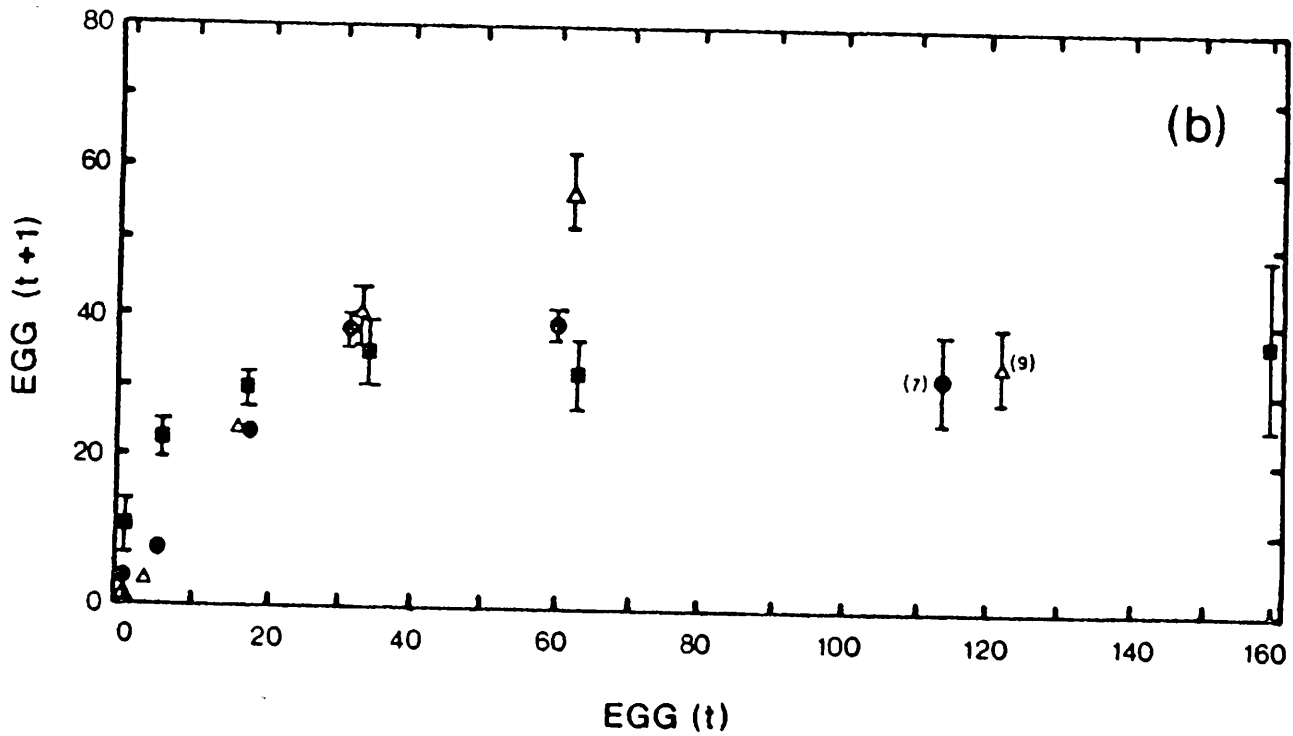
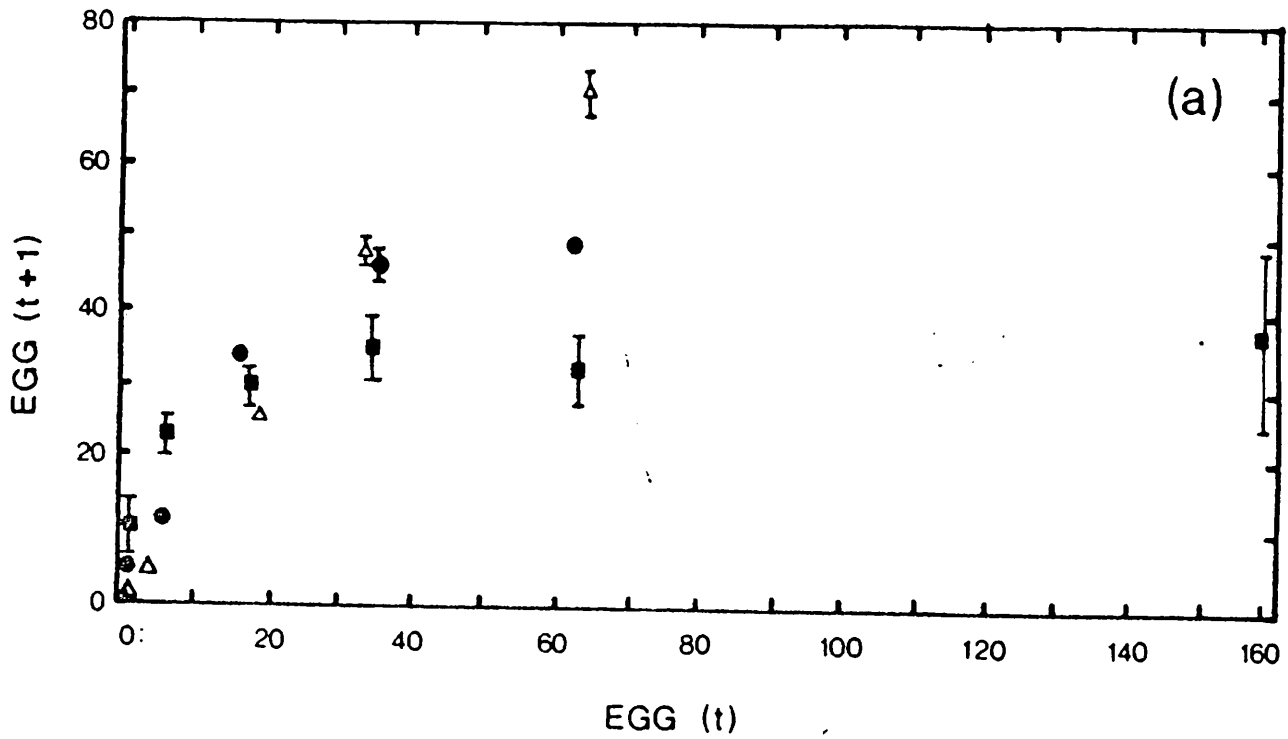




Fig. 7

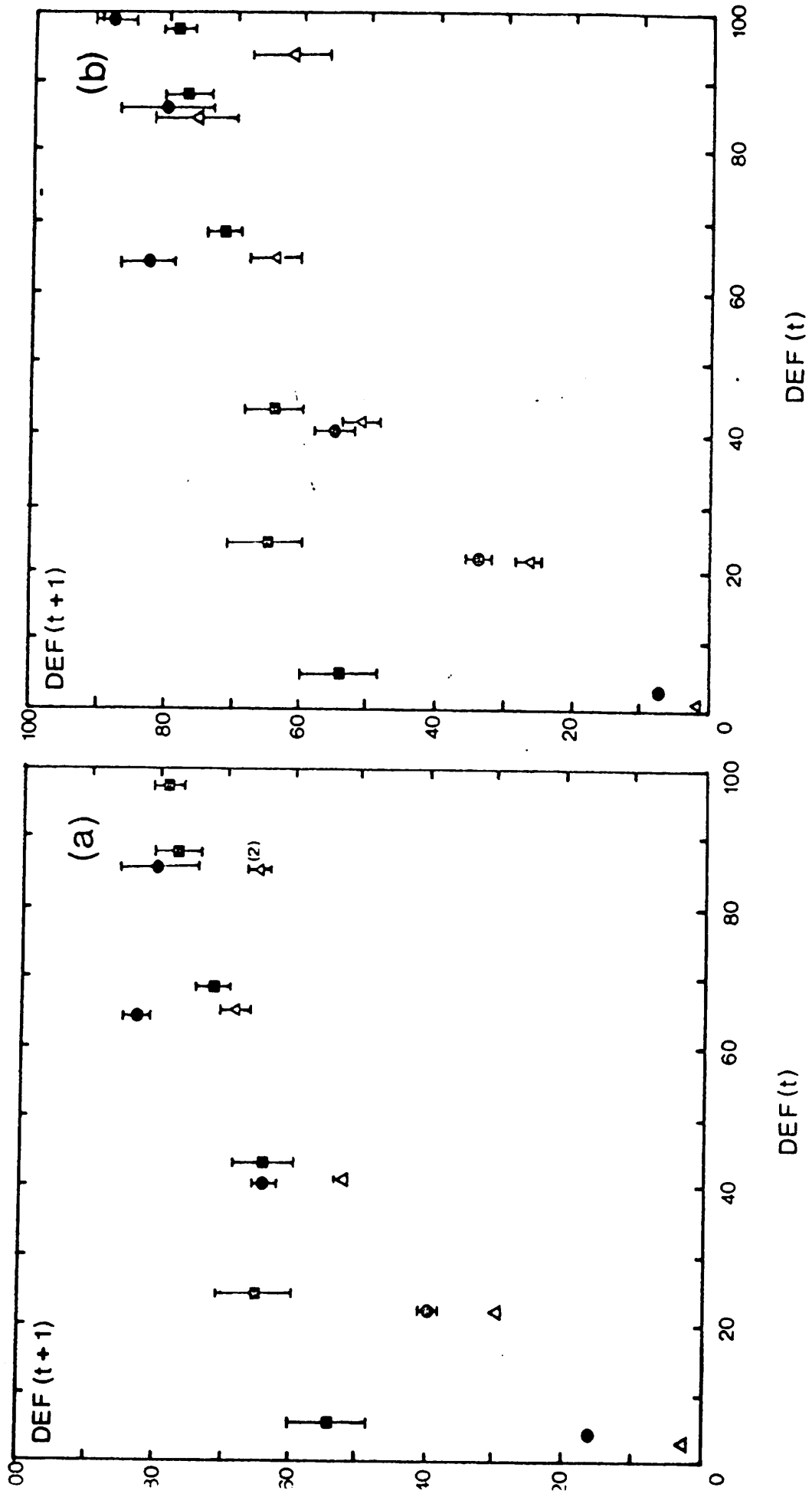


Fig. 8

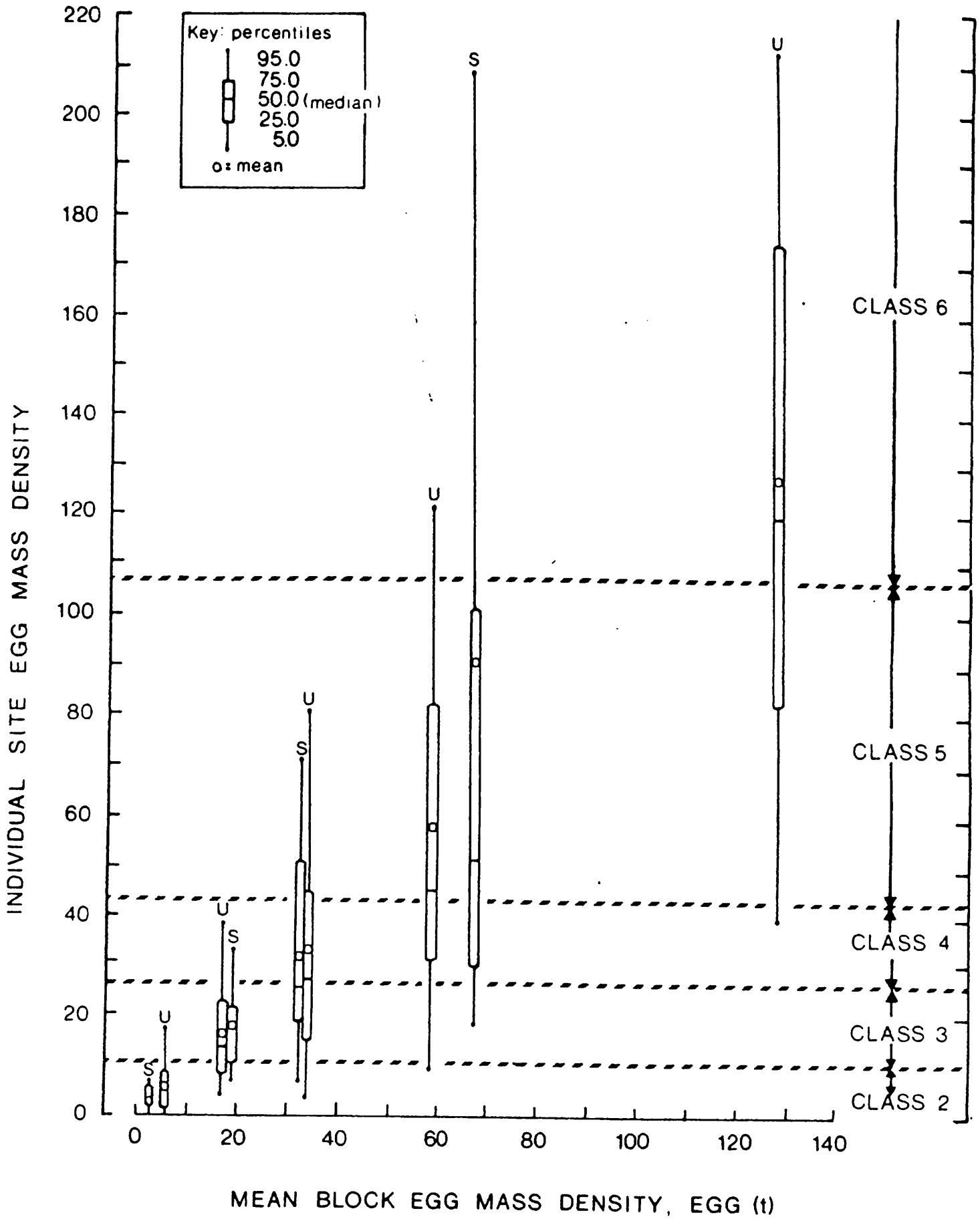


Fig. 9

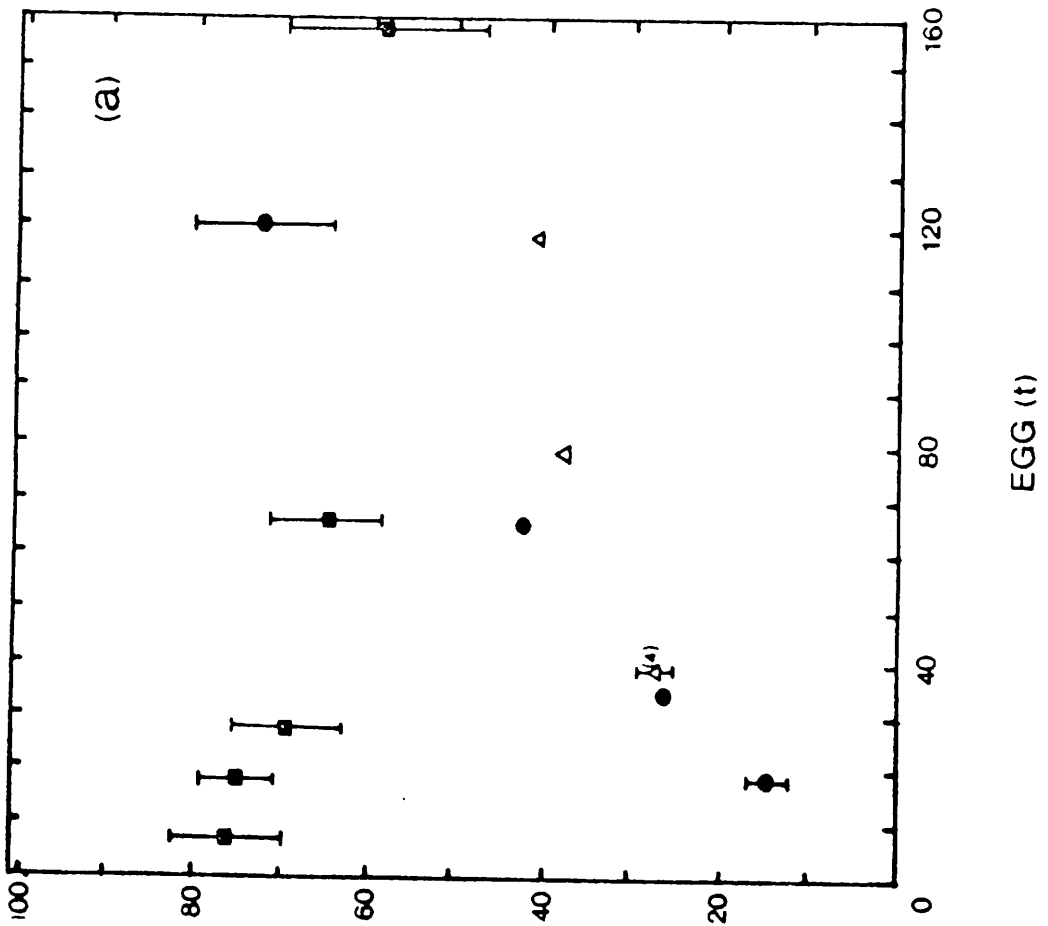
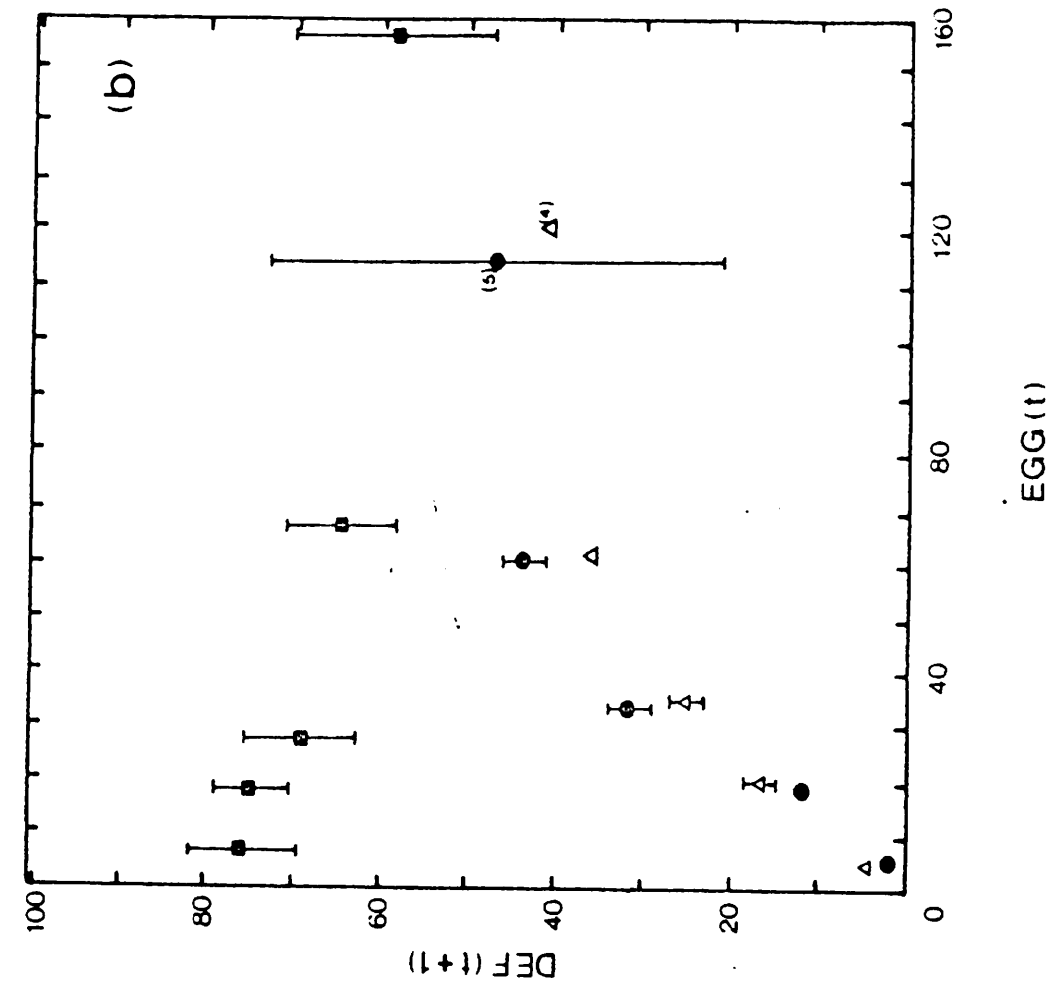


Fig 10

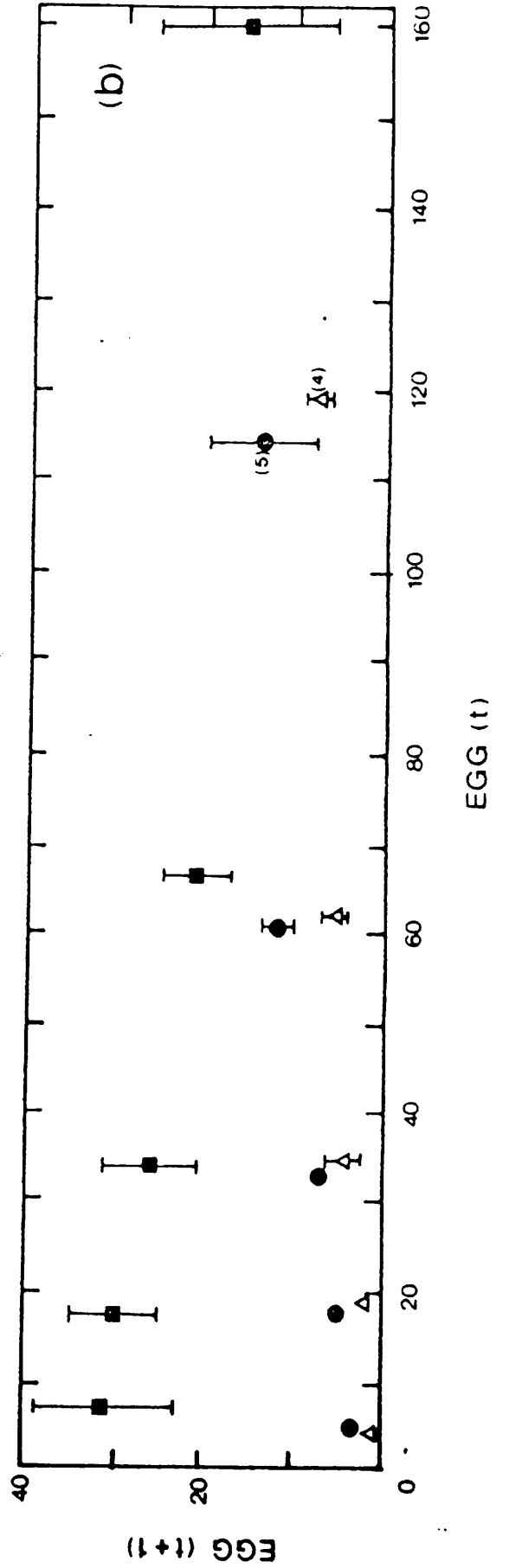
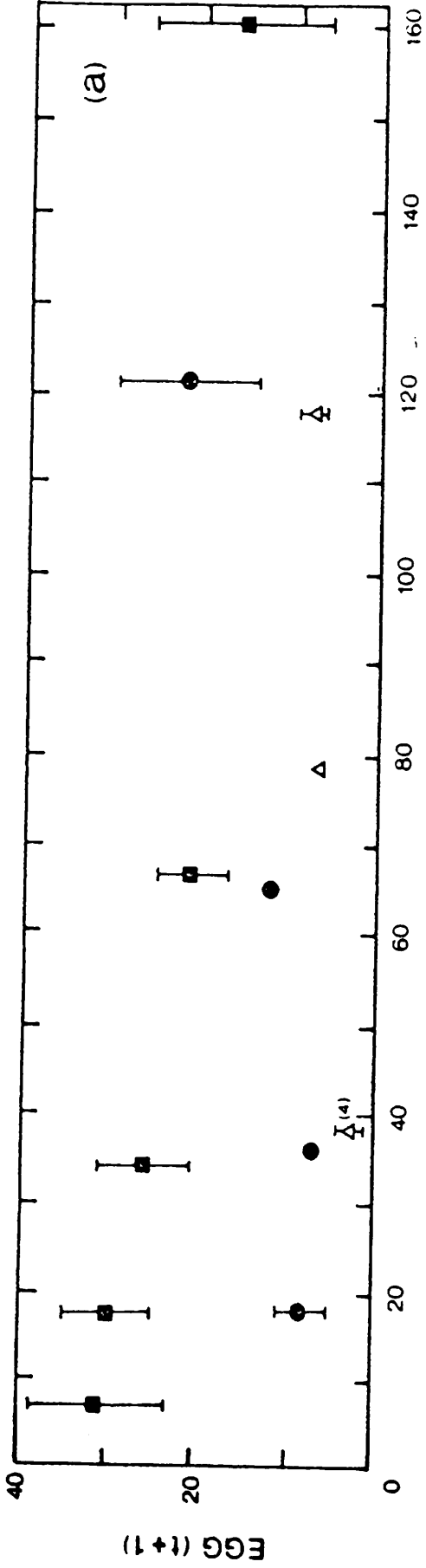


Fig. 11

