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RESEARCH MEMORANDUM

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This paper describes the natural history of a simulation model. The model was constructed to illuminate the determinants of the dynamic behavior for a pest/forest system with particular reference to the New Brunswick Budworm experience. It cannot reproduce the real system in all its richness. Rather, it is meant to be an analog of the important links between the budworm and its principal host, balsam fir.

Parental foundations of the present work are credited to a modelling workshop conducted by members of the Institute of Resource Ecology, Vancouver, and the Canadian Forest Service. The original model is described in a manuscript by Stander [4]. The basic superstructure of the present model remains much the same as the original. The flowchart in Figure 1 shows the basic features.

The original model has been reworked to eliminate some minor errors and incorporate recent interpretations of data. The principal aim of this revision is to elucidate the interplay between the primary state variables--budworm and fir. Within-year feedbacks between foliage and feeding larvae are emphasized.

The enormity of the budworm system required a long-term heroic effort just to observe and understand the natural course of events. Much of this experience is contained in a monograph by R.F. Morris [3]--hereafter referred to as "the monograph" or MG. A consequence of being limited to observations of a relatively unperturbed system is that we are restricted to a limited subset of phase space. We can expect that perturbations to the real system as well as to our model will move the state variables into combinations that have not yet been experienced. Such distortions of the system into "uncomfortable" configurations yield important and necessary information about the nature of the internal machinery. It is not always practical, reasonable or prudent to carry out a full scale perturbation experiment on the real world. The spraying studies fall into this class of experiment but it was impossible to control all the variables that we would have liked.

Since the primary variables (budworm and fir) were observed as they rode together through their natural progressions, the complete nature of the relationships that link these variables cannot always be extracted. We want to use our model to suggest or test pest management policies--or at least our ideas about such policies. If the policies affect the state variables in "unnatural" ways (which, almost by definition, they will) then we must explicitly include all of the important links between the variables.

The relationships used in the original model were not necessarily "wrong." Theoretically they should reproduce the natural sequence of the events as well as the model proposed here. We have expressed the interactions as explicit causal links rather than as implicit final effects. This more explicit model should be applicable to a wider range of events, perturbations and manipulations of the system than the original version would allow. Implicit relations are all right as long as we stay within the range of experience that lead to the formulation of these relationships, but we wish to go beyond this range with the model.

A simple example will hopefully illustrate the goal and advantages of this explicit formulation. Suppose the following equations are an exact representation of some real world system.

$$\begin{aligned} \frac{dT}{dt} &= T - T \cdot B \\ \frac{dB}{dt} &= - B + T \cdot B \ . \end{aligned} \tag{1}$$

Further, suppose that an extensive field investigation indicated that this system could be represented by the following "model"

$$\begin{aligned} \frac{dT}{dt} &= T - T \cdot B \\ \frac{d^2B}{dt^2} &= (\dot{B}) + (1 - B)\ (\dot{B} + B) \ . \end{aligned} \tag{2}$$

Now, under "normal" conditions this model will exactly simulate the real system. (This is so because equations (1) and

(2) are mathematically equivalent.) However, if we perturb T on our model, (2), it will have no effect on B because we have failed to explicitly incorporate the causal relationship between T and B.

The advantages of explicitness are, of course, counterbalanced by our lack of supporting data. In many cases, however, we can draw on ecological experience to suggest the functional form of the components of interaction. Given the form of a relationship, the appropriate parameters can usually be estimated with acceptable accuracy.

The next section summarizes the general form of the model. As mentioned above the superstructural is very like the original described by Stander [4]. The control model remains as the original and is not described again here. The budworm, forest response and dispersal models received the most refinement. The forest response and budworm models are computed in parallel rather than in sequence but we describe the forest response model first to introduce some definitions that are needed in other models.

The model has not been programmed at this time so the obvious section on its performance is missing--to be added when available.

Overall Model Structure

A basic flow diagram of the model is shown in Figure 1. Spatial heterogeneity is accomodated with a system of 6 x 9 mile grids. These grids correspond to map survey areas and provide a common base for comparison with the real world. In the original model 265 grids out of a total 456 in New Brunswick were used. We are, of course, not restricted to this number.

Within each grid--or "site"--conditions are assumed homogeneous. Trees of different age and species are assumed uniformily distributed. Even though it is known the budworm is differentially associated with different types of host trees we will assume that they are distributed according to their average.

The sequence of operations within the budworm, foliage response and dispersal models is presented schematically in Figure 2. The start of a year's iteration begins with the budworm in the egg stage. The trees at this point are in the state of defoliation caused by the previous generation. The yearly tree mortality, although not yet fully realized in nature, is anticipated and those trees removed from each site. The individual elements and operations of Figure 2 are described in the following sections.

Foliage Response Model

We consider two components of foliage: first, foliage area as a piece of real estate upon which the budworm live, measured in units of 10 square feet; second, foliage as a quantity of needles (and staminate flowers) that is a source of food and oviposition sites. This component could be expressed in units of mass, but for our purposes we define a a relative measure--the foliage unit (f.u.). A foliage unit is that amount of new-growth needles on ten square feet of branch in the absence of budworm exposure.

Foliage area (FA) is assumed a function of a stand's mean age of trees on a site and their defoliation history. The normal (without defoliation) relation between mean age (A) and foliage area was originally given as (Stander, Figure 9)

$$FA = \frac{FMAX * A}{KF + A} \quad . \qquad (3)$$

This area is reduced below its potential due to accumulated defoliation. We assume this to be a linear function of a defoliation index, ID, (defined below). Thus,

$$FA = \frac{FMAX \cdot A}{KF + A} \cdot \left(1 - \frac{ID}{IDMAX}\right) \quad . \qquad (4)$$

Henceforth, we shall call the second component--foliage as a quantity of needles--simply "foliage." This is further distinguished as "new" and "old" foliage. As stated above, one foliage unit is equivalent to the amount of new foliage on ten square feet of unmolested fir branch. Under these conditions new foliage averages 25% of the total; thus total foliage equals 4 f.u. New foliage joins the old foliage at the end of each season. And at equilibrium the old foliage looses 1 f.u. each year. When all new foliage is removed the tree responds by losing less than one foliage unit. Let F_1 and F_2 be the quantity of new and old foliage respectively, on each 10 square feet. Then the

$$\text{Old foliage lost} = \frac{1}{3}\cdot(1 + 2\cdot F_1) \quad . \qquad (5)$$

The rationale for this relationship is that nine years of total new foliage removal are required to eliminate all old foliage.

Additionally the amount of new foliage produced each spring depends upon the extent of past defoliation. The new foliage input function, F_0, is a function of total foliage, $F_1 + F_2$ and is shown in Figure 3. This function implies a 25% compensatory response to one unit of defoliation ($F_1 + F_2 = 3$). After four years of complete removal of new foliage F_2 is reduced to 5/3; no new shoots are produced and the tree puts all of its efforts into maintenance.

Foliage is represented schematically in Figure 4. The standing stocks are F_1 and F_2. Large larvae defoliation is removed from these stocks as DEF_1 and DEF_2. The new foliage that remains ($F_1' = F_1 - DEF_1$) joins the old and a quantity of old foliage, equation (5), is lost. The net amount of old foliage remaining is

$$F_2 = F_2 - DEF_2 + \frac{1}{3} F_1 - \frac{1}{3} DEF_1 - \frac{1}{3} \quad . \qquad (6)$$

Total defoliation (DEF) depends on large larval density and the total foliage available. This function is described below when we discuss large larval survival. Since the budworm prefers new foliage we apportion it as follows:

$$\text{if } DEF \leq F_1 \quad \begin{cases} DEF_1 = DEF \\ DEF_2 = 0 \end{cases} \quad ,$$

$$\text{if } DEF > F_1 \begin{cases} DEF_1 = F_1 \\ DEF_2 = DEF - F_1 \end{cases} .$$

If we remove all the new foliage but none of the old F_2 will have the following sequence:

Year:	1	2	3	4	5	6	7	8	9
F_2 :	$2\frac{2}{3}$	$2\frac{1}{3}$	2	$1\frac{2}{3}$	$1\frac{1}{3}$	1	$\frac{2}{3}$	$\frac{1}{3}$	0 .

This suggests an accumulated defoliation index defined as

$$ID = 3 \cdot (3 - F_2) = 9 - 3 \cdot F_2 \quad . \tag{7}$$

In the above scenario ID would take the sequence (1, 2, 3,...,9). After an extended period of severe defoliation the older, more susceptible trees begin to experience increased mortality. The defoliation mortality is taken from Miller [2] and is shown in Figure 5.

This concludes the major restructuring of the foliage response model. Points not covered here remain as they were described in Stander [4].

Budworm Model

A multitude of factors affect the survival of the budworm. If we are to maintain a manageable level of complexity, we must restrict ourselves to those factors that illuminate particular questions. To highlight the dynamic interactions between the budworm and its host, balsam fir, processes that directly link these two state variables have been emphasized as explicitly as possible. Supporting field data are not always available, leaving the weak criteria of no contradictions with established relationships. In some cases the functional form of a process is well established by independent ecological experience and only the parameters need be estimated; in other cases we can only hypothesize the general form of the relationship. Weather, as it affects large larval survival, is the only external factor that is explicitly included in the budworm survival functions. All other functions (e.g. parasitism and predation) are only implicitly included.

In order to model the generation survival of the budworm, it is most convenient to examine each life stage separately. We can later aggregate some of these stages for computational convenience. By examining the stages individually we can compare our results with field data and we can more accurately identify the assumptions that we must make.

In many respects the natural point to begin a budworm generation is with the third instar larvae. The emergence of this stage closely coincides with the emergence of new foliage. Timing makes this a logical point with which to begin a model iteration. However, much of the field work has been oriented toward the egg stage as the initial reference of each generation. We will continue with that lead and describe the budworm processes beginning with the eggs.

Egg to Small Larvae

The egg stage begins after the eggs have been deposited.

Any factor affecting egg disposition is attributed to the previous generation. Eggs are laid in late July or early August and the first instar larvae emerge 8 to 12 days later. At this time defoliation by the previous generation has occured but no new foliage has been generated.

Although tree quality, e.g. age, aspect, defoliation history, etc., could affect egg success, there is not sufficient evidence to suggest what form this would take. Likewise, egg survival very likely depends on egg density through such processes as predation, parasitism, and disease. Here again there is not sufficient evidence to suggest the form of this density relation. Its effect would be most pronounced at low egg density where data are most lacking.

The egg survival, S_E, used in this model is taken as a constant fraction independent of forest condition and egg density. The average survival in unsprayed study plots, was

$$S_E = 0.81 \quad ; \qquad (8)$$

(MG, Section 8). We shall adopt this value.

Small Larvae to Large Larvae

This period is from emergence as first instars in mid-August through the moult to third instars the following May. Sampling difficulties prevent precise differentiation of the first two instar stages.

Dominant events for small larvae are the autumn and spring dispersals. These dispersals though passive, occur over large distances (MG, pg. 187) and are affected by forest conditions throughout a site. During each dispersal larval survival depends upon the probability of successful dispersal to a susceptible host--i.e. fir older than nine years. The fraction of a site containing susceptible hosts is

$$\text{SUSCEP} = \text{PFIR} * (1 - T(1) - T(2) - T(3)) \quad , \qquad (9)$$

where PFIR is the proportion of fir and T(i) is the fraction of fir in age group i.

A critical, but unknown, factor is the fraction of larvae actually dispersed from their native tree. It is known that weather affects the probability of dispersal and it is likely that larval density does also. Lacking a better estimate we shall assume that 50% of the small larvae are subject to dispersal. That is, survival of first instars is proportional to

$$S_1 \propto 0.5 + 0.5 \cdot \text{SUSCEP} = 0.5 \cdot (1 + \text{SUSCEP}) \quad .$$

If the same assumptions apply to the second instar then

$$\begin{aligned} S_2 &\simeq 0.5 \cdot S_1 + 0.5 \cdot S_1 \cdot \text{SUSCEP} \\ &= 0.5 \cdot S_1 \cdot (1 + \text{SUSCEP}) = 0.25 \cdot (1 + \text{SUSCEP})^2 \quad . \end{aligned} \qquad (10)$$

The second instar larvae mine the one- and two-year-old needles, and their survival depends on their success in locating these needles. The host trees at this time are in the defoliation condition left by the previous generation of large larvae, therefore survival should decrease as F_2 decreases. The small larval search success (SLSS) (Figure 6) attempts to portray this factor.

When there is a full complement of old foliage, $F_2 = 3$, SLSS = 1. Even when half of the old foliage is removed the larvae can search over the short distances necessary to find needles. However, when defoliation goes beyond this point SLSS drops off. It does not reach zero because of alternate mining sites (e.g. black-spruce needles or balsam staminate flowers).

The SLSS function bears qualitative agreement with field experience (MG, Sections 9 and 21). Precise comparison is not possible without establishing the value of SUSCEP for the test plots.

Thus far we have only considered small larval losses due to dispersal. Escape from other sources of mortality must be considered. The unsprayed check plots (MG, Section 21) indicate that the maximum survival experienced was about 0.75. In the unsprayed area the maximum observed survival was about 0.67 (MG, Figure 9.4). The only available evidence for density dependence is displayed in Figure 9.2 of the monograph. The curve fitted to these points is justified by certain assumptions about dispersal, but since we have already extracted the dispersal process we would be amiss to use this function for our present requirements. A very rough eyeball projection would place $S_s = 0.2$ when N_s is about 1000. The appropriateness of this can be checked with other data and its sensitivity in the model.

Short of more complete knowledge we take the non-dispersal losses to be

$$S_s \propto 0.7 - \frac{0.5}{2000} \cdot N_s = 0.7 - 2.5 \times 10^{-4} \cdot N_s \ .$$

Finally, small larval survival is

$$S_s = \frac{1}{4} \cdot (1 + \mathrm{SUSCEP})^2 \cdot \mathrm{SLSS} \cdot (0.7 - 2.5 \times 10^{-4} \cdot N_s) \ . \quad (11)$$

Large Larvae to Pupae

Large larvae include the third through the sixth instar stages. The normal period is from early June to early July. Large larval survival is the most important in explaining variations in overall generational survival. It is also during this stage that weather has its most pronounced effect--warm dry weather promoting survival and cool wet weather reducing it.

Weather effects are important to all the large instars stages. The primary feeding occurs, however, only in the fifth and mainly the sixth stages. Since it is very difficult to separate the effects of each stage, large larvae are treated as one group and factors affecting survival are assumed to act concurrently.

A model for net large larval survival is shown in Figure 7 (Miller, Personal Communication). The weather classes correspond to the number of warm-dry days during this phase of budworm development. The precise criterion for this index is described elsewhere.

The common wisdom behind the shape of these curves is as follows. At low densities the survival is controlled by the action of predators, parasites, etc. At very low densities (below about 0.05 larvae per 10 sq. ft. of foliage--too low to be seen on the above graph) the larvae escape efficient predation and the population avoids extinction. As the population increases above 0.05/tsf survival is again enhanced because of the limited response of the predators. The explanation for the drop in survival at high densities is starvation due to limited foliage. The final leveling of the survival curves represents the effect of alternate food sources.

The effect of available foliage on starvation and survival is only implicitly included in Figure 7. In order to make this explicit we must know how much foliage the larvae consume and how this consumption affects larvae survival.

The amount of foliage consumed as a function larval density we call a feeding curve. A direct evaluation of this curve has not been found so we must rely on indirect evaluations. Recent survey data from a wide range of locations were converted and plotted in Figure 8. Here D is the total defoliation (called DEF in the previous section) expressed as a per cent of current foliage--100% correspondes to removal of one foliage unit. These points are so scattered that the only safe conclusion we can draw is that total defoliation increases with larval numbers. The corresponding foliage consumed per larvae ($d = D/N_L$) is plotted in Figure 9. Despite the scatter of these points there is a downward trend. Although these plots do not provide much guidance they do not preclude the adoption of a standard feeding relationship. We therefore assume that the large larval defoliation follows a Michaelis-Menten relation of the form

$$D = \frac{V \cdot N_L}{K + N_L} \tag{12}$$

or

$$d = \frac{V}{K + N_L} \quad , \tag{13}$$

where V and K are parameters to be determined. Miller [2] gives the following values as typical.

Budworms per tree	Defoliation of Current Shoots(%)
1,400	20
5,600	65
16,800	100 + old foliage

The first two population levels together with the condition that the curve for d passes through the centroid of the points in Figure 9 gives

$V = 260 \quad (\%)$

$K = 275 \quad (\text{Larvae/tsf}) \quad .$

These parameter values imply that larvae respond to the foliage as if there were only 2.6 f.u. present rather than the 4.0 f.u. of unstressed trees. If this is caused by a lower propensity to consume old foliage we can express V as

$$V = F_1 + \alpha \cdot F_2 \quad , \tag{14}$$

where α is a weighting factor for old foliage.
Unstressed conditions give

$$2.60 = 1 + \alpha \cdot 3$$

or

$$\alpha = .533 \quad .$$

When V changes due to changes in F_1 and F_2 then we must change K to preserve $d_o = d(N_L = 0)$, a physiological "constant." Thus

$$K = \frac{V}{d_o} \quad .$$

The equations we use are

$$\alpha = .533 \tag{15}$$

$$d_o = 260/275 = .945 \tag{16}$$

$$V = F_1 + \alpha \cdot F_2 \tag{17}$$

$$K = V/d_o \tag{18}$$

$$D = \frac{V \cdot N_L}{K + N_L} \tag{19}$$

$$d = D/N_L = \frac{V}{K + N_L} \quad . \tag{20}$$

D and d are plotted as dashed lines through the empirical points of Figures 8 and 9, with $F_1 = 1$ and $F_2 = 3$.

Now that a defoliation relation has been established we return to consideration of the survival of large larvae. For each weather situation let

$$S_L = f(N_L) \cdot g(d) \quad . \tag{21}$$

The second function, g(d), accounts for starvation. In reality there would be a distribution of foliage consumption--some larvae would get a larger amount than others and these would have a higher survival potential. In practice, however, we shall assume that the average consumption, d, determines the average survival.

There is some level of feeding, d_{min}, that would cause complete starvation. Further, we normalize $g(d_o) = 1$. That is, g(d) measures the reduction in survival as N_L increases. There is no compelling reason to use anything other than a linear relationship, i.e.

$$g(d) = (d - d_m)/(d_o - d_m) \quad . \tag{22}$$

If the descending branch of Figure 7 (w_1 case) is extended it crosses $S_L = 0$ at $N_L = 400$. Thus we define

$$d_m = d(400) = \frac{260}{275 + 400} = 0.385 \quad . \tag{23}$$

The increasing function, $f(N_L)$, is also assumed linear:

$$f(N_L) = a + b\,N_L \quad . \tag{24}$$

The parameters a and b (there are 3 sets for the three weather classes) are selected so that S_L passes through the inflection points of Figure 7 (i.e. where $N_L = 0$, 150 and 300). A plot of $f(N_L)$ is at Figure 10a. Note that all weather variation occurs in this function and does not interact with the feeding level d. A plot of $S_L = f(N)\ g(d)$, when $V = 260$, is shown in Figure 10b; it should be compared with Figure 7.

Pupae to Adults

The extensive study of unsprayed plots revealed an average survival of pupae of

$$S_p = 0.66 \quad . \tag{25}$$

This survival was not found to be strongly affected by either pupal density or forest condition (MG, section 11). There was an effect due to weather (expressed as mean temperature) but this is not included in the present model.

Unsprayed check plots in Area 2 (MG, section 23) showed a strong dependence on larval survival ($S_p = 0.3495 + 0.8281 \cdot S_L$). However no mechanism for this connection was suggested. We shall use $S_p = 0.66$ in this model with the understanding that we should test our results for sensitivity to a dependence on S_L.

Fecundity

Fecundity is strongly determined by the physiological state of the adult female. The chief factor affecting this within our model is the amount of food consumed during the larval stages. Turnbull found that fecundity is a linear function of food consumption for spiders. The equivalent measurements for the budworm were not made but it has been shown (Miller [1]) that fecundity varies linearly with pupal size. The relationship for normal populations is (MG, Eq 13.4)

$$F = 165.64\ x - 328.52 \quad , \tag{26}$$

where x is pupal length (mm.). The average maximum fecundity under field conditions is 200 eggs per female. According to the above equation this corresponds to $x_o = 3.2$mm.

The missing ingredient is the relationship between food consumption, d, and pupal size, x. We assume that mass (as x^3) and d are related as

$$x^3 = a + b \cdot d \quad . \tag{27}$$

If $x = x_o$ when $d = d_o$, $r = d/d_o$ and $x = 0$ when $r = r_1$, then

$$x = x_o \left[\frac{r_1 - r}{r_1 - 1} \right]^{\frac{1}{3}} \quad . \tag{28}$$

To establish the extrapolated point where $x = 0$ we solve the N_L vs. x equation (MG, eq 13.5) for zero size. This equation is

$$x = 3.07 - 0.0018 \cdot N_L \tag{29}$$

or $N_L = 1706$, which is equivalent to $d = d_1 = 0.131$ and $r_1 = 0.139$.

Note that we can write equation (29) in terms of d rather than N_L as

$$\begin{aligned} x &= 3.07 - 0.0018\cdot(\frac{V}{d} - K) \\ &= 3.57 - \frac{0.468}{d} = 3.57 - 0.492\cdot\frac{1}{r} \quad . \end{aligned} \tag{30}$$

This equation and equation 28 are plotted in Figure 11. The close agreement supports the use of equation 28.

The relationship we use in this model for fecundity is

$$F = 82.82\ x - 164.26 \quad . \tag{31}$$

When

$$\begin{aligned} x &= x_0 \left[\frac{r_1 - r}{r_1 - 1}\right]^{\frac{1}{3}} = 3.36 \cdot (r - 0.139)^{\frac{1}{3}} \quad , \\ F &= 278.58 \cdot (r - 0.139)^{\frac{1}{3}} - 164.26 \quad . \end{aligned} \tag{32}$$

We have divided by 2 so that fecundity becomes eggs as per adult.

The field surveys in heavily defoliated areas showed decreased pupal size and fecundity with extent of defoliation. This aspect should manifest itself through the foliage response and reduced food consumption.

Egg Laying and Dispersal

The evaluation of interactions between egg laying and dispersal are elusive in field populations. A female's physiological state and prevailing weather affect her mobility and thus her propensity for being dispersed. These same factors also affect male mobility and consequently mating success. Further, a female's mobility increases after she begins to lay eggs. She will usually not leave the neighborhood of her native tree until she has deposited at least one egg mass of 15-20 eggs. Females caught in traps, and therefore mobile, had already laid an average of 25% (or about 50) of their eggs.

Field studies found the net effective survival of adults to be 51% during the initial stages of an outbreak. It was not possible to separate dispersal losses (failure to locate oviposition sites, etc.) from other losses (predation, weather related mortality, etc.). However, to model this system, we must attempt this separation. First, we would like to know the survival rate for adults from the time of pupal emergence to completion of egg laying. Second, we would like to know how stand condition over space affects egg laying success. We lack this information and therefore must resort to some reasonable hypotheses.

We shall assume dispersal occurs on three spatial scales. The reader should refer to the diagram in Figure 14 while working through the following sections on dispersal. First, we assume the first eggs laid are on or near the tree from which the female emerged. The consequence of this assumption is that the female has a very high probability of locating a susceptible host. However, heavy defoliation reduces her chances of locating an oviposition site. We portray this by an oviposition search success (OSS) function (Figure 12). We assume that 20% of the potential eggs on any site are in this initial category. Eggs from this initial group which are not laid because of heavy defoliation are lost rather than dispersed further. The contribution to the egg stock from short-range dispersal is

$$0.2 \cdot \mathrm{OSS} \quad . \tag{33}$$

Following the deposition of these first eggs, the female increases her activity. The degree of activity is related to the weight of her remaining eggs. If she was a well fed larva and has many eggs she will be less prone to fly until she has deposited some of the weight. One effort of this mechanism is to encourage dispersal away from poor feeding areas and to promote residence on good ones. Eggs laid to reduce weight are subject to mid-range dispersal--away from the native tree but within the native site.

Mid-range dispersal applies to the eggs following the first 20%. The fraction of eggs desired (FED) to be laid by the female is a function of the level of feeding experienced by the large larva. The linear relation used is shown in Figure 13. At the maximum feeding rate ($d = d_o$), the female will be very heavy and attempt to lay all of her eggs in the native site. At or below a level of starvation which produces zero fecundity FED = 0. We determine this point from equation (32); $r' = .344$ and $d' = .325$.

A proportion $0.8 \cdot \mathrm{FED}$ of the eggs are subject to this mid-scale, within site dispersal. The oviposition success of this group is additionally proportional to the amount of susceptible fir (SUSCEP) and the oviposition search success (OSS).

The total proportion of available eggs laid on site is

$$P.E. = (0.2) \cdot OSS + (0.8)\ FED \cdot OSS \cdot SUSCEP\ . \qquad (34)$$

Eggs subject to mid-range dispersal which were not laid locally are "cast to the winds" and carried to other sites. From a potential fraction of 0.8, FED • OSS • SUSCEP have been laid in mid-range dispersal. The remainder, (0.8) • (1.0-FED • OSS • SUSCEP) are subject to long-range dispersal to other sites. The essence of the dispersal algorithm for allocating these eggs to specific (sink) sites is a matrix of transfer probabilities from any particular source site to all possible sink sites. The fraction of eggs landing on a new site which are successfully laid is again proportional to

$$OSS \cdot SUSCEP\ , \qquad (35)$$

where these factors apply to conditions on the sink sites.

We assume that adults make only one long-range dispersal and those that are unsuccessful in finding suitable oviposition sites after this flight are lost. It is possible that more than one flight is made, but supporting data do not warrant modelling this possibility.

We note in passing that if all the stands are in the same foliage condition, the proportion of eggs laid for all sites would be

$$\begin{aligned} P.E. = {} & (0.2) \cdot OSS + (0.8) \cdot OSS \cdot SUSCEP \\ & \cdot [1.0 + FED \cdot (1.0 - OSS \cdot SUSCEP)]\ . \end{aligned} \qquad (36)$$

As a numerical example, a moderate infestation could have OSS = 1, FED = 0.6, SUSCEP = 0.5 and

$$P.E. = 0.72 \quad .$$

This development is meant to portray the effect of spatial variation in forest condition on dispersal and egg laying. As mentioned above, field data do not allow separate evaluation of non-dispersal related losses. We shall set the adult survival from all other factors equal to unity (i.e. $S_A = 1.0$). Later, we may wish to adjust this value by simulating the conditions of the field test plots and adjusting S_A so that the net effect of mortality and dispersal produces a survival of 0.51. That is

$$S_A \cdot (P.E.) = 0.51 \quad . \tag{37}$$

Conclusion

Any model is hypothesis. At this stage we have a hypothesis for a model. We conclude now with some general comments concerning the steps we should take to establish a level of confidence for what we have done. Traditional procedures are available to us--qualitative assessment of the model's behavior and various tests against real world historical data.

The initial stage of most ecological modelling "validation" is usually an aesthetic appraisal of the model *in vacuo.* Do the dynamics look and feel right? The standard for judgment is usually a very qualitative picture of the real world. A harder test is a one-to-one comparison against historical records. Necessary data exist from 1949 to 1972--a period covering an outbreak and decline. It is an open question at this point what techniques and criteria we should use to establish goodness-of-fit.

Quantitative measures which capture the qualitative aspects of an outbreak may have to be invented. We will want to investigate various indices which portray the essential development in space and time of a budworm episode--thresholds, rates of growth, spread and decline, etc.

Other opportunities arise for diagnosis of the budworm model. None is definitive in itself but *in toto* they can be considered with all other evidence. First, we can relate the components of this version to the forms used in the original (Stander [4]). The original was the synthesis of considerable field experience and if our present version is not congruent with it, we must look further to find the reasons. Specifically, we should compare the two versions of foliage response. Additionally, the life stage survivals can be related directly to their corresponding densities, and fecundity related to adult density.

The next step is to aggregate the survival and fecundity relations into a generational survival and a reproduction curve. These aggregations must at least appear reasonable. Various other analytical probes of sections of the model can be made to see if the important controlling factors appear reasonable.

Finally, there is considerable field experience available for comparison. Particularly, the studies of the sprayed plots should correspond to the essential features of our model. There are many other relationships in the monograph and associated literature which should be brought into the picture. With the model as our real world, we can perform some of the same "experiments" and derive comparable statistics.

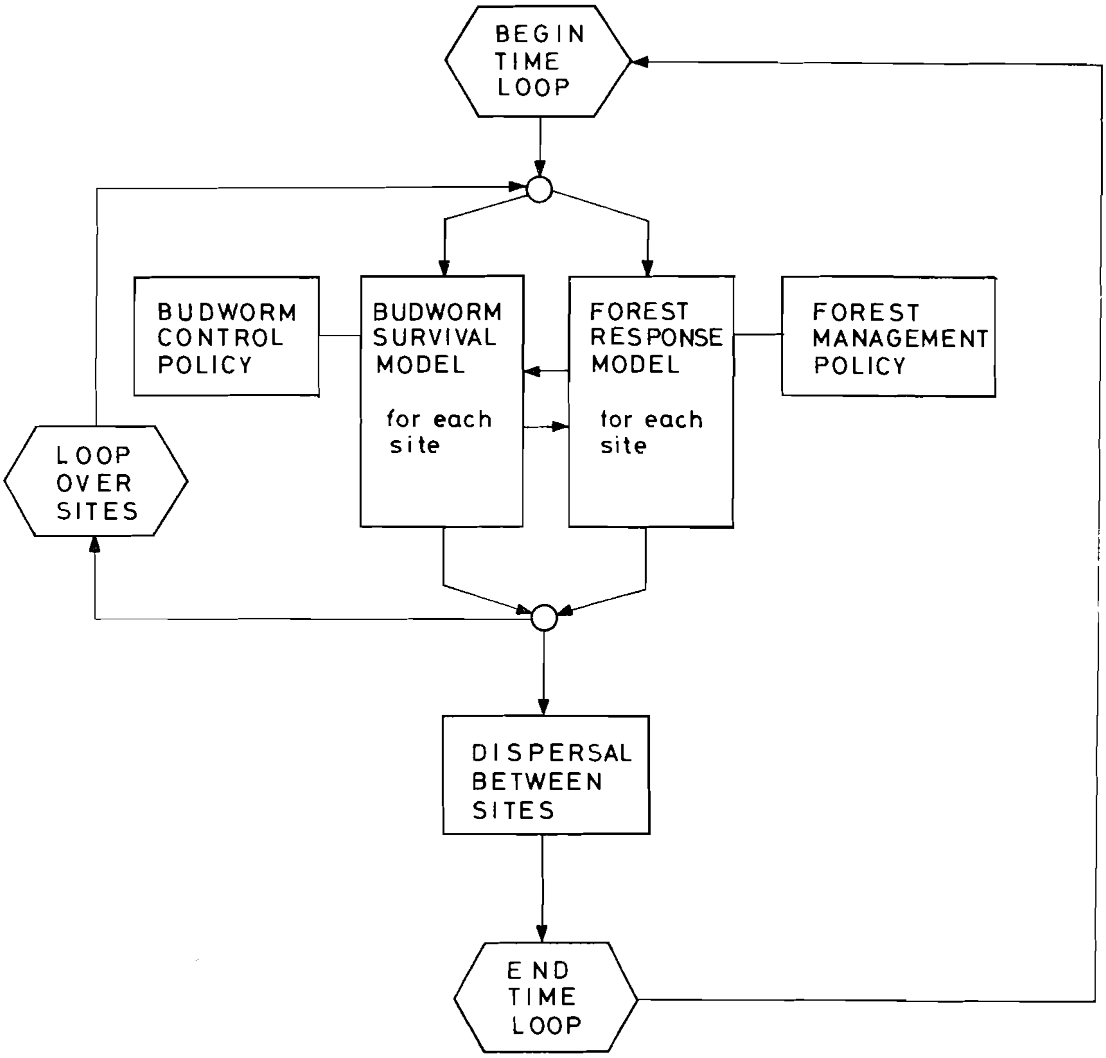

FIGURE 1. BASIC MODEL STRUCTURE

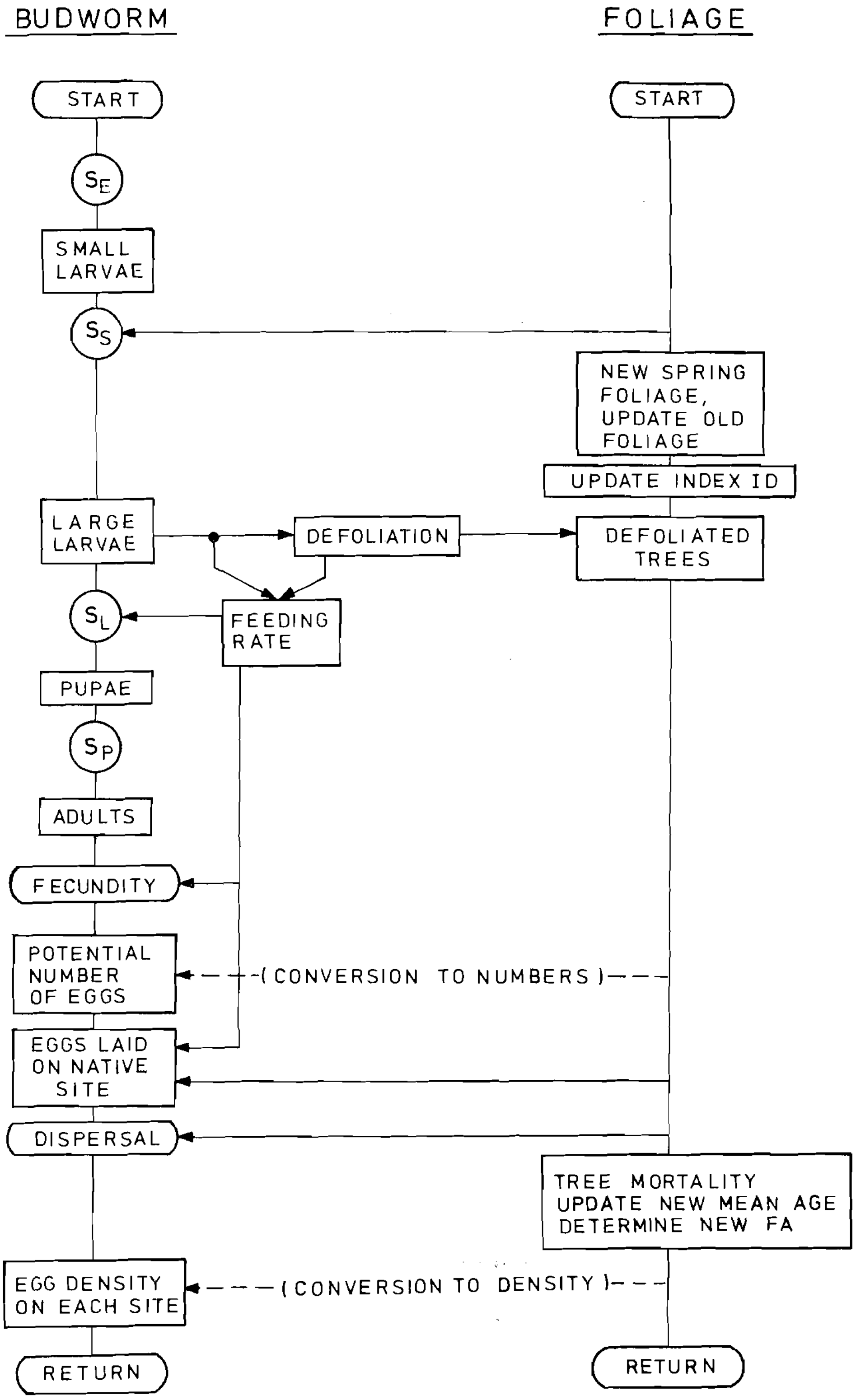

FIGURE 2. COMPUTATION SEQUENCE FOR BUDWORM AND FOLIAGE

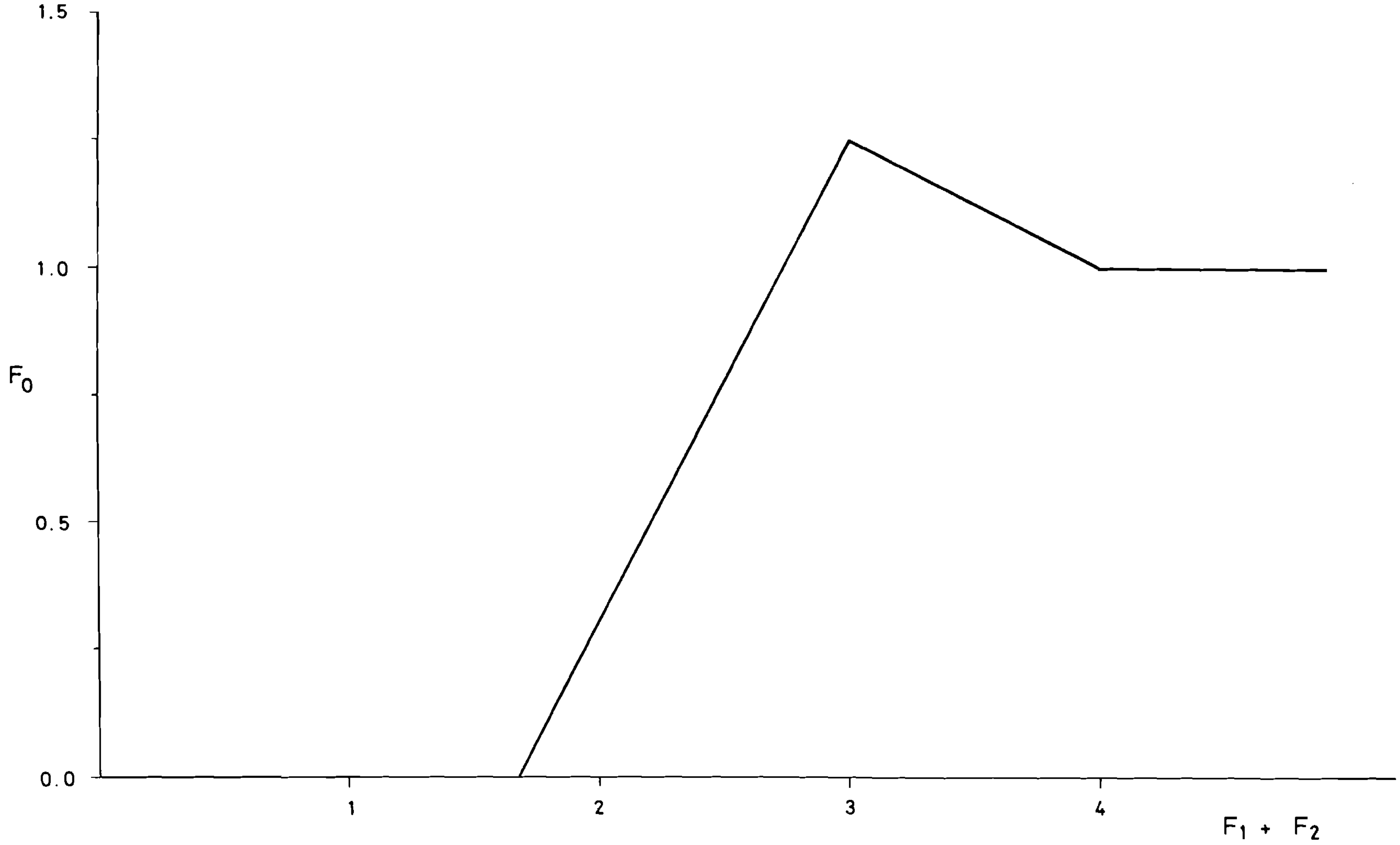

FIGURE 3. NEW FOLIAGE GENERATED PER 10 SQ. FT. AREA

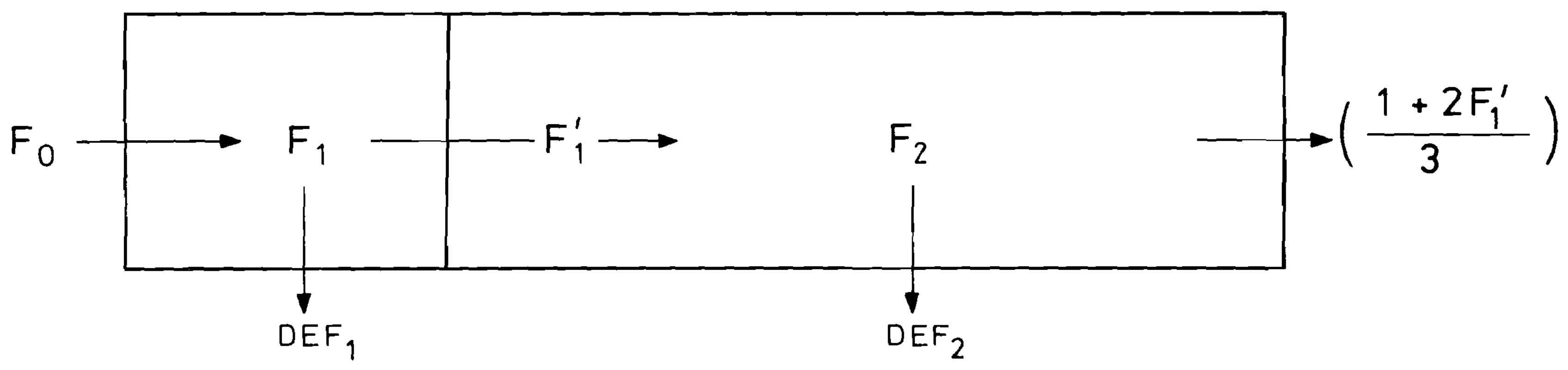

FIGURE 4. SCHEMATIC OF FOLIAGE

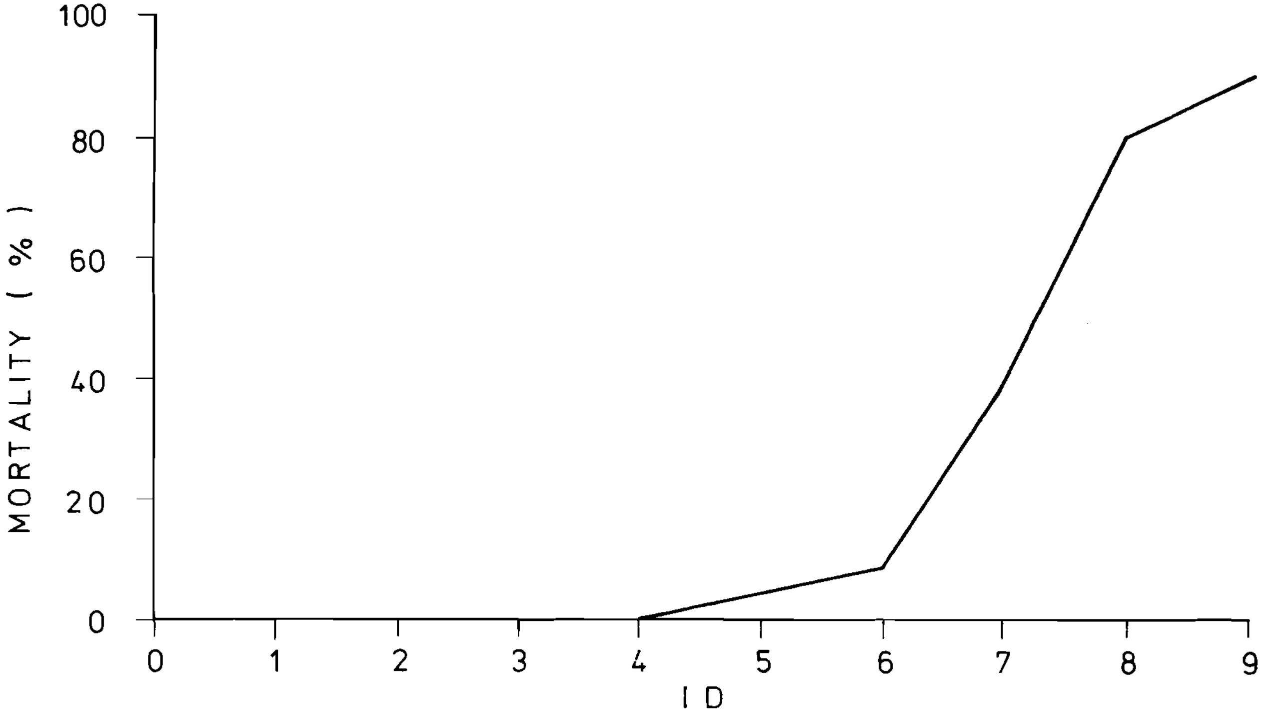

FIGURE 5. TREE MORTALITY VERSUS ACCUMULATED DEFOLIATION INDEX

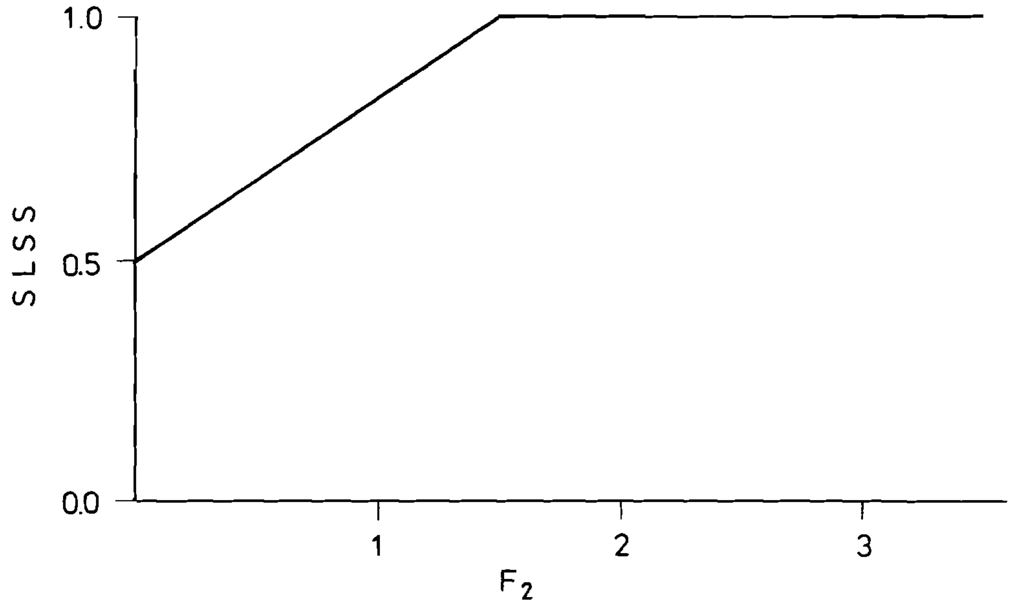

FIGURE 6. SMALL LARVAL SEARCH SUCCESS

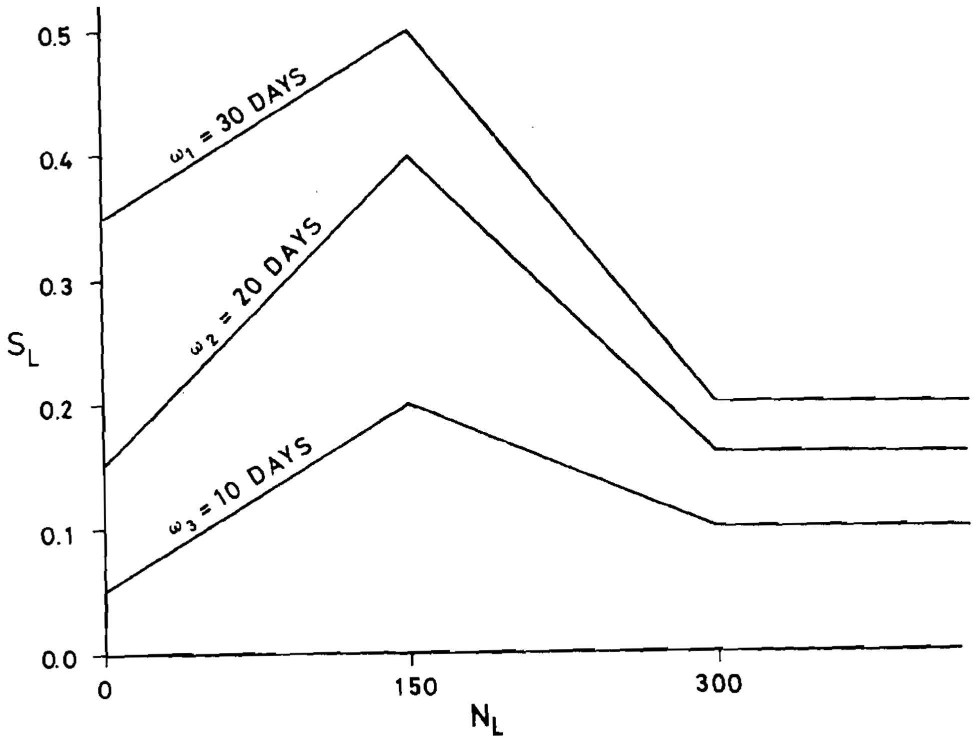

FIGURE 7. SURVIVIAL OF LARGE LARVAE NET EFFECTS FROM FIELD EXPERIENCE

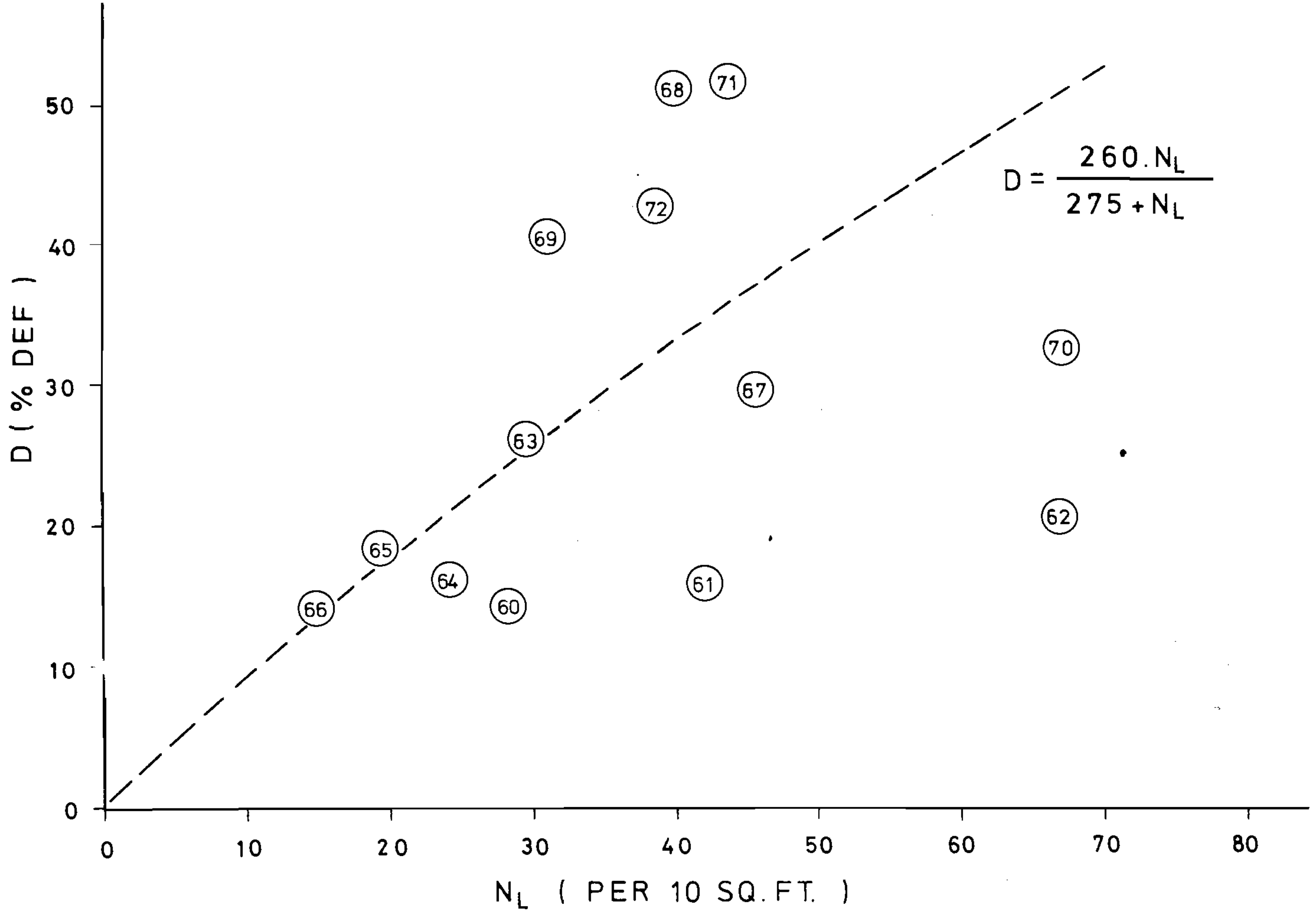

FIGURE 8. DEFOLIATION FROM SURVEY DATA

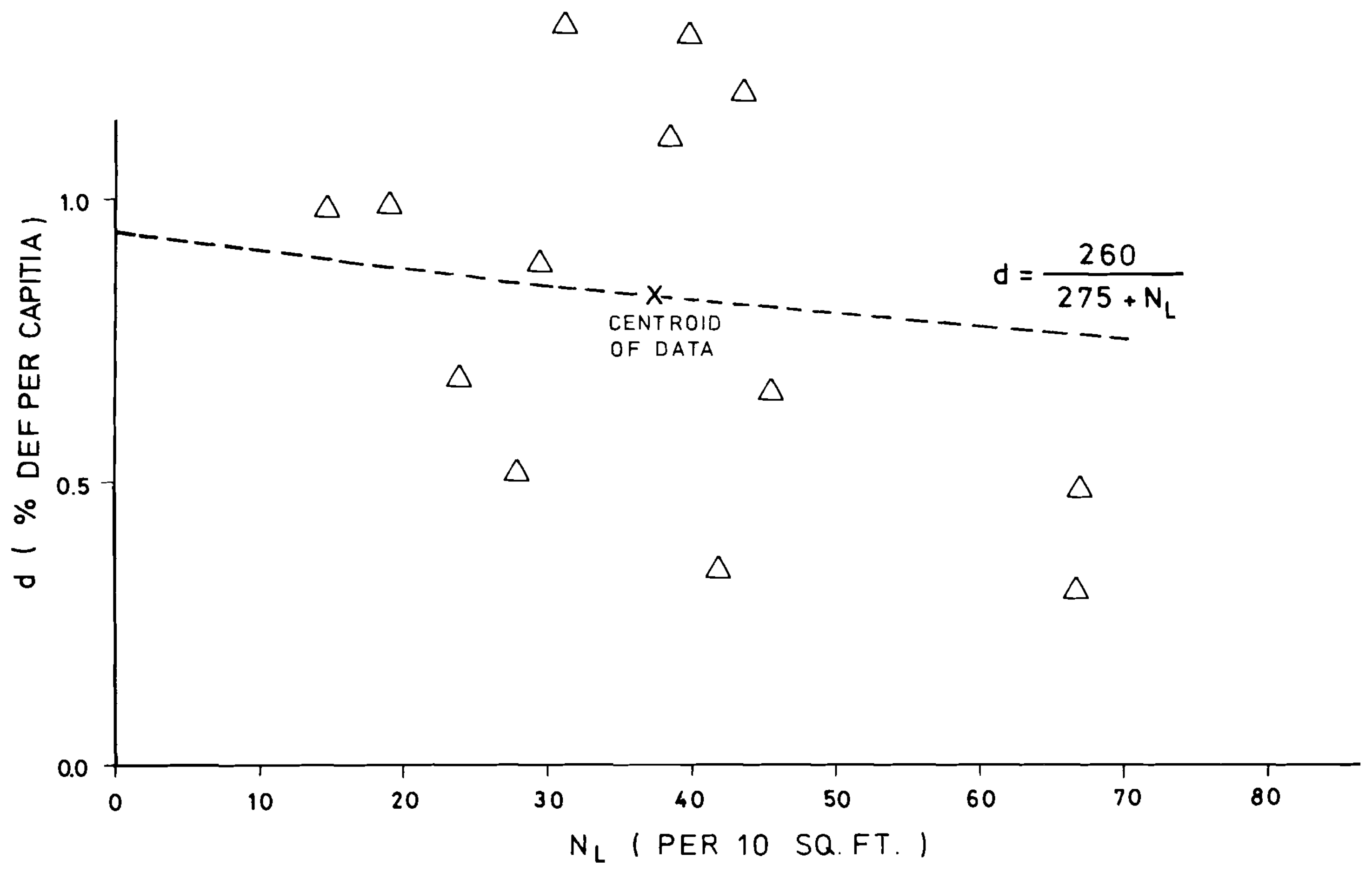

FIGURE 9. FOLIAGE CONSUMPTION FROM SURVEY DATA

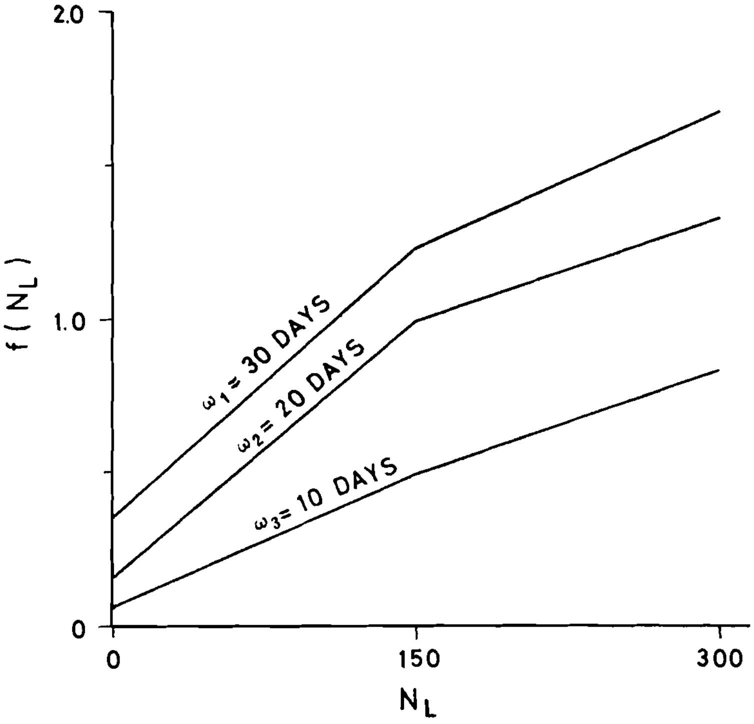

FIGURE 10a. FOLIAGE- INDEPENDENT SURVIVAL
FACTOR LARGE LARVAE

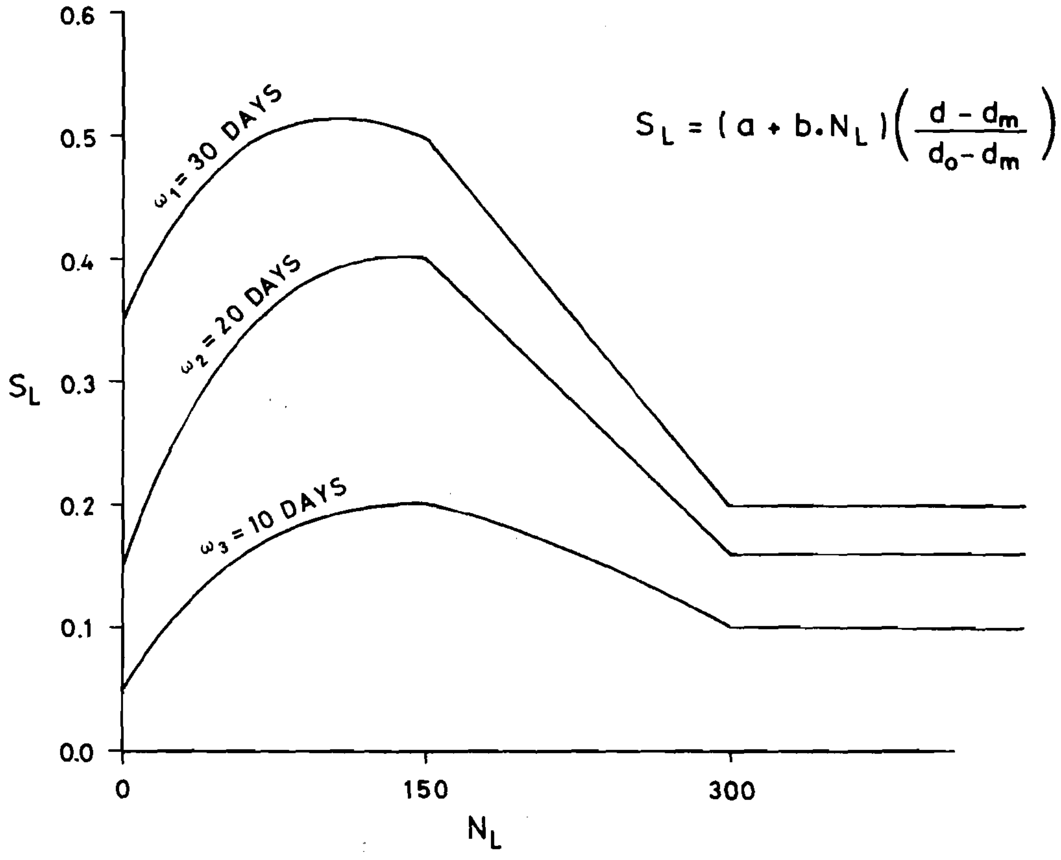

FIGURE 10b. COMPOSITE LARGE LARVAL SURVIVAL
($V = F_1 + \alpha F_2$ HELD AT 260)

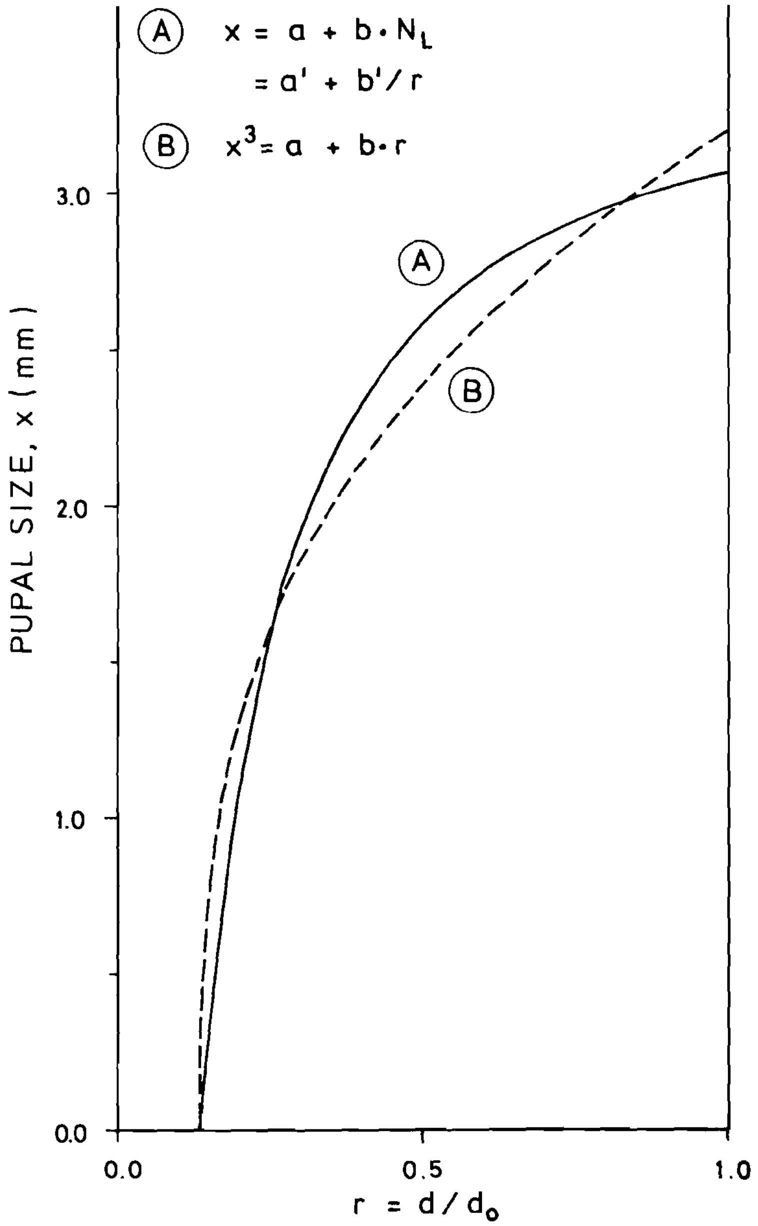

FIGURE 11. ALTERNATIVE MODELS FOR PUPAL SIZE VS. FOOD CONSUMPTION

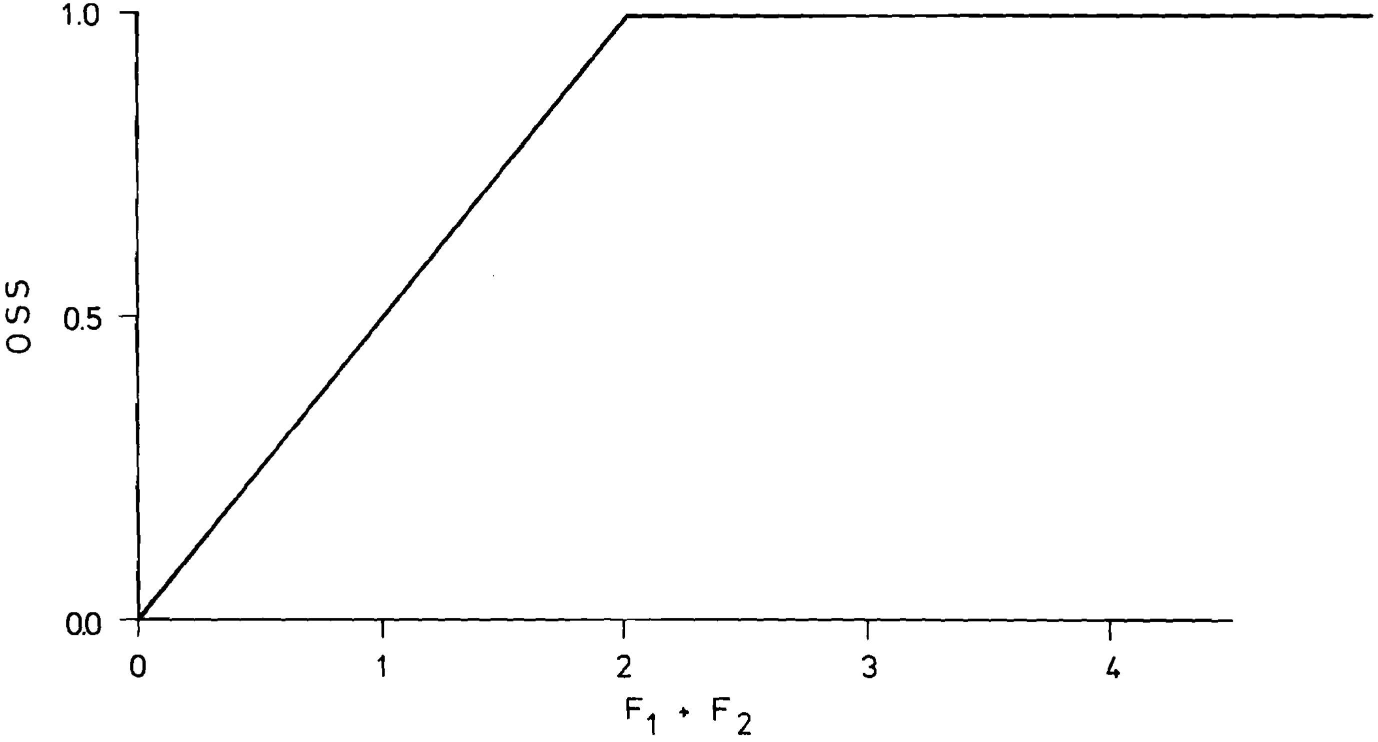

FIGURE 12. OVIPOSITION SEARCH SUCCESS (OSS) AS A FUNCTION OF TOTAL FOLIAGE AVAILABLE

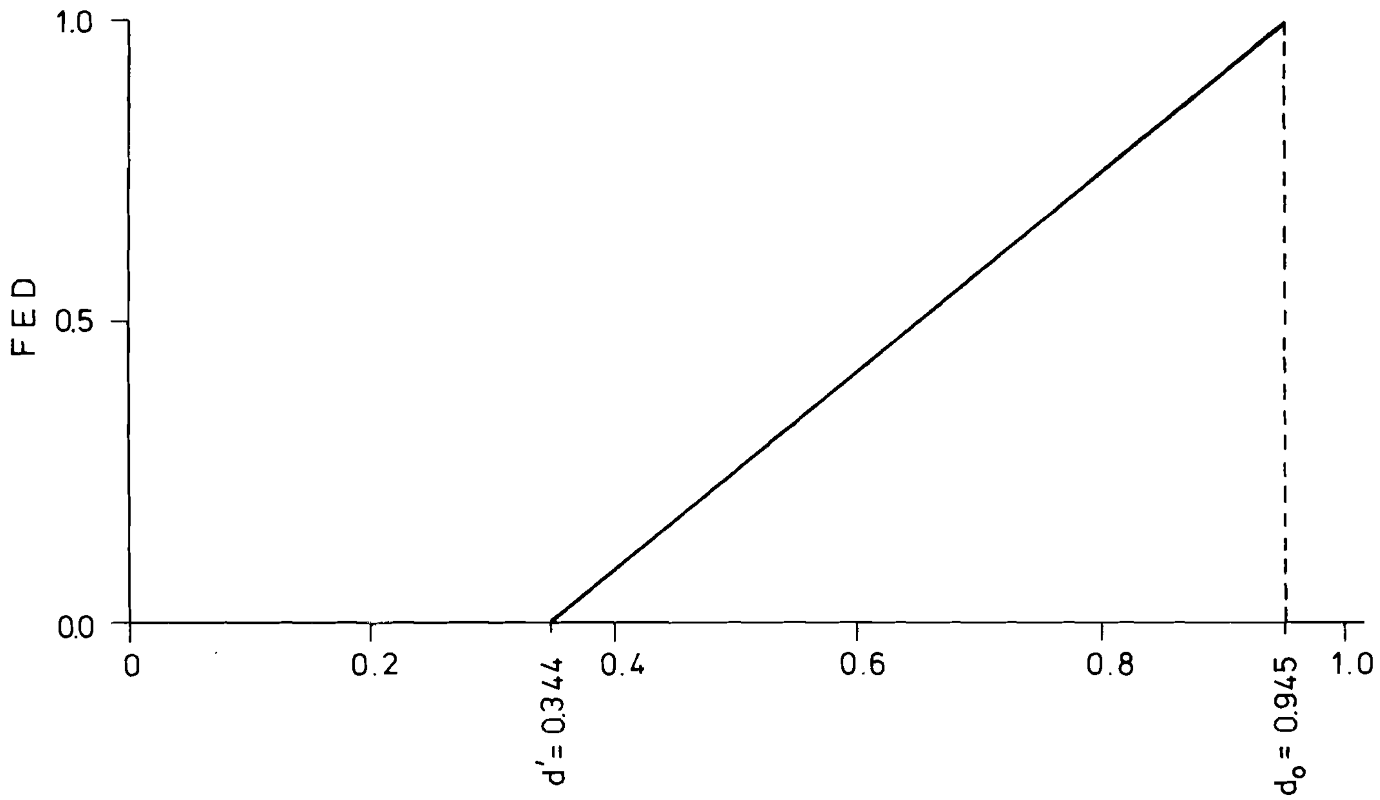

FIGURE 13. FRACTION OF EGGS DESIRED (FED) TO BE LAID ON NATIVE SITE

d' ⇒ ZERO FECUNDITY

d_o ⇒ MAXIMUM FECUNDITY, MAX. FOLIAGE CONSUMPTION

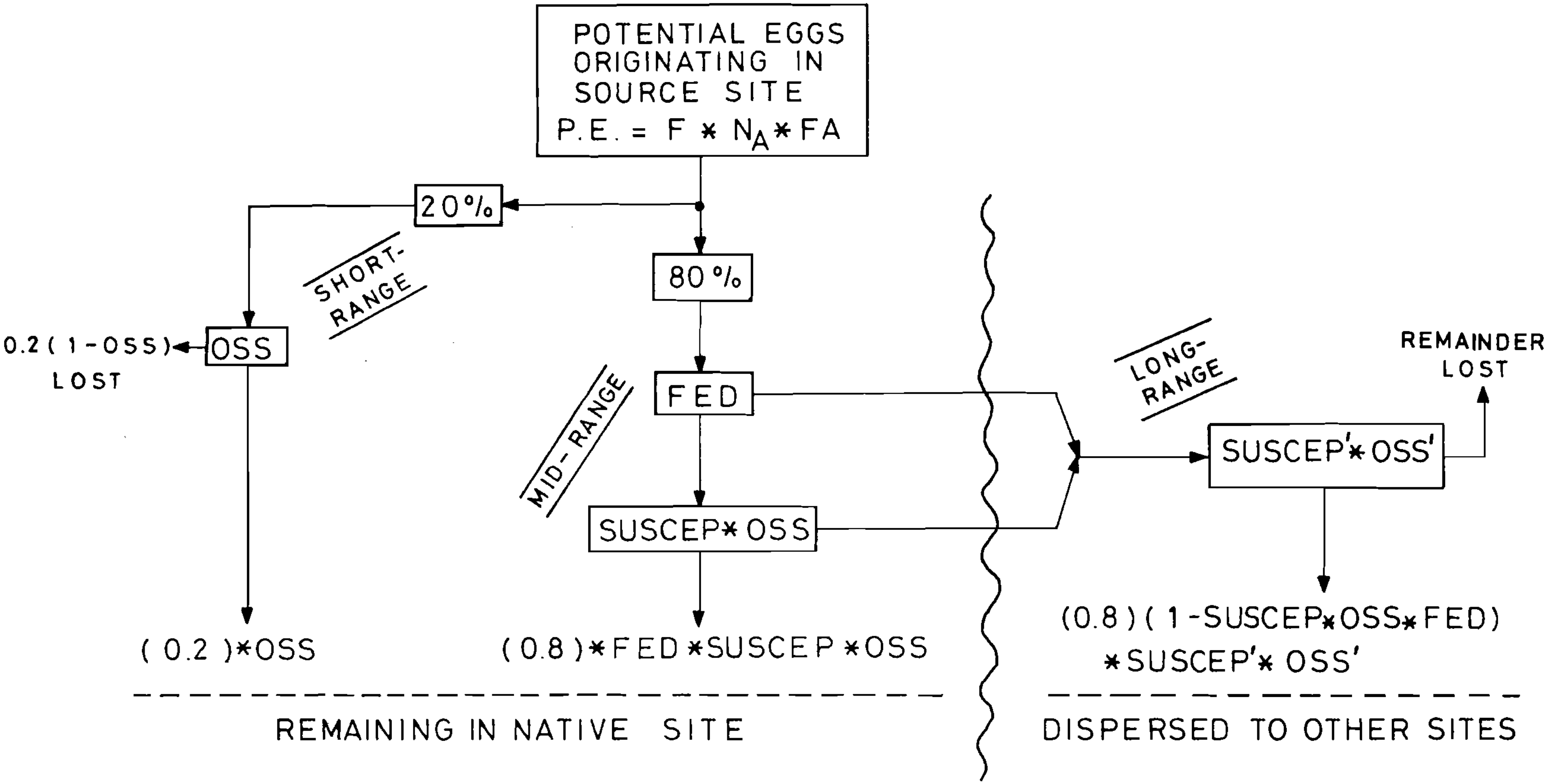

FIGURE 14. DIAGRAM OF EGG DISPERSAL SCHEME

References

[1] Miller, C.A. "A Technique for Estimating the Fecundity of Natural Populations of Spruce Budworm," Can. J. Zool., 35 (1957), 1-13.

[2] Miller, C.A. "Brief Comments on the Budworm, the Forest, and Forest Protection," Forest Research Laboratory Internal Report M-51. Fredericton, New Brunswick, 1969.

[3] Morris, R.F. "The Dynamics of Epidemic Spruce Budworm Populations," Memoirs of the Entomological Society of Canada, No. 31, 1963.

[4] Stander, J.M. "A Simulation Model of the Spruce Budworm and the Forest in New Brunswick," MS, Inst. Res. Ecol., University of British Columbia, 1973.