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A MODEL FOR PLANT-HERBIVORE INTERACTIONS
INCORPORATING HETEROGENEITY AMONG HOST PLANTS IN HERBIVORE SURVIVORSHIP

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What is the point? If such heterogeneity exists it is highly stabilizing. It has robust implications even in graphical form.

Q: is hostplant mosaic real?

A: are some members of host plant population protected from herbivory, and others not? Is difference 2-3 orders of magnitude or not?

Populations of insect herbivores are controlled by the availability and dispersion of host plant (Caughley and Lawton 1981, Dempster 1983, Kareiva 1983), by susceptibility to predators (Hairston et al 1960, Hassell 1978), and by weather (Strong 1984, Kareiva 1983). In addition, recent evidence suggests that many plants are highly variable with respect to qualities which may affect herbivore success (including chemical constituents, nutritive quality, and plant dispersion), and heterogeneity in these qualities appears to reduce the severity of insect attack (Denno and McClure 1983). In general, variability in plant quality reduces herbivore fitness by (1) reducing the probability that a given insect will encounter plant foliage that it can successfully consume (Whitham 1983, Schultz 1983, Kareiva 1983), and (2) by preventing the evolution of a single insect genotype which can severely damage the plant population (Hare 1983). The effect of variability on evolving populations of insects has been modeled (see Mitter and Futuyma 1983, Gould 1983 for reviews). However, the effect of this variability on insect populations in ecological time has not been explicitly modelled.

Athough most authors do not report within- or between-plant variation in herbivore survivorship, available data suggest that the variability may be very great. Alstad and Edmunds (1983) have shown that artificially transferred colonies of pine scale insects have very low survival (less than 1% of colonies become established) on individual pine trees other than the one they were removed from, and Whitham (1983) showed that the fitness of Pemphigus aphids ranged over an order of magnitude between different host trees and between different branches of the same tree. Denno (1983) reported large differences in population density of Prokelisia leafhoppers as being a response to local variability in nutritive value of Spartina foliage. These studies suggest that plant quality, as measured by herbivore fitness or survivorship, may frequently vary over a range of 1-2 orders of magnitude or more. In general, variability of this magnitude will result when one portion of a plant population is effectively resistent to herbivore attack while another portion is vulnerable.

Survival of herbivores on plants is frequently found to be dependent on the presence or absence of ants (Messina 1981, Buckley 1982, Laine and Niemela 1980), and Smiley (in press) has shown that spatial variation in ant attendance to the extrafloral nectar glands of Passiflora results in differences among plants in the average suitability for herbivores, ranging from 40 to 90% daily survival rates of Heliconius caterpillars. Other herbivores require the presence of certain species of ants. Pierce and Elgar (in press) and Smiley et al (in prep.) found that fitness of caterpillars of the lycaenid butterfly Jalmenus evagoras was virtually zero unless Iridomyrmex anceps was present, and Atsatt (1981) showed that females of another lycaenid Ogyris amaryllis require ants for oviposition. These examples suggest that spatial variability in the predator community may be as important to herbivore success as other sources of variability discussed in Denno and McClure (1983). Many predators are not uniformly distributed in space, and, although little data is available, the vulnerability of herbivores on plants are likely to be affected by the plant's location in the habitat with respect to factors such as the nests of ants (Bartlett 1961, Laine and Niemela 1980, Leston 1978), microhabitats suitable for spiders (Robinson 1981), lizard foraging ranges (Schoener 1970), other plants (Atsatt and O'Dowd 1976), or nests of birds, wasps, and other predators. Spatial variation in the average distribution of predators may be described as a "predator mosaic", in which areas or "patches" of the mosaic differ in the composition of the local predator community. This definition focuses on spatial heterogeneity rather than territorial interactions between species, which are used to define the analogous "ant mosaic" (Leston 1978, Jackson 1984).

Since host plant nutritive and chemical quality will usually be independent of the "predator mosaic", the effects of the two sources of variability will be approximately multiplicative. For example, if each source of mortality independently caused herbivore survival to range over two orders of magnitude, then the combined effect would range over four orders of magnitude. In general, addition of new sources of variability will tend to increase this range in a multiplicative fashion unless there are compensating interactions among the factors. This could occur if mortality caused by one agent increase in response to a decrease in another mortality agent, or when the force of mortality is a rapidly increasing function of the density of the herbivores. In theory, an "optimally" foraging predator should act as a compensating agent of mortality, since it should selectively feed on prey in a density-dependent fashion (Hassell 1978), "culling" aggregations of herbivores on plants which are otherwise poorly defended. However, Morrision and Strong (1980), Dempster (1983), Strong (1984), and Kareiva (1983) reviewed the effects of predators on insect herbivores under natural conditions, and concluded that density-dependent predator responses were rare. This suggests that herbivores on plants with an ineffective predator community or other form of defense will usually not be "culled" by compensating predation. Since most other forms of mortality are unlikely to interact with herbivore density (at natural densities), variation among plants in nutritive, chemical, microclimatic, and "predator" quality will probably result in large-magnitude variation in the expected probability of survivorship.

In this paper, I develop a model for plant-herbivore interactions which incorporates large-magnitude heterogeneity among plants in herbivore survivorship. I begin by analyzing the stability properties of a simple system consisting of the herbivore population and two categories of plants, and then proceed to analyze multiple-plant systems using computer simulation and algebraic arguments. From this I develop a graphical analysis and analyze two examples from my own research. Finally, I discuss some of the implications of the models for understanding the interaction between plants and herbivores.

MODEL FOR PLANT-HERBIVORE INTERACTION

Plants typically interact with insect herbivores on two time-scales. Herbivores remove foliage or otherwise affect plant biomass over a very short time scale, usually days, and they may affect plant reproductive success over a much longer time scale, typically several years or longer. Insect herbivores typically respond to plants on a time scale of one year or less. In the present model I examine the interaction between plant biomass and populations of insect herbivores over a short time scale (Caughley and Lawton 1981), and do not specifically examine the effects of plant reproduction.

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$$\frac{ds}{dt} = rs - nbcp$$

$$\frac{dn}{dt} = \frac{nbcp}{p} - nu = n(bc-u)$$

To begin, I modelled a homogeneous plant population. I assumed that changes in plant size or biomass (s) may be modeled as plant growth rate (rs) minus herbivory rate (H), expressed as:

$$ds/dt = rs - H \qquad (1)$$

I also assumed that changes in the number of mobile adult insect herbivores (n) may be modeled as the rate of production of new adult herbivores (H/p, where p is the amount of plant material required to produce one adult herbivore) minus the death rate of adult herbivores (nu):

$$dn/dt = H/p - nu \qquad (2)$$

Finally I assumed that the rate of herbivory (H) is determined by:

$$H = nbcp \qquad (3)$$

where b equals the herbivore per capita birth rate (=egg production rate for most insect herbivores) and c equals the probabability that newborn herbivores survive on the plant. 'c' is thus the parameter which expresses the suitability of plants for herbivore survival on the plant. Table 1 lists these terms, with definitions.

Equation (3) assumes that juvenile herbivores have an equal chance of survival on all plants (c), i.e. that plants are homogeneous. For this model (equations 1-3), the herbivores undergo exponential decline or growth, depending on the sign of (bc-u) and the availability of host plant.

Plants which are effectively protected against herbivory cannot grow indefinitely. I assumed they could grow to some maximum size s0, beyond which growth ceases. I incorporated this into the model as exponential plant growth up to a cutoff at s=s0:

$$r=r0 \text{ (constant) for } s < s0,\ r=0 \text{ for } s > s0 \qquad (4)$$

or, alternatively, as logistic plant growth:

$$r = r0(1-s/s0) \qquad (5)$$

where r0 is the growth rate of small plants. Equations (4-5) represent extremes and probably bracket more realistic functions which would have growth rates decline rapidly but not abruptly near s=s0.

With either equation (4-5) combined with the model in equations (1-3), herbivores always decline to zero (except for the unlikely case when bc = u). This happens because when bc > u, herbivores increase until the plants are defoliated, and then the herbivore population "crashes," i.e. goes to zero and when bc < u the herbivores decline immediately to zero. These models incorporate very simple assumptions about the interaction between plants and insect herbivores, and are highly unstable. In order to provide more useful, stable models, Noy-Meir (1975) and Caughley and Lawton (1981) made additional assumptions about the effects of plant and herbivore density. Their models are most applicable to vertebrate grazing systems, which exhibit measurable density-dependent effects. As discussed above, populations of insect herbivores in natural systems typically do not exhibit measureable density-dependent components at most densities. Strong (1984) and Dempster (1983) have suggested that most populations of insect herbivores are not regulated by density-dependent effects except when they occasionally reach high densities, defoliating their hosts. I have followed this reasoning in the present paper, and do not explicitly incorporate density dependence into the

$$ds_i/dt = rs_i - nbpc_i \frac{s_i}{S}$$

$$dn/dt = nbc_i \frac{s_i}{S} - nu$$

at equilibrium when $ds_i/dt = 0$

$$r\hat{s}_i = nbpc_i \frac{\hat{s}_i}{S}$$

$$\hat{s}_i = \frac{nbpc_i \hat{s}_i}{rS}$$

$$u = bc_i \frac{\hat{s}_i}{S}$$

equations for herbivore numbers.

I incorporated heterogeneity among plants in herbivore survivorship into equations 1-5 by assuming that the habitat contains n categories of plants (1,2,..i..n), each with biomass s_i and probability of juvenile herbivore survivorship c_i. I assumed that c_i is a constant for each plant, and that two plants with the same c_i ~~were~~ are identical in terms of the model and may be treated together. Thus, I assigned each plant within a habitat to plant categories based on the suitability of plants for survival of juvenile herbivores. Equations (1-3) then take the form:

$$ds_i/dt = rs_i - nbpc_i D(i) \qquad (6)$$

$$dn/dt = nbc_i D(i) - nu \qquad (7)$$

D(i) is a function which distributes newborn herbivores (eggs) across the host plants. I initially assumed that the distribution was random with respect to foliage biomass, i.e. that each unit of foliage biomass has an equal probability of receiving eggs. In that case,

$$D(i) = s_i/S \qquad (8)$$

where S equals the total biomass of all plants summed together.

Equations (6-8) require that the values of c_i be equal to juvenile survivorship, and that all surviving herbivores are identical. If juveniles die in the pupal stage or otherwise after leaving the host plant (with survivorship probability = Q), the additional mortality has the effect of increasing the average amount of plant biomass (p) required to produce one adult herbivore ($p = p'/Q$, where p' is the

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setting (9) and (10) to zero:

(and $s_1 = s$ $c_1 = c$

$$rs = \frac{nbcps}{s+s_0}$$ from (9)

plant

$$rs(s+s_0) = nbcps$$

$$rs + rs_0 = nbcp$$

$$s = \frac{nbcp}{r} - s_0 = (11)$$

$$un = \frac{nbcs}{s+s_0}$$ from (10)

herbivore

$$u = \frac{bcs}{s+s_0}$$

$$us + us_0 = bcs$$

$$us_0 = (bc-u)s$$

$$\frac{us_0}{bc-u} = s \quad (12)$$

amount of host plant consumed by one surviving herbivore). If adults are not identical, but have fecundity or adult survivorship influenced by the host plant (Rausher 1983), another function would be required in the equation for herbivore change (7). I have not modelled such functions in the present work.

STABILITY ANALYSIS OF TWO-PLANT MODEL

To investigate the qualitative stability of the model in equations 4-6 I analyzed a two-plant model in which plant 1 has few predators and conditions are favorable for herbivore increase but plant 2 has a highly effective defense and $c_2=0$. In such a case, s_2 increases to maximum size s0:

$$ds_1/dt = rs_1 - nbc_1 ps_1/(s_1+s0) \qquad [s_2=s0] \qquad (9)$$

$$ds_2/dt = 0$$

$$dn/dt = \{nb\, c_1\, s_1\}/\{s_1+s0\}-un \qquad [c_2=0] \qquad (10)$$

The zero isoclines of model 7-8 were found by setting equations 7 and 8 equal to zero and solving for s (letting $s_1=s$ and $c_1=c$):

$$s = bcpn/r - s0 \qquad \text{[plant growth isocline]} \qquad (11)$$

$$s = us0/(bc-u) \qquad \text{[herbivore population isocline]} \qquad (12)$$

↑ yes, see fig 1

A positive equilibrium can exist only if (bc-u)>0, i.e., per capita production of new adults (bc) must be greater than the per capita death rate (u). This means that the herbivore must be able to increase when feeding on the most favorable plant in its habitat.

To evaluate the behavior of the model away from equilibrium the signs of equations 7 and 8 were evaluated at various points in the phase-plane (see figure 1). As with most predator-prey models (May 1981) the point trajectories were found to move tangentially around the equilibrium point, suggesting that the model is oscillatory. The angle of crossing of the isoclines also suggested that the system is unstable, using the method of Rosenzweig and MacArthur (1963). However, the signs at $n = 0$ and $s >> 0$ indicated that as n approaches zero, the decline in herbivore numbers is slowed without affecting the increase in s, allowing both the plants and the herbivores to recover. Likewise at $s = 0$ and $n >> 0$ the decline in plant size is slowed while n continues to decline, allowing the plants to persist until the herbivore population becomes rare enough that the plants can recover. Thus, although the equilibrium point is apparently unstable, the system appears to be protected against either s or n collapsing to zero.

A stability analysis around the equilibrium point:

$$\hat{s} = s0/(bc-u) \tag{13}$$

$$\hat{n} = rs0 / (bc-u)p \tag{14}$$

revealed that the sign of the real part of the eigenvalues of the associated Jacobean matrix was positive for $(bc-u)>0$ (Appendix I). This means that the model is unstable near equilibrium, confirming the result of graphical analysis. Computer simulation revealed that plants and herbivores in model 7-8 oscillate in cycles with increasing amplitude (figure 2; solid line). A global stability analysis revealed that the cycles increased indefinitely when $bc > r+u$, but were finite in number when $bc < r+u$ (Y. Iwasa, personal communication). In the latter case, both plants and herbivores grew indefinitely after a finite number of cycles.

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$$r(1-s/s_0)s = \frac{nbpcs}{s+s_0}$$

$$r(1-s/s_0) = \frac{nbpc}{s+s_0}$$

$$(1-s/s_0)(s+s_0) = \frac{nbpc}{r}$$

$$s + s_0 - \frac{s^2}{s_0} - s =$$

$$s_0 - \frac{s^2}{s_0} = \frac{nbpc}{r}$$

$$\frac{s^2}{s_0} = s_0 - \frac{nbpc}{r}$$

$$s^2 = s_0^2 - \frac{nbpc\,s_0}{r} \longrightarrow ?$$

Plant growth limitation was not imposed in the above model. The effect of the plant growth ceiling (equation 4) was to impose a limit cycle on the otherwise diverging system, as shown by computer simulation in figure 2 (dashed line). Incorporating the logistic plant growth model (equation 5) modified equation (9) as follows:

$$ds/dt = r(1-s/s0)s - nbcps/(s+s0) \qquad [r=r0 \text{ in } (5)] \qquad (15)$$

The plant growth isocline for this model (equations 10, 15) was determined to be:

? → $s^2 = s0^{\textcircled{2}\,?} - \{bcp(s0)/r\}n$ [plant growth isocline] (16)

with the herbivore population isocline remaining unchanged (equation 11). When both isoclines were plotted as in figure 3 and analyzed using the method of Rosenzweig and MacArthur (1963), the oscillatory nature of the model was seen to be preserved. However, the angle of the isoclines was changed so that the equilibrium point appeared by inspection to be stable. Stability analysis around the equilibrium confirmed this, with the real parts of the eigenvalues always being less than zero for $(bc-u) > 0$ (Appendix II). The stable equilibrium points were:

$$s = \{u\ (s0)\} / \{bc-u\} \qquad (17)$$

$$n = \{r(s0) / p(bc-u)\}\ \{1 - u/(bc-u)\} \qquad (18)$$

Computer simulation incorporating logistic plant growth revealed cycles of decreasing amplitude converging on the equilibrium points, as predicted by the stability analysis.

This analysis of the two-plant heterogeneity models (equations 9,10 and 15) revealed that they have very different stability properties from the analogous models without heterogeneity (equations 1-5). In heterogeneous systems, herbivores cycled in abundance or reached an equilibrium with the host plant population. When vulnerable plants became rare, the herbivores began exploiting the protected plants. Herbivore production then declined at the same time as the plants began to recover. This process conforms to that in other types of models in which density-dependent effects have been explicitly formulated to allow plants and herbivores to recover when rare (e.g. Caughley and Lawton 1981).

probably

MULTIPLE PLANT MODEL: SIMULATION AND ANALYSIS

In nature, multiple factors interact to determine the average survivorship c_i of herbivores on a given plant, and the values of c_i lie along a continuous spectrum of herbivore survivorship probabilities. Since the effects of independent sources of mortality on survivorship are multiplicative rather than additive, and because values of c_i are typically very small (<0.1) it is most useful to represent the spectrum of plant suitability on a logarithmic scale (Varley 1975). For simplicity, I initially modelled 10 categories of plants which were uniformly distributed across a range of this spectrum. For example, the plants in the simulations in figures 4 and 5 have c_i values equal to 0.003, 0.005, 0.009, ..., 0.333. Here, the values of c_i ranged over two orders of magnitude from 0.003 to 0.333 in a geometric (multiplicative) series. The range of these values encompasses estimated survivorship probabilities for <u>Heliconius</u> feeding on <u>Passiflora</u> plants with (p=0.006) and without (p=0.11) attendant ants (see below). Other model parameters used initially were r=0.05/day, s0=100 leaves/ha., b=2 female eggs/day,

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It is important to note that, in spite of the parameter values being taken from nature, the simulations are unrealistic in that they assume that each plant suitability category contains equal numbers of plants. This will be addressed below in the introduction of the graphical analysis.

In spite of [illegible]

p=5 leaves, and u= 0.07/day. These values correspond approximately to parameters estimated for populations of *Passiflora* and *Heliconius* species (Smiley 1978 and Mallet 1984), which maintain low-density populations in rainforest habitats in the neotropics (Ehrlich and Gilbert 1973). insert It is important to note that the multiple plant model presented here is unrealistic in that the number of plants in [illegible]

Some of the plants represented in the multiple-plant model may become defoliated ($s_i \overset{\approx}{=}* 0$), and since growth rate is proportional to size (equation 1), these plants cannot recover quickly from defoliation. Since plants in nature generally have stored reserves which enable them to recover from defoliation, I incorporated a minimum plant size of 1.0 leaves into the simulations. This procedure allowed plants to recover from defoliation if herbivores were not too numerous, but did not otherwise affect the outcome of the model. I assumed that these "reserve" leaves were unavailable to the herbivores, as would be the case if their biomass were in the form of stored reserves rather than actual foliage.

When simulated with the plant growth cutoff model (equation 4), the 10-plant system converged to a limit cycle of small amplitude (figure 4~~)~~ solid lines. The three most-suitable plants (8-10) became defoliated at equilibrium, while the six least-suitable plants (1-6) grew to full size (figure 5 top). Plant 7, the "marginally suitable" plant, cycled in size with the herbivore population. When simulated with the logistic plant growth model (equation 5), the system came to a stable equilibrium (figure 4~~)~~ dotted line. The three most-suitable plants were nearly defoliated, and the 4-5 least-suitable plants grew nearly to full size (figure 5~~)~~ bottom. Plants 6 and 7, the marginally suitable plants, remained at stable, intermediate sizes. Thus, a similar pattern resulted from both models.

[illegible] assume [illegible] to be equal. This is unlikely [illegible] in most cases. The graph [illegible] is presented [illegible]

$$ds_i/dt = rs_i - nbpc_i D(i) \qquad (6)$$

$$ds_i/dt = r\left(1-\frac{s_i}{s_0}\right)s_i - \frac{nbpc_is_i}{s_i+s_0} \qquad (15)$$

$$ds_i/dt = r\left(1-\frac{s_i}{S_0}\right)s_i - \frac{nbpc_is_i}{S} \qquad \text{modified } (15)$$

$$r\left(1-\frac{s_i}{S_0}\right)s_i = \frac{nbpc_is_i}{s_i+S} \qquad \left[ds_i/dt = 0\right]$$

$$r\left(1-\frac{s_i}{S_0}\right) = \frac{nbpc_i}{rS}$$

$$s_i = s_0 - \frac{nbpc_is_0}{rS} \qquad (19) \longrightarrow$$

$$s_i = s_0 - \frac{nbps_0c_i}{rS} \qquad (19)$$

$$s_0 = \frac{nbps_0c_m}{rS} \qquad \left[c_i = c_m \text{ at } s_i = 0\right]$$

$$\frac{1}{c_m} = \frac{nbp}{rS}$$

$$(19)$$

$$a(i) = nb\frac{[s_i]}{S}c_i = nb\left[s_0 - \frac{nbp}{rS}c_is_0\right]c_i/S$$

$$= nb\left[s_0 - \frac{c_i}{c_m}s_0\right]c_i/S$$

$$= \left\{nb\left[s_0 - \frac{s_0}{c_m}c_i\right]/S\right\}c_i \qquad (20)$$

The least suitable (best protected) plants grew unhindered by herbivory, the most suitable (least protected) plants become defoliated and were unavailable for the herbivores, and the marginally suitable plants were partially defoliated. This suggests that the marginally suitable plants support most of the production of herbivore adults, and constitute the principal host plant resource for the herbivore population at equilibrium.

To quantify which plants were producing most of the adult herbivores, I determined the position and breadth of the peak in herbivore production along the logarithmic axis of plant suitability ($x = \ln[(c_i])$. I first considered the logistic plant growth model, which converges to a stable equilibrium. For this model, equilibrium plant sizes may be derived by ~~setting~~ modifying equation ~~(6)~~ (15) for multiple plant categories, setting to zero and rearranging:

$$s_i = s0 - \{nbps0 / rS\} c_i \qquad (19)$$

and may include negative values of s_i when $c_i > c_m$. c_m is defined as...

This is a linear function of c_i. ~~If c_m is defined as~~ the value of c_i for the marginal plant 'm' (i.e., the x-intercept of the line in equation 16? 17 or the curve in Figure 5), i.e. where $s_i = 0$. Then, herbivore production (a(i) by host plant i at equilibrium will be:

$$a(i) = \{nb[s_i]/S\} c_i = \{nb[s0 - (s0/c_m)c_i]/S\} c_i \qquad (20)$$

?

Converting to the logarithmic scale and integrating (Appendix IIIA), this function yields approximately 80% of herbivore production by plants positioned along the axis of plant suitability within 2.3 log units of X_m, where $X_m = \ln[c_m]$. Similar calculations using the plant growth cutoff model revealed that over 90% of the egg production occurred on plants within 2.3 units of X_m (Appendix IIIB). This is an overestimate,

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* Note: converting the plant growth equation from s_0 to S_x by dividing s_0 by w ("width of c_i categories) is a way of scaling the plant growth equation to the x-axis of hostplant suitability. This allows integration of plant production (growth) along the x-axis, which is crucial is combining the herbivore production of multiple plant categories

To determine how model parameters (such as herbivore death/ oviposition rates, and plant sizes) might affect c_m, thus determining which plants become defoliated and which plants produce most of the herbivore population, I solved for the points at which herbivore death rate is equal to the total herbivore production rate. This is approximately (Appendix III-5):

note - $2\frac{\delta x}{S}$ is the ratio of "well-placed" eggs ~ $2\delta x$ to the total S. low ratios mean many eggs are "wasted" i.e. like mortality - Hence ~ log unit offset in fig 6.

since I assumed that the sizes of the "marginally suitable" host plants have size s0 when in fact they cycle in size. Cycling should tend to spread the herbivore production over more plants. However, the simulations show that this effect is small (Figure ~~5)~~ 5 top). Thus, a relatively small subset of host plants (within an interval of 2 along the logarithmic axis of plant suitability) contributes 75-90% of the production of new herbivore adults to the herbivore population.

[illegible] model parameters (birth and death rates, plant sizes) might [illegible] growth model [illegible] host plant [illegible]

To determine) which plants ~~become defoliated under a given set of model parameters, (plants i where $c_i > c_m$),~~ I ~~determined~~ calculated ~~the position of X_m~~ along the logarithmic ~~axis of plant suitability. For the logistic plant growth model~~ at equilibrium, the herbivore population death rate equals the production of new herbivore adults (a), which is approximately (Appendix ~~III~~ III-5):

$$un = a =* (nb\, S_x\, c_m)/2S \qquad (21)$$

* see note

with c_m as defined above, S equals the total plant biomass at equilibrium, and $S_x = s0/W$, where W is the interval along the x-axis included within plant category i (W =* ln[1.7] = 0.5) for the models in figures 4 and 5). add note here ~~This~~ Equation (21) may be solved for c_m or X_m, respectively:

$$c_m =* 2(u/b)(S/S_x) \quad \text{or} \quad X_m =* \ln[2(u/b)(S/S_x)] \qquad (22)$$

The inverse of u/b is equal to the oviposition rate times the expected lifespan of a newly eclosed adult (1/u). This ratio should be sensitive to changes in the habitat of the adult herbivores, since factors such as plant spacing, predators, and weather conditions which increase b are likely to reduce u, amplifying the effects. In contrast, S/S_x should be

=* = ~ = approx

$$n=\{rS_o/p(bc-u)\}\{1-u/(bc-u)\} \qquad (18)$$

relatively stable, since environmental factors which decrease S, the total plant biomass, should also decrease S_x, a subset of the total plant biomass. The calculations above also suggest~~s~~ that variation in the u/b ratio is likely to alter the position of X_m in the model, without affecting the width of the peak in herbivore production.

I ~~tested~~ modelled these predictions using the 10-plant simulation model with logistic plant growth. As illustrated at the bottom of Figure 5, over 75% of the production of new herbivore adults was produced by plants 4-7, a "span" of 4 plant categories. The value of x ($x = \ln[c_i]$) increased by 0.5 in each successive category, which, added together, gave an overall span of 2.0 between the highest and the lowest value. This is close to the predicted value of 2.3 for the logistic plant growth model. The same span produced over 90% of the new adult herbivores in the plant growth cutoff model at the top of Figure 5, also as predicted. To ~~test~~ model equation (22), I simulated changes in the u/b ratio for a system in which c_{min} =0.001 and c_{max} =1.0, with ~~all~~ other parameters remaining ~~constant~~ the same. S_x/S changed from 0.48 to 0.20 as a result, illustrating that large changes in the u/b ratio cause only a small change in the S_x/S ratio. In figure 6 (thick line) I plotted X_m, the log-suitability of the marginal plant, as a function of the u/b ratio. ~~for several models including the the random oviposition model considered here~~. As predicted by equation (22), X_m varied in proportion to u/b, and was approximately 2 log units greater since $2(S/S_x)$ ranged from 4 to 10. These simulations indicated that equation (22) accurately predicts equilibrium values of the model.

The form of equation (18) suggests that the equilibrium number of adult herbivores (^n) is directly proportional to plant productivity (rs0). I tested this by varying rs0 from 0.5 to 50 in the 10-plant simulation and found that $\hat{n}$ remained in exact proportion. Since plants with values of c_i near c_m produce most of the population of herbivore adults, I reasoned that the productivity of these specific plants actually determined the number of adult herbivores. To test this, I altered plant growth rates (r(i)) so that plant productivity (r(i)s0) declined as x increased. I then manipulated u/b to "move" the marginal plant along the x-axis. As predicted, $\hat{n}$ rose and declined in proportion to the changes in plant productivity subsumed by the peak of herbivore production, but was independent of the productivity of other plants.

In summary, the multiple-plant models suggest that systems with random oviposition and plant populations which are smoothly heterogeneous tend to be highly stable, with herbivore production primarily determined by the productivity of a set of "marginally suitable" plants. For such models, when a pulse of herbivores overconsume their food supply, they are forced to decrease their use of the most suitable plants. The assumption of random oviposition (equation 8) ensures that the use of low-suitability plants will thereby increase, lowering the mean fitness of eggs and ultimately reducing the population of adult insects. However, since most herbivores do not select among their host plants at random (Rausher 1983), I also examine the consequences of non-random oviposition.

NON-RANDOM OVIPOSITION

I simulated the effects of non-random oviposition using the 10-plant simulation models. I first simulated a "perfect forager" which could accurately locate the plant foliage with the highest value of c_i, deposit just enough eggs to defoliate it, locate the the next best foliage, oviposit, and so on, until the full egg complement (bn) of the population of adult herbivores was depleted. These simulations resulted in patterns similar to those in Figures 4 and 5, except that plants which were marginally defoliated in the random oviposition model become completely defoliated and the position ($X_m = \ln[c_m]$) of the marginal plant along the x-axis moved to the left toward ~~lesser~~ reduced values of plant suitability. Apparently, the ability to accurately locate and fully exploit the most suitable plants enabled the herbivores to defoliate plants with low values of c_i. At equilibrium, the small productivity of the "defoliated" plants produced most of the herbivore population, and the marginal plant was of such low suitability that very few herbivores were produced in spite of the large number of eggs deposited. This is illustrated in Figure 6, where $X_m < \ln[u/b]$, indicating that this plant alone could not support successful reproduction by the herbivore population. At this point the simulations become unrealistic, since hosp plants which are consistently defoliated should lose and their reserves and die.

The perfect forager" simulations incorporated the assumption that herbivores locate and accurately assess the suitability (value of c_i) of each host plant in the environment. The assumption that the herbivore can accurately assess host suitability is unrealistic because many aspects of host suitability are cryptic to herbivores (e.g. Singer 1972). In particular, the distribution of some types of predators may not be apparent to searching adults. For example, Smiley (1978) and Longino (1984) reported that <u>Heliconius</u> butterflies do not

$$D(i) = \frac{s_i}{S} e^{a(x+K)} \qquad (23A)$$

$$s_i = s_0 - \{nbps_0 / rS\} c_i \qquad (19)$$

$$a(i) \approx \frac{\hat{n}b\left(s_x - \frac{s_x}{c_m} c_i\right) e^{a(x+K)}}{g\hat{S}} \qquad (24)$$

preferentially oviposit on ant-free host plants, in spite of their greatly reduced fitness on plants with ants (Smiley, 1985 and in press). ~~Since~~ Ants are conspicuous, slow-moving, and use extensive chemical communication. Other types of predators are likely to be far more cryptic to insects. As a consequence, even a very efficiently foraging herbivore is almost certain to occasionally use host plants with low values of c_i. To model this possibility, I simulated a "preference" forager which has increased preference (PR(x)) for plants of higher suitability (higher values of $x=\ln[c_i]$), but nevertheless places some proportion of the eggs on plants with low values of x:

$$PR(x) = \frac{e^{a(x+K)}}{g} \qquad (23)$$

$a(x-x_{min})$

$$\text{and} \quad D(i) = \frac{s_i\, e^{a(x+K)}}{gS} \qquad (23a)$$

Here, 'K' equals $-\ln(\text{minimum value of } c_i)$, ensuring positive values for all (x+K), 'a' is a "preference coefficient" with a=0 indicating random foraging and a=1 indicating preference directly proportional to the value of c_i, and 'g' equals a proportionality constant. For these simulations, K usually had a value of about 7 (actually 5.9 for the simulations in figures 4 and 5, and 6.9 for figures 6-8). Incorporating this with equation (8) and using equation (19) for approximate plant size at equilibrium, the production of herbivores by plant (i) is approximately:

$$a(i) \approx \frac{\hat{n} b \left(S_x - \frac{S_x}{c_m} c_i \right) e^{a(x+K)}}{g\hat{S}} \qquad (24)$$

Integrated between -K and 0 along the logarithmic scale, the function for the percent of herbivore production within Z log units of c_m is approximately:

$$\% \approx 100\left\{1-(a+2)e^{-Z(a+1)}+(a+1)e^{-Z(a+2)}\right\} \tag{25}$$

For a=1, equation (25) predicts that 97% of the adult herbivores will be produced by plants with values of x (=ln[c_i]) within Z=2.3 log units of X_m. Thus, for this degree of preference, the peak of herbivore production is more narrow than that of a "random" forager with the same parameters. a=1 represents a strong degree of preference since approximately 90% of the eggs would be deposited on the "best" three plants out of 10 if all plants were equally abundant.

I derived the position of the marginal plant along the x-axis (the axis of plant suitability) for the preference forager using equations analogous to those derived for the random forager (see appendix IV):

$$\overset{a+1}{c_m^{a+1}} \approx \frac{\mu}{b}\,\frac{a+2}{a}\left\{c_m^{a}-(a+1)e^{-aK}\right\} \tag{26}$$

With 'a' near zero, this equation approximates equation (22) for random foraging herbivores (see appendix IV). When a>1 and $K \overset{-}{>} 7$:

$$c_m \approx \frac{\mu}{b}\,\frac{a+2}{a} \tag{27}$$

This equation shows that, at equilibrium, as the preference coefficient a increases to large values and the width of the herbivore production peak narrows (equation 23), c_m approaches u/b, the mean per capita death rate for juvenile herbivores on the host plant (figure 7). However, equations (23-25) do not incorporate the possibility, permitted in the simulations, that small "defoliated" plants produce herbivores. The

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To summarize this far, the multiple plant models and simulations have shown that, as long as there is a continuum of host plants that smoothly vary in suitability over a wide range (2-3 orders of magnitude), several robust results follow. (1) An equilibrium will be established that includes a set of marginally suitable plants which are responsible for supporting most of the herbivore population. (2) The marginally suitable plants will be, those in which per capita on-plant herbivore mortality (c_m) balances herbivore per capita reproduction ($\frac{b}{u}$), adjusted for oviposition selectivity, which reduces c_m by 1-2 log units at most. (3) The marginally suitable plants which span approximately 2 log units produce 75-90% of herbivore production, and their biomass and productivity determine the equilibrium herbivore population.

values predicted by the equations therefore diverge from the simulations for extreme degrees of preference ($a>1$). Figure 7 illustrates peaks of herbivore production for $a=0,1,2,4$ as predicted by equations (25) and (26). The peak for $a=1$ is about 2/3 as wide as the peak for $a=0$.

As the width of the peak in herbivore production narrows, the amount of plant productivity subsumed by the peak should be correspondingly less, which should result in lower population densities for the adult herbivores. The results of simulations suggest that this is indeed the case. As the value of the preference coefficient (a) was increased, herbivore population density at equilibrium was observed to decline (Figure 8).

Equations 21-25 and the results of simulations in Figures 6 and 8 suggest that the primary effect of host plant discrimination is to narrow the peak of herbivore production, reduce the value of $X_m=\ln[c_m]$ (the suitability of the marginal host plant), and to reduce equilibrium population density for the herbivores. The reduced population density is primarily caused by the defoliation of plants which were marginally suitable under random foraging, making them less available to the herbivore population. At very high levels of preference (i.e. the "perfect forager" model), all plants may be defoliated which can sustain the herbivore population, and the herbivores subsist probably [illegible] on the very small plants which are regenerating from defoliation.

add paragraphs

GRAPHICAL MODEL

The multiple-plant models suggest a graphical model for plant herbivore interactions incorporating heterogeneity among plants in

21a

$$a(i) = \left\{ nb\left[S_i \right] / S \right\} c_i = \left\{ nb\left[S_0 - (S_0 / c_m) c_i \right] / S \right\} c_i \quad (20)$$

$$a(i) = \left\{ nb\left(S_x - \frac{S_x}{c_m} c_i \right) e^{a(x+k)} \right\} / gS \quad (24)$$

$$\% = 100 \left\{ 1 - (a+2) e^{-2(a+1)} + (a+1) e^{-2(a+2)} \right\} \quad (25)$$

herbivore survivorship, as follows. Let the horizontal axis of the graph be the logarithmic spectrum of plant suitability 'x' for a given population of herbivores, and let the vertical axis be the biomass of plants. Plot the distribution of plant biomass along the spectrum (see Figure 9). Use the u/b ratio and equations (20, 24, and 25) to approximate the position of the marginally defoliated plant ($X_m = \ln[c_m]$) along the x-axis. 'X_m' will usually be 1-2 log units to the right of u/b along the x-axis (see figure 7).

The $\hat{s}_i$ may then be calculated from their position along the x-axis. Assume that the production of adult herbivores takes place in the region of the spectrum spanned by X_m and X_m-Z, where Z ranges between 1 and 2 depending on the estimated preference function (equation 23). To the left of X_m-Z, the $\hat{s}_i$ will be equal to the values on the graph, between X_m and X_m-Z the $\hat{s}_i$ will be declining from the values on the graph toward zero, and to the right of X_m, the s_i will be equal to zero. Calculate the productivity (P) of the plants in the region of herbivore productivity as approximately:

$$P = (r0/2)(S_x Z/2) = r0S_x Z/4 \qquad (28)$$

where $S_x Z/2$ and $r0/2$ are the the estimated biomass and growth rates, respectively, of plants which are 50% defoliated, on average. For the plant growth cutoff model, r0 should be used in place of r0/2, but the corresponding reduction in the width of the herbivore production peak partially compensates for this, and I suggest that equation (28) be employed, regardless of plant growth model. At equilibrium, P/p (where p equals the amount of plant biomass required to produce one adult herbivore), will approximately equal the rate of production of new herbivores. This equals the population death rate (nu). Solving for n yields:

$$\hat{n} = [P/p][1/u] = rS_xZ/4pu \qquad (29)$$

For the simulations in Figure 8, S_xZ was 133 and 89 for a=0 and a=1, respectively. Using equation (29), $\hat{n}$ = 9.5 and 6.4, respectively, which correspond closely to the values in figure 8 (9 and 6, respectively). Below, I analyze two examples using this technique.

Smiley (1985 and in press), Smiley and Wisdom (1985), Longino (1984), and Mallet (1984) investigated species of Heliconius butterfly caterpillars which feed on species of Passiflora at Corcovado National Park in Costa Rica, Central America. Based on the evidence from field studies of Passiflora vitifolia in Smiley (1985, and in press), I calculated the probability of caterpillar survivorship on plants by extrapolating the survivorship over a four-day period to the full twelve days required for larval development. This procedure assumes that mortality rates do not decline as the larvae grow, which is supported by the data in Smiley (1985 and in press), and does not include relatively infrequent forms of juvenile mortality such as egg and larval parasitism, or egg and pupal predation. 10% of P. vitifolia plants at the field site were relatively ant-free, with an estimated caterpillar survivorship of 0.11 (x=-2.2). The other 90% of plants were ant-tended, and averaged 0.0057 survivorship (x=-5.1). This average included some large, contiguous patches of host plant with a mean survivorship of 0.00013 (x<-10). Ant-free plants tended to be small in comparison with ant-tended plants, and I estimated the distribution of biomass along the x-axis to be that illustrated in figure 9. I additionally represented

200

.05 Area / [illegible] 10 / [illegible]

the presence of large-biomass canopy foliage by a dotted line. This foliage is usually not oviposited upon by the species of Heliconius investigated, which prefer small vines and understory portions of large vines (Mallet 1984). The methods in Smiley (in press) were not precise enough to determine the c_i values for individual plants, and the actual spread in values of c_i may be greater than that illustrated.

Gilbert (unpublished data) determined the local population density of Heliconius in the "horsepasture" at the field site. Mallet (1984) estimated the total biomass of P. vitifolia in a five hectare patch of secondary forest ajacent to that site to be 2000 leaves/ha. Since about one tenth of this biomass lay in the herbivore-producing portion of the spectrum (see figure 9), and using equation (29), assuming r0=0.05/day, p = 5 leaves/herbivore and u=0.07/day, the estimated population density (^n) for H. hecale, a species which primarily uses P. vitifolia, was 7/ha, or 35 for the five-hectare area. This figure agrees well with actual estimates of population density from that site (n =* 40, ranging from 10 to 100, depending on seasonal fluctuations; L. Gilbert, unpublished data). This analysis indicates that the model is capable of predicting realistic values of ^n from crude estimates of plant biomass and the birth and death rates of adult herbivores.

I also employed the graphical model to analyze cases in which plant protection may evolve, i.e. in systems with heritable host resistence (Mitter and Futuyma 1983). If the curve of potential plant biomass (in the absence of herbivory) is plotted, any area under the curve and to the right of X_m, the marginally defoliated plant, will be absent or defoliated after the herbivore population is introduced and comes to equilibrium with the host plant. This vacant area represents "empty habitat" for the plant population, which may be filled by recruitment from the surviving, resistent population if resistence is heritable and is not genetically correlated with other, deleterious, traits. Such recruitment will tend to shift the curve of potential plant biomass to the left of X_m, the marginally defoliated plant. As a consequence, these systems should evolve until the zone of herbivore production lies on the right-hand margin of the curve of potential plant biomass. Since most natural systems will have a component of resistence which is not heritable, actual curves may have "tails" which extend to the right or left of the predicted shape.

For example, Smiley et al (1985) found that late-instar larvae of Chrysomela aenicollis survived well (90%) on willow trees with high concentrations of the bitter phenol glycoside salicin, but survived poorly (30%) on trees with low concentrations of the chemical. It is likely that survivorship increases rapidly above some threshold of salicin concentration, which results in a bimodal distribution of plant biomass along the axis of herbivore survivorship. Smiley and Rank (in prep.) and Smiley (in press) found that cold stress caused severe mortality to the larvae, which shifts the curve of plant biomass to the left at increasing elevations (see Figure 10). As a consequence, only at low elevations do beetle populations defoliate the salicin-rich willow genotype. This selection pressure favors low-salicin plants or branches, and, assuming salicin concentration to be heritable, high-salicin genotypes should become rare. The beetles then persist at very low numbers on the few remaining plants which are vulnerable. In the transition zone where cold stress is intermediate in severity, beetles defoliate some but not most of the high-salicin willows, and there is a polymorphism in salicin concentration among the willows. The beetles are very abundant at this elevation (Smiley et al 1985). At the highest elevations, where cold stress is severe enough that the beetles only persist on a small subset of host plants growing in suitable microhabitats, there is minimal selection against plants which contain high levels of salicin. At this elevation, most of the plants contain high amounts of salicin, and beetles are common but not abundant.

When resistence to herbivory is not heritable, the curve of potential plant biomass may extend far to the right of X_m, the log survivorship of the marginally defoliated plant. For example, the pre-herbivory distribution of introduced weeds such as the Klamath weed in California or the prickly pear cactus in Australia had very high plant biomass. The introduction of _Chrysolina_ beetles and the cactus moth, respectively, brought about extensive defoliation of the plant populations, which never recovered their former densities. These examples illustrate that the distribution of potential plant biomass may be very different from the post-herbivory distribution, and may be very difficult to estimate. However, for many purposes it is sufficient for the researcher to estimate values in the presence of the herbivore, since these consitute the state of the system near equilibrium.

DISCUSSION

The algebraic modelling, computer simulations, and graphical analysis presented above suggest that heterogeneity among plants in herbivore survivorship has profound effects on the interaction between plants and insect herbivores. With reasonable assumptions about plant growth, the location-specific

presence of a sufficiently wide spectrum of survivorship (1-3 orders of magnitude) is a sufficient condition for the establishment of a relatively stable relationship between plants and insect herbivores. That portion of the host plant population which is highly resistent to herbivory provides a sufficient range of of variability, and the presence of multiple agents of location-specific mortality which act independently ~~ensures~~ should ensure that a continuum of survivorship probabilities will be established. This latter point

The relationship established is relatively insensitive to the randomness of herbivore searching behavior. The critical parameters which determine most of the quantitative properties of the relationship are the distribution of plant productivity or biomass along the spectrum of plant protection, and u/b, the ratio between the per capita death and birth rates for the population of adult herbivores. A knowledge of these three elements is sufficient to predict the distribution of plant sizes and the numbers of adult herbivores at equilibrium. Although the model is severely unrealistic is some respects, such as the assumption that fractional herbivores can oviposit fractional eggs or the assumption of instantaneous herbivore feeding and growth on the plant, application to field data from Heliconius and Passiflora suggested that the model can yield realistic quantitative values for some systems. At the very least, the model provides a guide for examining the effects of variability among plants on plant-herbivore systems.

For plant-herbivore systems such as those modelled here, a pulse in herbivore population size does not result in an immediate increase in death rates of juvenile herbivores. The increase in mortality of juveniles only takes effect after defoliation of the more susceptible plants, forcing the herbivore population to use less suitable hosts.

Analysis of life-table data from individual plants or small plots in such a plant-herbivore system will show density-independent fluctuations,in spite of the fact that as a whole, the population tends to return to equilibrium densities. This indicates that detection of density-dependence may depend on the scale of investigation (Kareiva, in press).

Dempster (1983) and Kareiva (1983 and in press) cited numerous examples in which an increase in the u/b ratio apparently caused reduced population densities for herbivores, while a decrease in the ratio caused an increase in population density. This result is intuitively reasonable as an immediate response to changes in u and b, but it is not evident that the long term responses of the population should reflect the u/b ratio. Since many of the examples cited involve long-term differences, there remains the question of why the herbivores with the increased u/b ratio do not go extinct and why the ones with the low u/b ratio do not eventually defoliate their host plants. Dempster (1983) suggests that locally, such density-independent events may be common, but Strong (1984) and Kareiva (1983) suggest that the dependence of population size on the u/b ratio may be real but difficult to measure. The model in Figure 9 reconciles both these points of view, since local extinction and defoliation occur on individual plants, yet increasing the u/b ratio causes a decrease in population density at equilibrium. This happens because herbivores with high death rates and/or low birth rates (high u/b ratio) can only subsist on the "tail" of plant biomass which is relatively unprotected from herbivory (far to the right on the axis of plant protection), while herbivores with low death rates and/or high birth rates (low u/b ratio) successfully exploit the the relatively more numerous plants which are better-protected against herbivory.

I have not attempted to model systems with two or more herbivore species coexisting on the same host plant species. One way to accomplish this would be to define n separate axes along which each of n types of herbivores interact with the population of host plants, and to define the host plants is as being distributed across the n-dimensional surface, interacting with all n types of herbivores simultaneously. In such a system, if two herbivore species share the same major sources of mortality they should be modelled as sharing the same axis of plant suitability. This may bring them into competition, since their population densities are limited by the same set of host plants, and the winner will probably be determined by the species with the lower value of u/b. However, if two herbivore species differ greatly in the source of mortality, including vulnerability to different types of predators, weather conditions, or chemicals, they should be modelled on different axes. Then, the two species will be limited by the availability of different subsets of the host plant population, and should be more likely to coexist, regardless of differences in u/b. Smiley and Spencer (in prep.) suggested that differential vulnerability to predators may explain the remarkable pattern of coexistence between <u>Heliconius</u> caterpillars and <u>Passiflora</u>-feeding flea beetles described in Smiley (1982). In this system, two types of herbivores have developed highly parallel communities while sharing the same plant parts (new growth) of <u>Passiflora</u>, and they appear to coexist using different individual plants of the same species. Jeffreys and Lawton (1984) have argued that competition in herbivorous insects may often be for "enemy-free space" rather than for edible host plant, because density-dependent predation should increase when two herbivores share a host plant. This preliminary analysis suggests that the effects predicted by Jeffries and Lawton (1985) can occur even when predator species do not respond to changes in herbivore density, and that competition for "enemy-free host plant" may be the key to understanding the structure of many insect communities.

In summary, in complex habitats such as [illegible] individual host plants or host plant subunits may be highly heterogeneous in terms of the survivorship of herbivore eggs or juveniles placed upon them by the parent insect. If the mean probability of survivorship ranges over two orders of magnitude or more, which is likely when ~~one~~ part ~~component~~ of the host plant population is well-protected against herbivory, and with reasonable limitations on plant growth, then relatively stable populations of insect herbivores ~~may~~ become established. For this to happen, the inverse of the expected per capita egg production of adult herbivores (u/b) must lie well within the range of plant variability in herbivore survivorship. Constraints on the width of the peak in herbivore production (along the axis of plant protection) allow quantitative predictions to be made from a graphical version of the model, predictions which were shown to produce realistic values. The model predicts that the population density of adult herbivores depends primarily on abundance of suitable host plant in the habitat. Accurate use of the model depends on the ability to estimate the biomass or productivity of plants along the axis of plant suitability, supporting the hypothesis that plant variability is a critical component of the interactions between plants and insect herbivores (Denno and McClure 1983).

how to further test?

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symbol	definition
s	biomass (size) of plant foliage
t	time
r	mass specific growth rate of plant foliage
H	rate of herbivory (removal of foliage)
c	average probability of survivorship for juvenile herbivores on the plant
p	biomass of foliage required to produce one adult herbivore
n $\hat{n}$ equil?	number of adult herbivores
b	per capita rate of egg production (birth rate) of adult herbivores
u · μ	per capita death rate of adult herbivores
r0	maximum growth rate (r) for plants
i	category of plants for which average survivorship of juvenile herbivores on plant (i) equals a specified range of values
s0	maximum biomass for plant category (i)
s_i	biomass (size) of plant category (i)
c_i	average value of c for plant category (i)
D(i)	function for distribution of herbivore eggs among plant categories
S $\hat{S}$ equil	total plant biomass, summed over all plant categories
m	"marginally defoliated" category of plants, such that plants with values of ci>cm are defoliated and plants with values of ci<cm are not. Also
c_m	value of ci of "marginally defoliated" plant (m)
x	value of ci along the logarithmic axis of herbivore survivorship (x = ln[ci])
X_m	value of x for "marginally defoliated" plants
S_x	biomass of full-grown plants integrated between x+(1/2) and x-(1/2). Also equal to s0/W, where W is the interval along the x-axis of plant category (i)
Z	"width" of peak of herbivore production
PR(x)	function by which plants with higher values of x are preferred for oviposition
K	equals $-x_{min}$, the smallest value of x modelled
g	proportionality constant for scaling PR(x)

Table 1. Symbols appearing in text, with definitions.

P = productivity of the subset of plants which produce most of the herbivore adults

A(x) = ?(A#)

FIGURE LEGEND

Figure 1. Phase plane diagram for equations (11) and (12). The (n,s) trajectories indicate that the system will oscillate in time with increasing amplitude (see text).

Figure 2. Simulation of plant-herbivore inteaction in which two plants differ in their susceptibility to herbivores (equations 9,10; solid line). Effects of cutoff model for limitation of plant growth (equation 4; dashed line) and logistic plant growth (equation 5; dotted line) are to stabilize the model to a stable limit cycle or a stable equilibrium, respectively.

Figure 3. Phase plane diagram for logistic plant growth model (equations 10 and 15). The angle of crossing of the isoclines has changed from that in Figure 1, so that the (n,s) trajectories exhibit oscillations through time with decreasing amplitude (see text).

Figure 4. Simulation of plant-herbivore interaction in which ten plants differ in susceptibility to herbivores. Parameters approximate those estimated for populations of _Heliconius_ butterflies and _Passiflora_ vines, with the estimated spectrum in probability of herbivore survival ranging over two orders of magnitude from 0.003 to 0.333. * Bottom Trajectories of plant size are given for plant categories 1-10 (growth cutoff model; solid lines) and for plant 7 (logistic growth model; dotted lines). The trajectories indicate that the cutoff model converges to cycles of small amplitude, while the logistic model converges to a stable equilibrium.

Figure 5. Size and herbivore production of the ten plants simulated in Figure 4, after 1000 days, based on plant growth cutoff model (top) and

* Top? Trajectories of herbivore # are given for growth cutoff model (solid lines) and logistic model (dotted lines)

the logistic plant growth model (bottom). Most herbivores are produced by 2-3 of the ten plants which are "marginal" in terms of susceptibility to herbivores.

Figure 6. Relationship between X_m, the log-suitability of the marginal plant as determined by simulation, and u/b, the mean survivorship barely sufficent to support the herbivore population at equilibrium. As predicted by equation (22), X_m is about 2 log units greater than u/b for the random foraging simulation, but this difference declines as herbivore preference (a) increases (equation 25). X_m for the "perfect forager" is less than u/b. This is caused by the ability of such foragers to successfully exploit the production of "defoliated" plants, and are not dependent on the marginal plant for the production of new adults.

Figure 7. Shape and position of the peak in herbivore production along the axis of plant protection, as a function of the preference coefficient 'a' (equation 23). The peak becomes narrower and shifts toward ln[u/b] as 'a' increases.

Figure 8. Equilibrium population densities of adult herbivores as determined by simulation, as a function of u/b and preference function (a). Herbivores capable of exercising preference (greater values of a) and "perfect foragers" (see text) have reduced population density.

Figure 9. Quantitative graphical model for Heliconius-Passiflora interaction incorporating heterogeneity among plants in herbivore survivorship. The solid curve represents the estimated biomass of P. vitifolia along the spectrum of plant suitability. The hatched area represents the portion of the spectrum which produces herbivores; it is

2 log units wide as predicted for a random forager. This area is about one-tenth of the estimated total area of 2000 leaves/ha., which, using equation (29), gave an estimated population size of 7/ha. This figure is is close agreement with independently derived field estimates (see text).

Figure 10. Graphical model of *Salix*-*Chrysomela* interaction at three elevations. In this system herbivore survivorship is partially determined by the concentration of salicin in the plants, a trait which is probably heritable. The dotted lines represent plants which would be present if selection did not favor the alternate genotype. Predicted numbers of *C. aenicollis* shown to right.

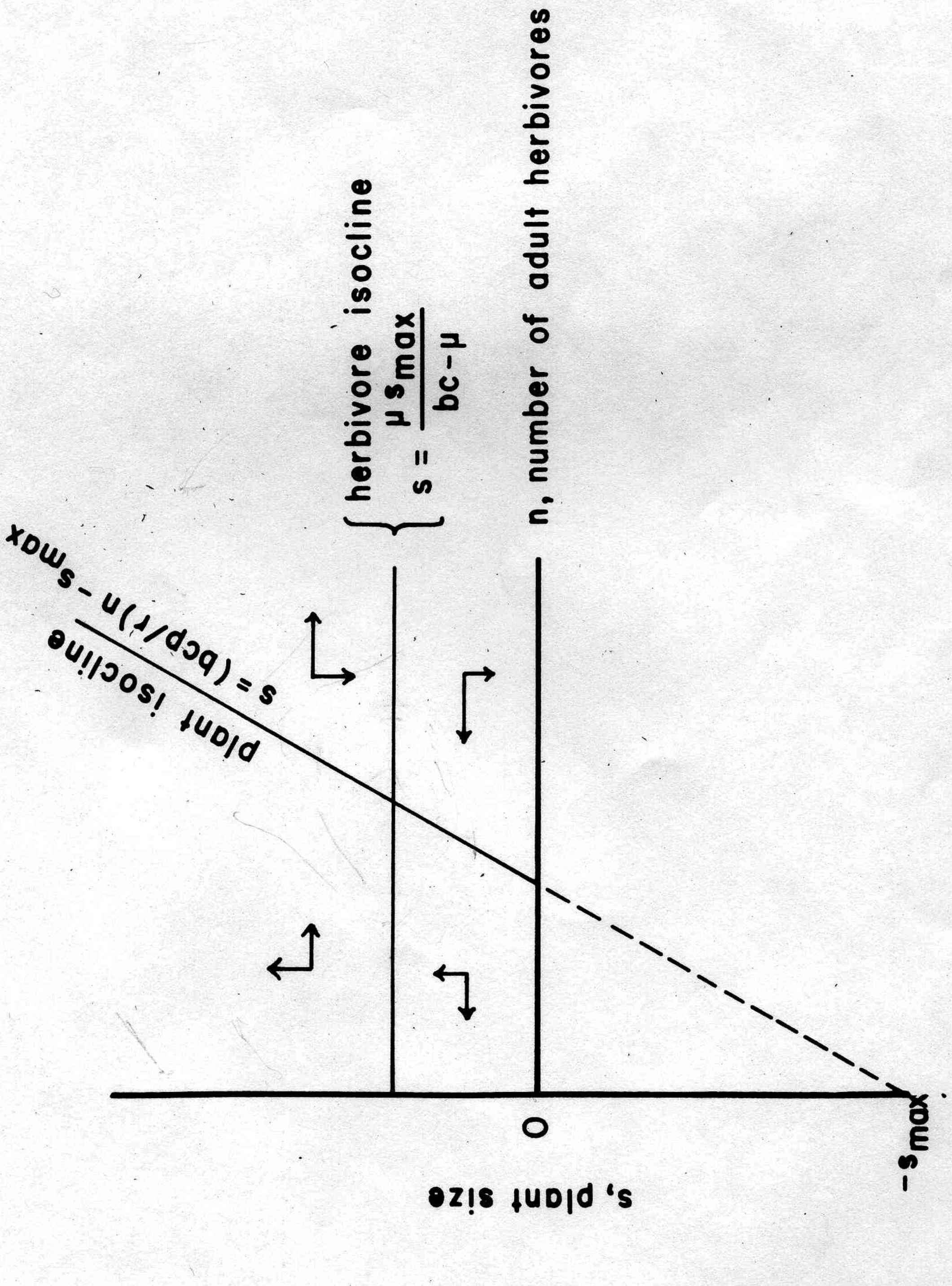

herbivore isocline
$s = \frac{\mu s_{max}}{bc-\mu}$
n, number of adult herbivores
plant isocline
$s = (bcp/r)n - s_{max}$
s, plant size
0
$-s_{max}$

FIG. 1

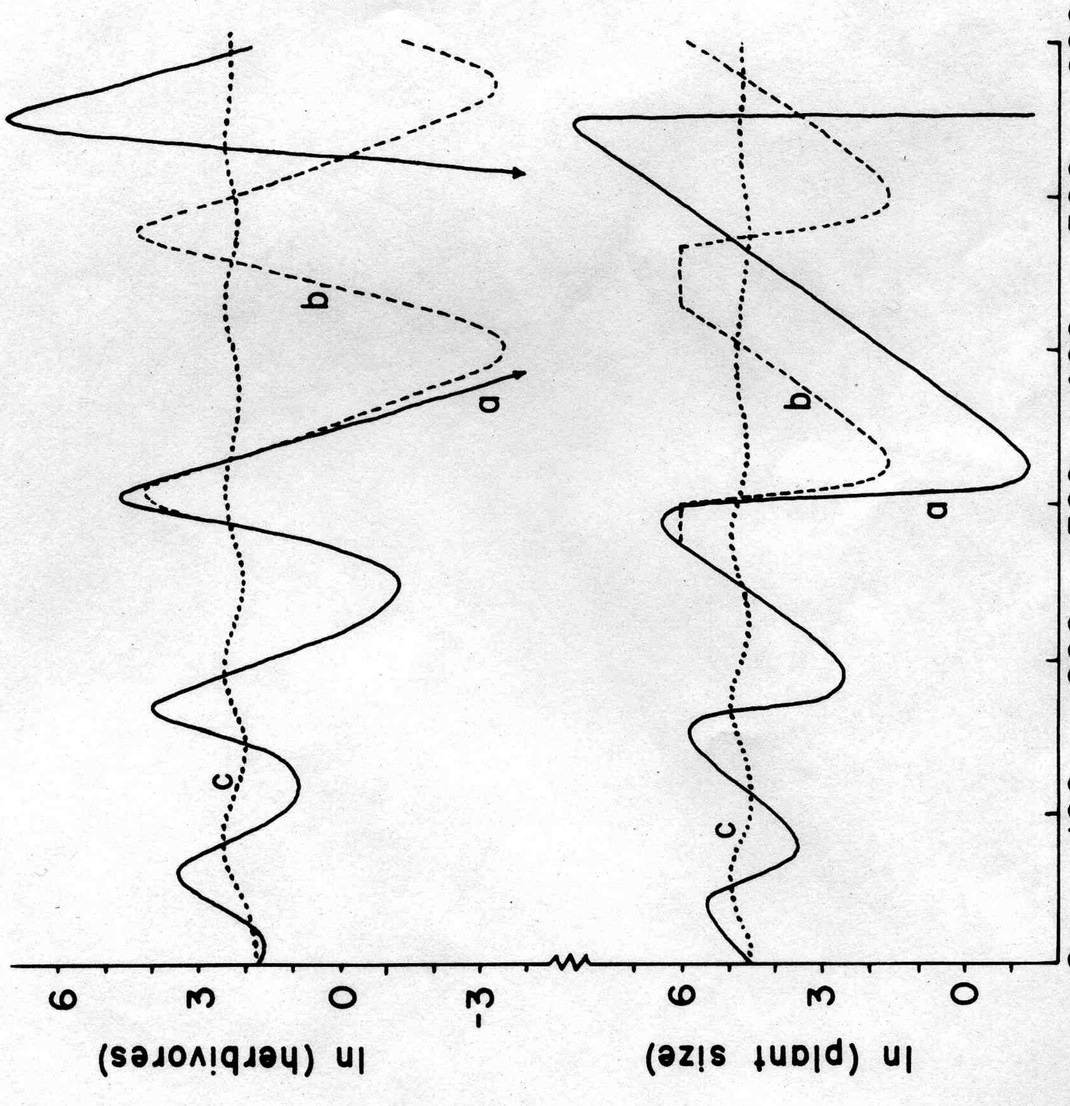

ln (herbivores)
6
3
0
-3
ln (plant size)
6
3
0
a
b
c
a
b
c
0
100
200
300
400
500
600
days

FIG. 2

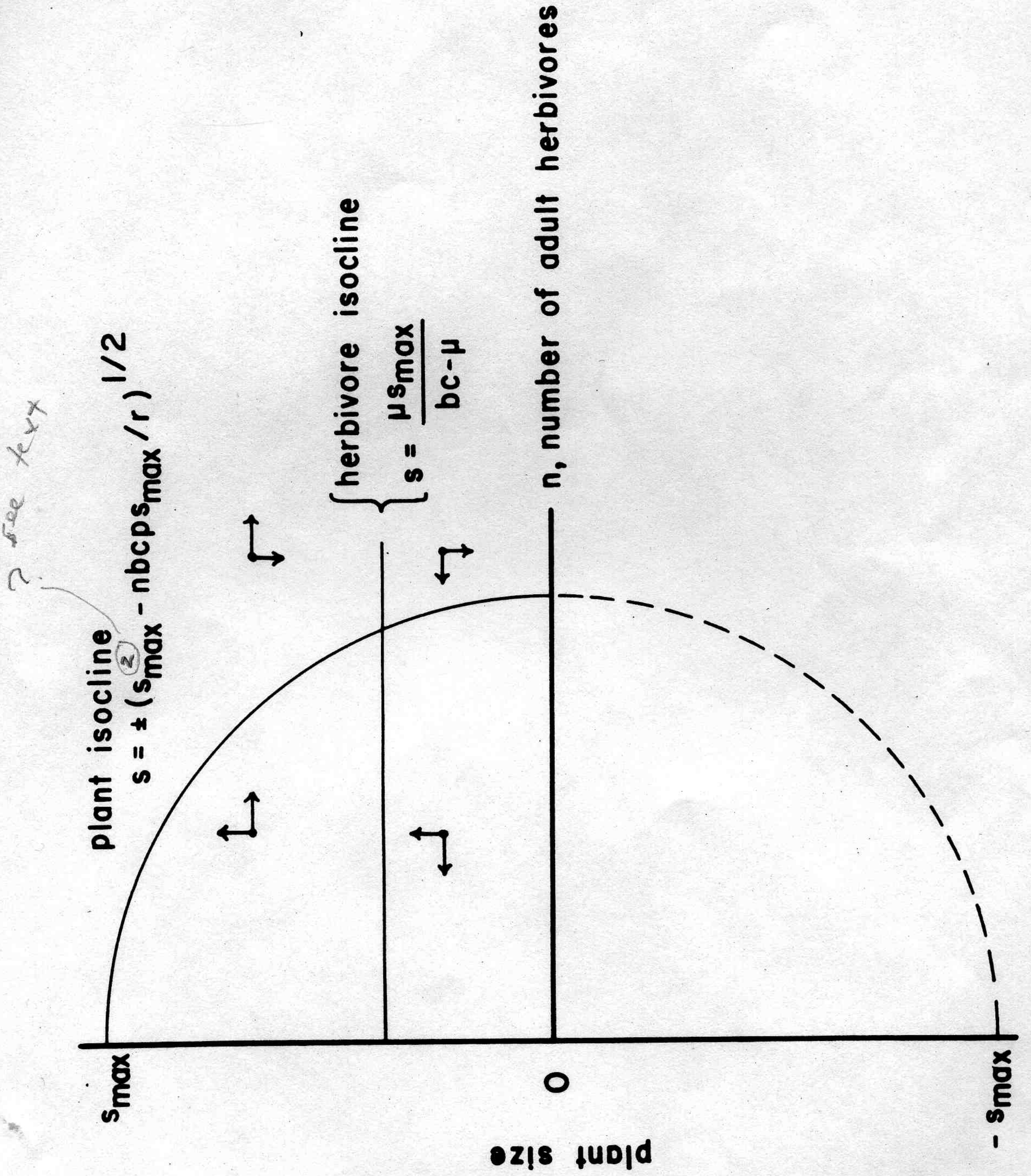

plant isocline
$s = \pm(s_{max}^{2} - nbcps_{max}/r)^{1/2}$
? see text
herbivore isocline
$s = \frac{\mu s_{max}}{bc-\mu}$
n, number of adult herbivores
plant size
s_{max}
0
$-s_{max}$

FIG. 3

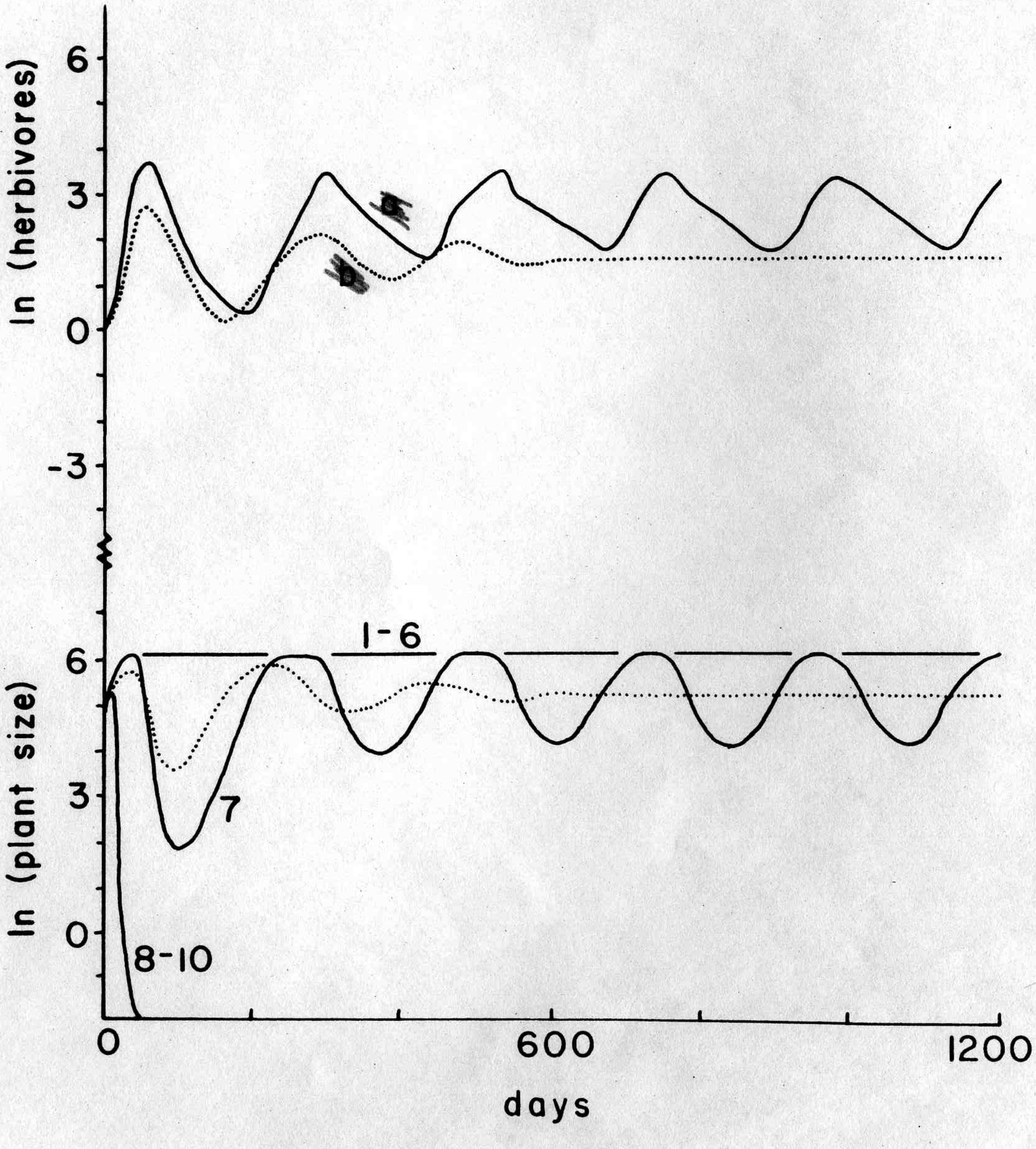


FIG 4.

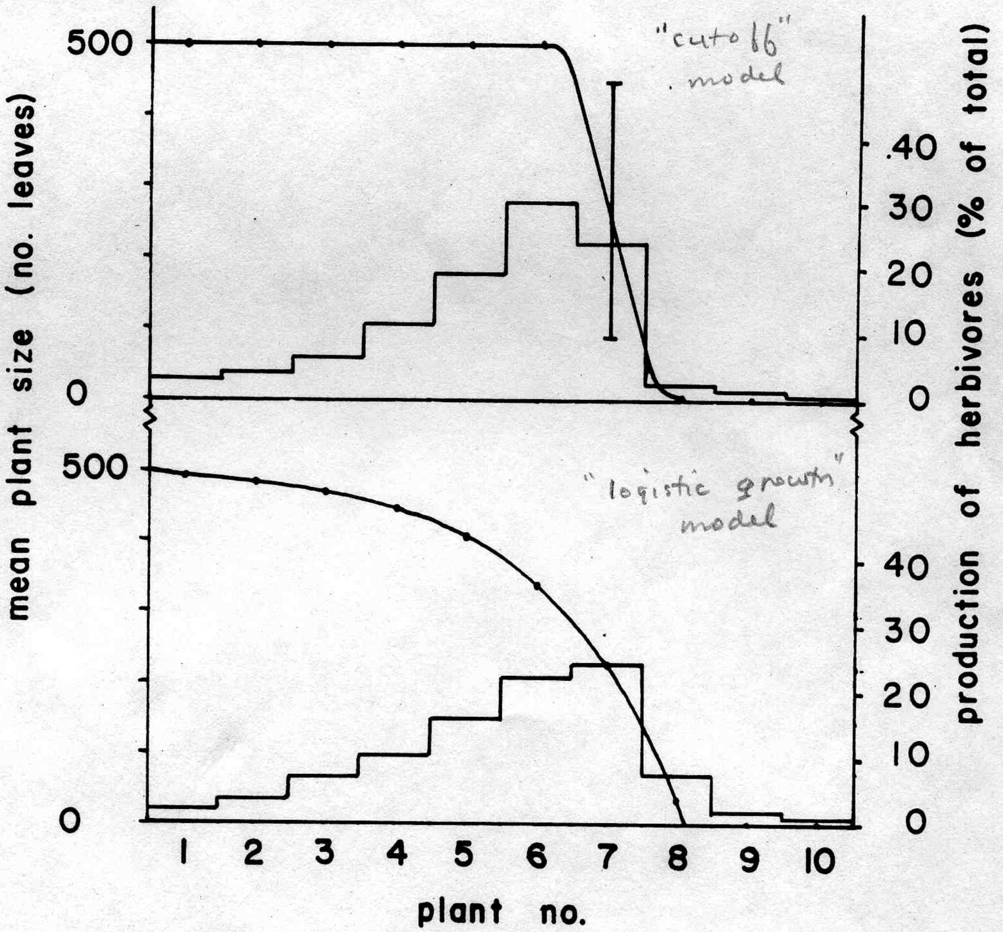

500
0
500
0
mean plant size (no. leaves)
"cutoff" model
"logistic growth" model
.40
30
20
10
0
40
30
20
10
0
production of herbivores (% of total)
1
2
3
4
5
6
7
8
9
10
plant no.

FIG. 5

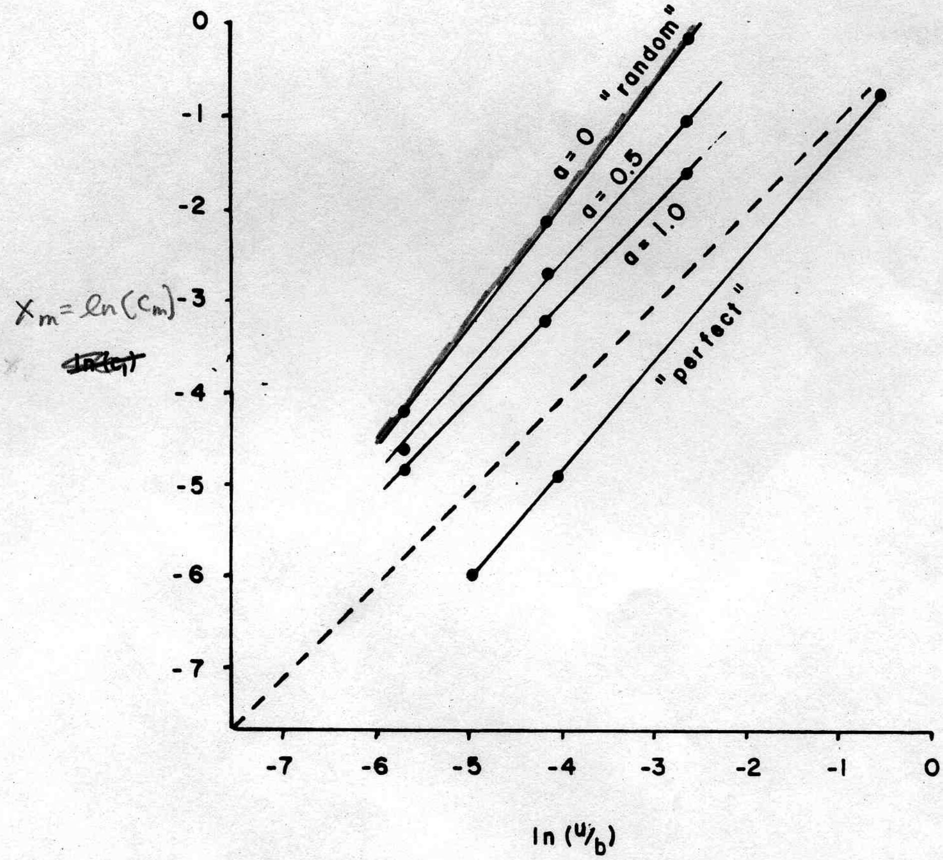
0
-1
-2
$X_m = \ln(C_m)$ -3
~~ln(c)~~
-4
-5
-6
-7
-7
-6
-5
-4
-3
-2
-1
0
ln (u/b)
a = 0
"random"
a = 0.5
a = 1.0
"perfect"

FIG. 6.

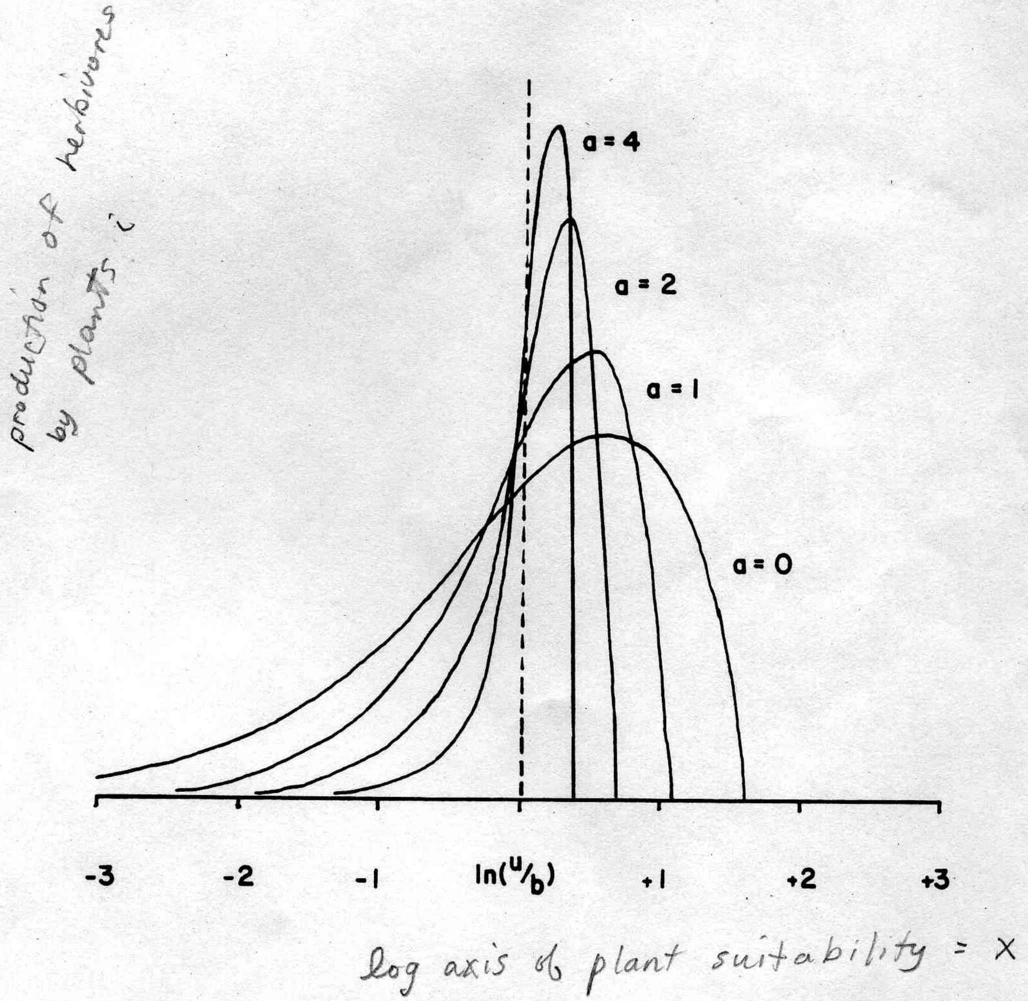
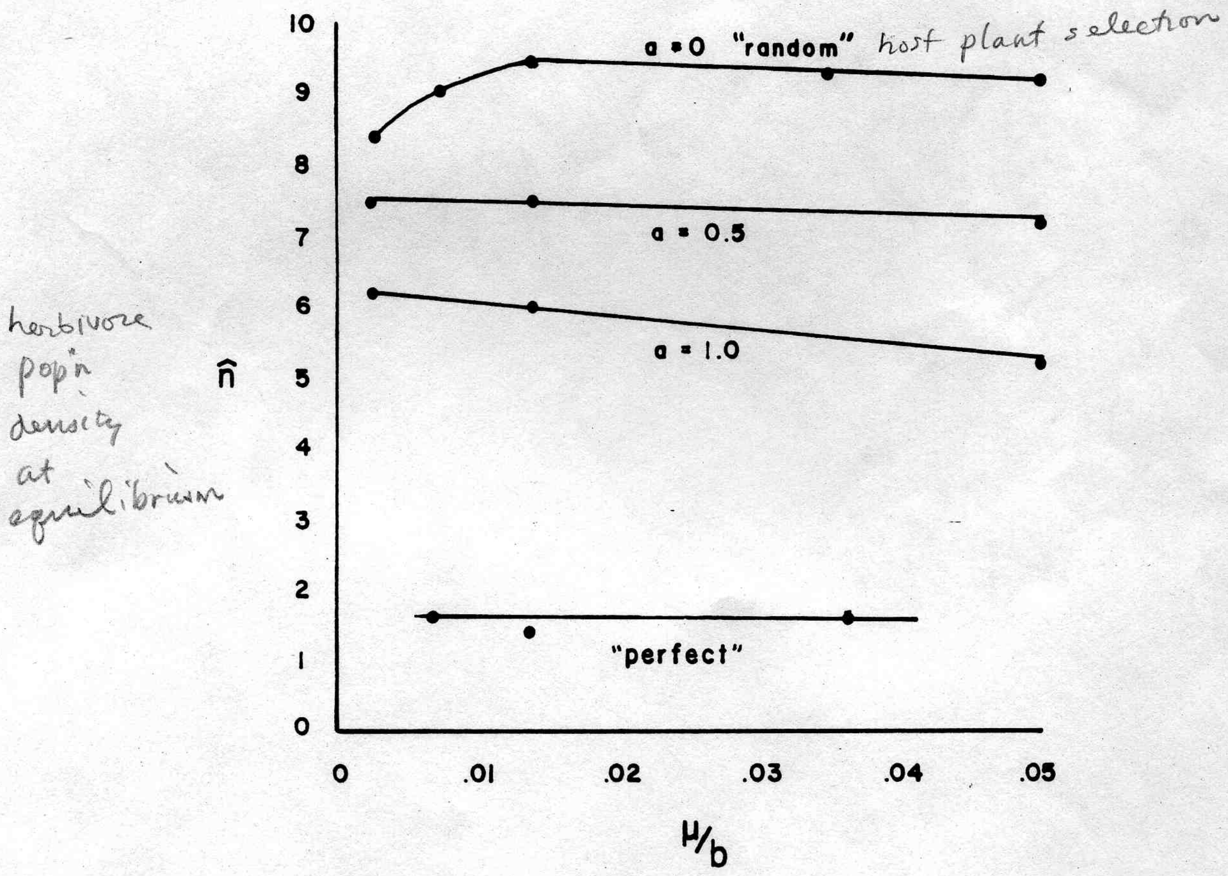

production of herbivores
by plants i
a = 4
a = 2
a = 1
a = 0
-3
-2
-1
ln($^u/_b$)
+1
+2
+3
log axis of plant suitability = X

FIG. 7



10
9
8
7
6
5
4
3
2
1
0
a = 0 "random" host plant selection
a = 0.5
a = 1.0
"perfect"
herbivore pop'n density at equilibrium
$\hat{n}$
0
.01
.02
.03
.04
.05
μ/b

FIG. 8

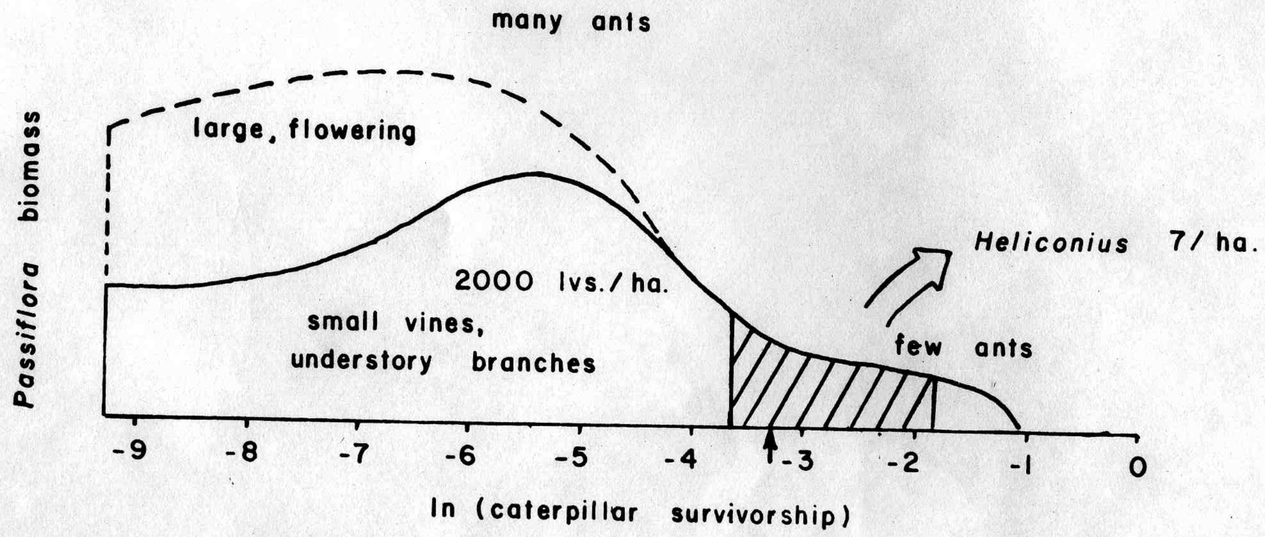

many ants
large, flowering
Passiflora biomass
2000 lvs./ha.
small vines,
understory branches
Heliconius 7/ha.
few ants
-9
-8
-7
-6
-5
-4
-3
-2
-1
0
ln (caterpillar survivorship)

FIG.9

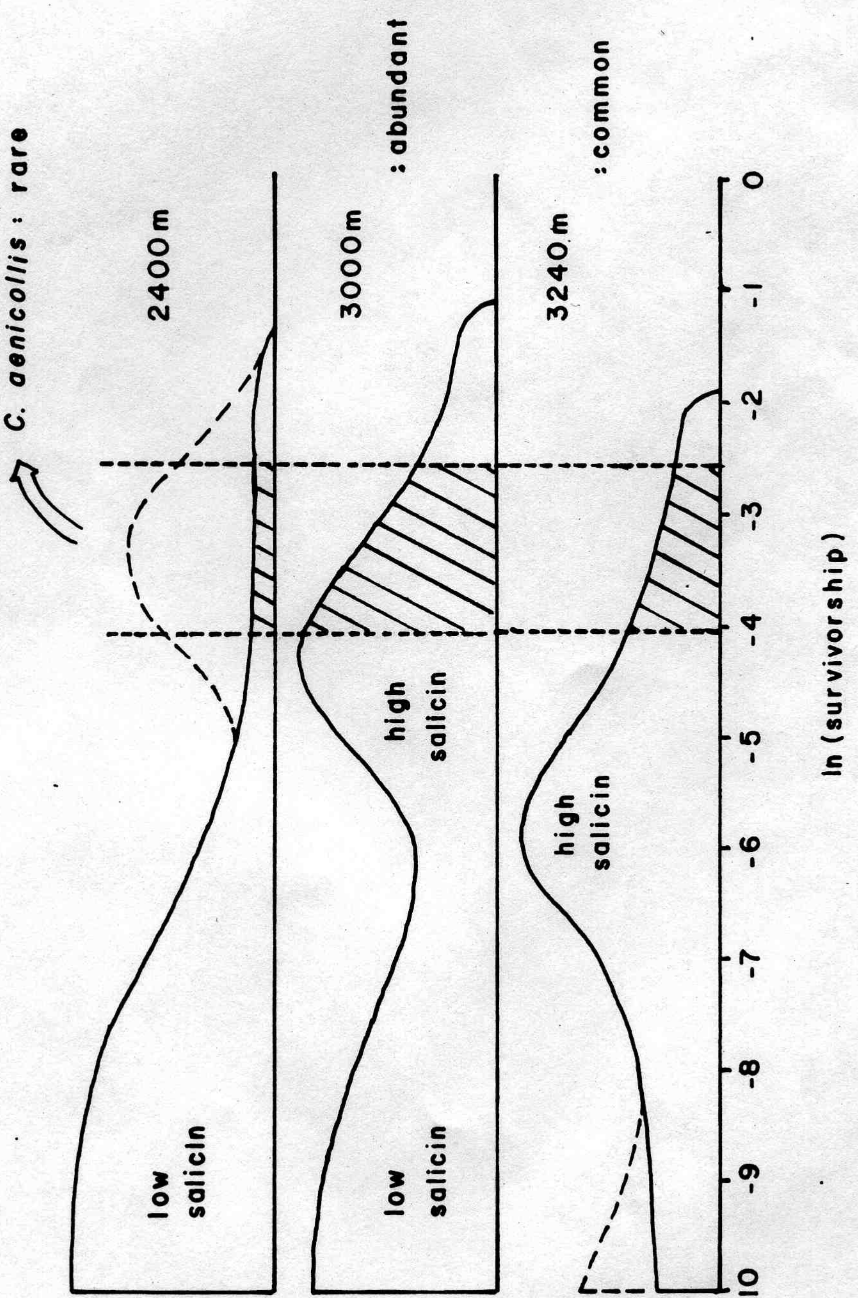

C. aenicollis : rare
2400m
3000m : abundant
3240m : common
low salicin
low salicin
high salicin
high salicin
willow biomass
ln (survivorship)
-10
-9
-8
-7
-6
-5
-4
-3
-2
-1
0

FIG. 10.

APPENDIX I

The Jacobean matrix of partial derivatives for equations (5) and (6) is:

$$J = \begin{pmatrix} r - \dfrac{s_{max} nbcp}{(s + s_{max})^2} & - \dfrac{bcps}{s + s_{max}} \\ \dfrac{bcn \cdot s_{max}}{(s + s_{max})^2} & \dfrac{bcs}{s + s_{max}} - \mu \end{pmatrix}$$

Substituting equations (9) and (10), the values of s and n at equilibrium yield:

$$J^* = \begin{pmatrix} \dfrac{r-\mu}{bc} & -\mu p \\ \dfrac{r}{p} \cdot \left(1 - \dfrac{\mu}{bc}\right) & 0 \end{pmatrix}$$

The eigenvalues for this matrix were evaluated by solving for L in:

$$\det \begin{vmatrix} \dfrac{r \cdot \mu}{bc} - L & -\mu p \\ \dfrac{r}{p} \cdot \left(1 - \dfrac{\mu}{bc}\right) & -L \end{vmatrix} = 0$$

Using the formula for roots of the quadratic equation, the eigenvalues were found to be:

$$L1, L2 = \frac{\dfrac{r \cdot \mu}{bc} \pm \left\{ \dfrac{r \cdot \mu}{bc}^2 - 4 \cdot \mu \cdot r\left(1 - \dfrac{\mu}{bc}\right) \right\}^{1/2}}{2}$$

The real part of the eigenvalues ((rμ/bc) is always positive. Therefore the two plant model without plant growth limitation is unstable, as suggested by the graphical analysis.

APPENDIX II

To evaluate equilibrium stability of the logistic plant growth limitation model (equations 11 and 6), substitute the equilibruim values for s and n (equations 13 and 14) into the Jacobian matrix of partial derivatives. The resulting matrix has the form:

$$J^* = \begin{pmatrix} \dfrac{-2r \cdot \mu}{(bc - \mu)\, bc} & \mu p(bc - \mu) \\ \dfrac{r}{P}\left(1 - \dfrac{2\mu}{bc}\right) & 0 \end{pmatrix}$$

and the resulting eigenvalues will then be:

$$L1, L2 = \frac{\dfrac{-2r \cdot \mu}{(bc - \mu)bc} \pm \left\{\left(\dfrac{2r\mu}{(bc - \mu)bc}\right)^2 + 4r \cdot \mu \cdot (bc - \mu) \cdot \left(1 - \dfrac{2\mu}{bc}\right)\right\}^{1/2}}{2}$$

The real part of these eigenvalues will always be negative, because:

$$\frac{-2r \cdot \mu}{(bc - \mu)bc} < 0$$

when $bc > \mu$, a necessary condition for herbivore existence. Therefore, the plant growth limitation model expressed in equations 11 and 6 is stable around equilibrium, as suggested by the graphical analysis.

$$= \frac{nbe^{x}s_x}{\hat{s}} - \frac{nbe^{2x}\frac{s_x}{cm}}{\hat{s}}$$

$$= \frac{nbs_x}{\hat{s}}\left(e^{x} - \frac{e^{2x}}{cm}\right)$$

$$e^{x} \quad \frac{e^{2x}}{2}$$

Logistic growth model

Appendix III. A. To derive the equilibrium estimated continuous distribution of production of new adults by plants distributed on a logarithmic scale, let $x=\ln[c_i]$, and let A(X : X-Z) equal the number of ~~eggs~~ adults produced by plants with values of x less than X but greater than X-Z. Then, a(x) dx, where a(x)=A'(x)/dx, is the number of new adults produced by plants at position x along the x-axis. This can be written as:

$$a(x)\,dx = \hat{n} b e^{x} D(x)\,dx \qquad [e^{x} = c_i] \qquad (III-1)$$

where D(x) equals the probability that any given egg will be placed on a plant with $c_i = \exp(x)$. By analogy with equation (8) and incorporating equation (19), D(x) is:

$$D(x)\,dx = \frac{\hat{s}(x)\,dx}{\hat{S}} = \frac{\left(S_x - \frac{S_x}{c_m} e^{x}\right) dx}{\hat{S}} \qquad (III-2)$$

$s_x = S_0/W$

where, as in equation (21), $S_x = S_0/W$, with W being the interval along the x-axis included within plant category i. Combining and integrating, the production of new adults is then:

$$\left(\int e^{2x} = \frac{e^{2x}}{2}\right)$$

$$A(x)\Big|_{x-Z}^{x} = \hat{n} b \frac{S_x}{\hat{S}} \left\{ \left(e^{x} - \frac{e^{2x}}{2c_m}\right) - \left(e^{x-Z} - \frac{e^{2x-2Z}}{2c_m}\right) \right\} \qquad (III-3)$$

To calculate the production of herbivore adults by plants with values of x ranging between $X_m = \ln[c_m]$ and $X_m - Z$:

$$A(x)\Big|_{X_m-Z}^{X_m} = \frac{\hat{n} b S_x e^{X_m}}{2\hat{S}} \left\{ 1 - 2e^{-Z} + e^{-2Z} \right\} \qquad (III-4)$$

The total herbivore production is then:

$$A(x)\Big|_{-\infty}^{X_m} = \frac{\hat{n}\, b\, S_x\, e^{X_m}}{2\hat{S}} \qquad \text{(III-5)}$$

and the proportion of the total produced by plants with values of x greater than $X_m - Z$ is:

$$\frac{A(x)\Big|_{X_m-Z}^{X_m}}{A(x)\Big|_{-\infty}^{X_m}} = 1 - 2e^{-Z} + e^{-2Z} \qquad \text{(III-6)}$$

This equals 0.82 (80%) when Z = 2.3 = ln(10). In other words, plants with values of c_i within an order of magnitude of that of the marginal plant produce over 80% of the new herbivore adults.

B. An analogous analysis of the plant growth cutoff model, assuming equilibrium plant sizes are equal to S_x for all plants with values of c_i less than c_m, yielded the proportion:

$$\frac{A'(x)\Big|_{X_m-Z}^{X_m}}{A'(x)\Big|_{X_m-\infty}^{X_m}} \approx 1 - e^{-Z}$$

This equals 0.90 (90%) when Z = 2.3.

APPENDIX IV

To derive equations describing equilibrium values of the logistic plant growth model incorporating foraging preference, I used equation (24):

$$a(i) = nb\left(S_x - \frac{S_x}{C_m} c_i\right) e^{a(x+K)} \qquad (24)$$

$$a(x) = \hat{n} b e^{aK} e^{ax} \left(1 - \frac{e^{x}}{e^{X_m}}\right)$$

Herbivore production by plants with values of x ($x=\ln(c_i)$ between X_m and $-K$ ($K = x_{min} = \ln$(minimum value of c_i) is then:

$$A(x) \approx \frac{\hat{n} b S_x e^{aK}}{\hat{S}_g} \left\{ \frac{e^{x(a+1)}}{a+1} - \frac{e^{x(a+2)}}{(a+2)e^{X_m}} \right\}$$

$$A(x)\Big|_{-K}^{X_m} \approx \frac{\hat{n} b S_x e^{aK}}{g\hat{S}(a+1)(a+2)} \left\{ e^{X_m(a+1)} - (a+2)e^{-K(a+1)} + (a+1)e^{-K(a+2)} \right\}$$

$$\approx \frac{\hat{n} b S_x e^{aK} e^{X_m(a+1)}}{g\hat{S}(a+1)(a+2)} \qquad [\text{for } K>7]$$

Herbivore production by plants with values of x between X_m and X_m-Z will be:

$$A(x)\Big|_{X_m-Z}^{X_m} \approx \frac{\hat{n} b S_x e^{aK} e^{X_m(a+1)}}{g\hat{S}(a+1)(a+2)} \left\{ 1 - (a+2)e^{-Z(a+1)} + (a+1)e^{-Z(a+2)} \right\}$$

and the proportion of total herbivore production by plants with values of x between X and X-Z will then be:

$$\frac{A(x)\Big|_{X_m-Z}^{X_m}}{A(x)\Big|_{-K}^{X_m}} \approx 1 - (a+2)e^{-Z(a+1)} + (a+1)e^{-Z(a+2)}$$

I calculated X_m, the log-value of c_i of the marginal plant, by combining the equation for $A(X_m:X_m -K)$ with the relation un = bA(X), and solving for c_m:

$$c_m^{a+1} = \frac{\mu \hat{S} g (a+1)(a+2)}{b S_x e^{aK}}$$

Using a relation derived from the fact that the integral of D(x) = 1 for plants **between X and -K:**

$$g = \frac{S_x e^{aK}}{\hat{S} a(a+1)} \left\{ e^{aX_m} - e^{-aK}\left(1 + a\left[1 - \frac{e^{-K}}{c_m}\right]\right)\right\}$$

$$\approx \frac{S_x e^{aK}}{\hat{S} a(a+1)} \left\{ e^{aX_m} - e^{-aK}(a+1) \right\}$$

and substituting into the above equation for c_m yields equation (26).

To show that equation (26) approaches equation (22) as a approaches zero, note that S/S_x =* K, and:

$$g \approx \frac{e^{aK} c_m - e^{-aK}}{aK(a+1)} \approx \frac{1(1 - e^{-aK})}{aK} \approx 1$$

Substituting into the above equation for cm^{a+1} gives equation (22):

$$c_m \approx \frac{\mu \hat{S} (a+1)(a+2)}{b S_x e^{aK}} \approx 2\left(\frac{\mu}{b}\right)\left(\frac{\hat{S}}{S_x}\right) \qquad [a \to 0]$$