

Variable chemical defences in plants and their effects on herbivore behaviour

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ABSTRACT

Most plants exhibit very high chemical variability from scales of within individuals to between populations and between species. This extraordinary variation has not yet been adequately explained. One potential explanation is that variability may benefit the plants by making them a more unpredictable environment for herbivores. I explored this possibility with a dynamic state variable model. I assumed a concave benefits curve and modelled the behaviour of a herbivore on two types of plants. Each plant type had the same mean level of toxins, but one had a variable distribution of toxins while the other was completely predictable. In each time step, the herbivore either foraged or reproduced. If it foraged, it could either accept or reject the plant encountered. The model predicted that, when herbivores had intermediate energy levels, they would reject variable-toxin plants, as long as there were constant-toxin plants in the environment and the benefits curve was sufficiently concave. This emphasized the importance of herbivore choice in plant defence and demonstrated that variability can be an additional level of defence for some plants.

Keywords: chemical variation, dynamic state variable model, herbivore choice, herbivory, plant defence theory, secondary metabolites.

INTRODUCTION

Plant secondary metabolites exhibit some of the highest diversity seen in nature. Variation exists at the level of species, populations and individuals, and within individuals. The chemicals expressed by a plant can change over time, over different parts of the plant and in response to the environment (Berenbaum, 1981a,b; Denno and McClure, 1983; Baldwin and Karb, 1995; Birch *et al.*, 1996; Merritt, 1996; Karban and Baldwin, 1997). The origin and purpose of this extraordinary level of diversity remain a mystery (Berenbaum, 1983, 1995; Denno and McClure, 1983; Schultz, 1983; Berenbaum and Zangerl, 1996).

One group of theories proposing to explain this variability is based on plant metabolism. One such theory is that most chemicals produced by plants are not active defences. The high diversity of chemicals in plants is maintained to increase the probability that some chemicals will be active, and to increase the rate of evolution of new chemicals (Jones and Firn, 1991). Thus, most chemicals produced by a plant are non-functional. This theory is

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not well supported by the evidence (Berenbaum, 1995). Another metabolism-based theory suggests the production of secondary metabolites is related to nutrient availability (Coley *et al.*, 1985; Coley, 1987) or the balance between different nutrients, especially carbon and nitrogen (Bryant *et al.*, 1983; Tuomi *et al.*, 1991). This is based on overflow metabolism, suggesting that plants put resources beyond those essential to growth and reproduction into defence. This assumes that plants are not able to precisely regulate their own metabolism. However, plants are capable of storing excess energy in the form of starch, and there is no reason to assume they are incapable of as precise metabolic regulation as animals (Berenbaum, 1995).

Another group of theories that has had somewhat more success in explaining the chemical variability of plants is based on herbivore responses. One possible explanation is that variable plants present a more uncertain environment to herbivores. This could make them less preferred food sources because an individual herbivore is unlikely to be adapted to all possible phenotypes at the same time (Whitham, 1981), or because the variability results in a lower average fitness for the herbivore (Karban *et al.*, 1997). Variability might also be important because of analogue synergism, where a combination of chemicals is more toxic than a single one (McKey, 1979; Berenbaum, 1985; Berenbaum and Zangerl, 1993), and because it slows the evolution of resistance by herbivores (Whitham, 1983).

In addition to constitutive variation in defences, induced responses – changes that occur in a plant in response to herbivory – tend to increase variability both within an individual and within a population. Induced responses take a variety of forms, but most commonly involve increasing morphological or chemical defences. These changes typically protect the plant from future herbivory by negatively affecting herbivores (induced resistance) or positively affecting the plant's fitness (induced defence), but they can sometimes result in increased susceptibility to herbivory (Karban and Baldwin, 1997). Although first noted only about 20 years ago, induced defences have since been discovered in a number of species. Karban and Baldwin (1997) list 115 species for which induced resistance has been demonstrated, and there are probably many more examples yet to be discovered.

Most theories explaining the use of induced defences rather than constitutive defences rely on metabolic costs (Feeny, 1976; Coley *et al.*, 1985; Harvell, 1986; Coley, 1987; Herms and Mattson, 1992). These theories assume that producing these defences requires energy that could otherwise be spent on growth and reproduction. In this case, a plant is more fit if it puts energy into defences only when they are truly needed, as signalled by early damage. However, costs of defences have been particularly difficult to find. Studies that show a cost to producing defences (Harvell, 1986; Baldwin *et al.*, 1990) are as rare as studies which have found no evidence of costs (Brown, 1988; Karban, 1993). A review by Bergelson and Purrington (1996) found costs for resistance to herbivory in only 29% of the studies they examined.

Karban *et al.* (1997) proposed a novel way to view induced defences that does not rely on costs, but instead relies on the function of the induced defences. They consider a defensive chemical with a particular dosage-dependent effect on herbivores: it has little detrimental effect on herbivores when present at a low or moderate dose, but has dramatic effects at higher concentrations. The outcome of any strictly concave function such as this, is that a plant which produces variable levels of defensive chemicals is better defended than one that always produces the mean level of toxin (Fig. 1). This phenomenon is often referred to as Jensen's inequality (DeGroot, 1970). For chemicals with this type of effect, a plant that can

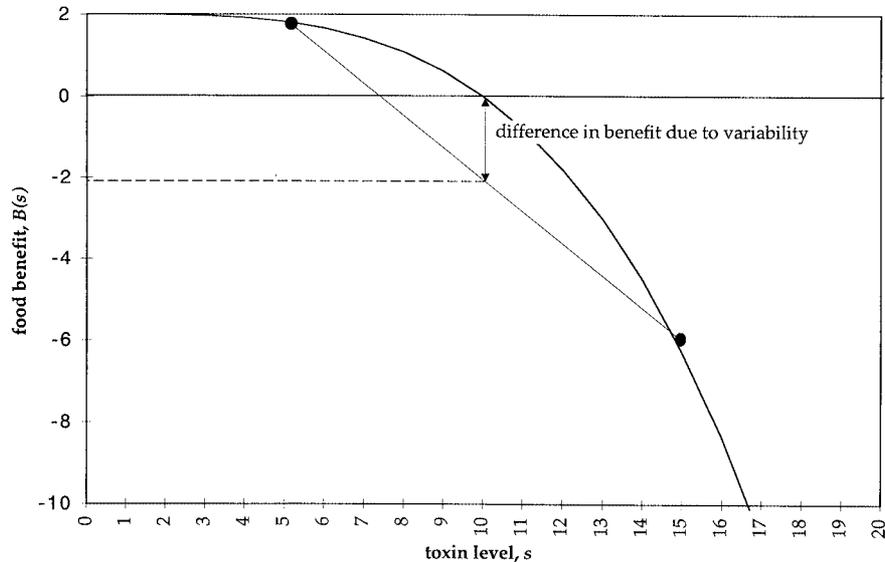


Fig. 1. I use a concave benefits function, $B(s)$, depending on toxin level, s . This results in rapidly decreasing benefit as the concentration of toxins increases. Therefore, a plant that produces two different levels of toxins in different parts will yield lower average benefit to a herbivore than a plant that constitutively expressed this mean level of toxins. For example, a plant that produces half of its leaves with toxin level 5 and the other half with toxin level 15 would have a mean toxin level of 10. If this were expressed constitutively, it would yield a benefit of zero, but due to the distribution, the benefit actually received by the herbivore is less than -2 .

exist in two states – induced or non-induced – yields a lower expected benefit to herbivores than a plant with only one state, even if both plants produce the same mean amount of toxin. I predict that herbivores that can detect this difference should be more likely to avoid the inducible plant because of the additional variability.

Although much research into plant defences has focused on costs, other explanations such as herbivore behaviour have not been explored adequately. Most studies on the effectiveness of various chemical defences have compared herbivores fed a diet containing the toxin to herbivores fed a diet that excludes the toxin. This ignores the possibility of behavioural avoidance of toxins, whether or not they have toxic effects on the herbivore, as an effective plant defence (Bernays, 1990; Wrubel and Bernays, 1990). Herbivore avoidance of certain plant parts could affect patterns of damage. In particular, if a plant is locally induced around a site of attack, herbivores might avoid the damaged area and produce a more dispersed pattern of damage than would otherwise occur. Dispersed damage has been shown in some studies to be less detrimental to the plant than clumped damage (Craig *et al.*, 1986; Mauricio *et al.*, 1993) and seems to be a preferred feeding method of some caterpillars (Faeth, 1986; Mauricio and Bowers, 1990). Avoidance can also be important at the population level, since a rejected plant escapes damage from herbivory, whereas its neighbours probably experience increased herbivory and therefore reduced competitive ability. Another perspective that has not been adequately addressed is the effect of adult feeding on reproduction. There is a large body of literature on adult oviposition choice in

response to plant chemistry and larval success on host plants (Renwick and Radke, 1983; Pereyra and Bowers, 1988; Huang *et al.*, 1993; Kouki, 1993; Du *et al.*, 1995; Nielsen, 1996; Nylin *et al.*, 1996). There have been very few studies on the effects of feeding choice on reproductive success.

To explore some of these alternative defence theories, I designed a dynamic state variable model (Houston and McNamara, 1985; Mangel and Clark, 1988) that compares the defensive strategies of two types of plants against a generalist herbivore. The first type of plant produces a constant level of toxin in all its parts, whereas the second type of plant produces the same average amount of toxin but distributes it unevenly throughout its parts. A herbivore that feeds on a constant-toxin plant will always consume plant tissue with a determinate amount of toxin, whereas a herbivore that feeds on a variable-toxin plant will consume tissue with a random toxin level selected from a distribution function.

I use the term 'toxin' to refer to the overall effect of a complex of chemicals expressed by a plant. This is admittedly an oversimplification of how plants are actually defended, but many studies suggest that the effects of defensive chemicals on herbivores is a result of synergistic effects between different chemicals (McKey, 1979; Berenbaum, 1985; Berenbaum and Zangerl, 1993), nutrient content of the leaf, and herbivore-specific responses (Lindroth, 1991). Thus, the actual effects of toxins on herbivores can rarely be predicted by measuring the levels present in the plant. However, the overall effects of toxins can be measured through bioassays with herbivores. I focus on the functional effects of the toxins to minimize the assumptions of the model.

The model investigates how herbivores respond to variability in plant defences and whether this variability benefits the plant by increasing herbivore avoidance. The principal assumption is that the benefit curve is concave, as explained above. It is unknown precisely how common this pattern may be in nature, since such a response is extremely difficult to measure. A concave dosage-dependent effect has, however, been found for several chemicals (Parr and Thurston, 1972; Elliger *et al.*, 1976; Byers *et al.*, 1977). Unfortunately, such studies are scarce. Determining the precise level of different toxins in a plant can be done by destructively sampling the plant, but most chemical analyses hide some of the micro-variations within a plant, both spatially and temporally. In addition, such tests do not reveal how much of the toxins a herbivore would actually consume, since many herbivores behaviourally avoid toxins (Karban and Baldwin, 1997).

THE MODEL

Dynamic state variable models can incorporate variation in energy states of organisms, temporal variation and environmental stochasticity, and yield a range of optimal decisions depending on the specific conditions of the organism and the environment over time (Houston and McNamara, 1985; Mangel and Clark, 1988). I have designed the simplest possible model that incorporates enough life-history information to be useful. The model optimizes behaviour by evaluating a fitness function, $F(x,t)$, which depends on the time in the season, t , and the energetic reserves of the herbivore, $X(t) = x$ (Table 1). The state variable is affected by the toxin levels encountered by the herbivore and its behaviour.

In each time step, there are two tiers of decisions. First, the herbivore either forages or lays eggs. Then, if the herbivore forages, it may either accept or reject the plant encountered. I assume that herbivores can distinguish between constant-toxin and variable-toxin plants,

Table 1. Parameters and functions used in the model, together with definitions and values used in most of the analyses^a

Parameters and functions	Definition	Standard value
x	metabolic state of herbivore	varies: 0–20
α	metabolic cost of foraging	0.5
t	time in season	varies: 1–20
T	final time step	20
$F(x,t)$	maximum expected reproductive success given state x at time t	varies
$F(x,T)$	reproductive success at end of season (end condition)	varies
s	toxin concentration in plant	varies: 0–20
s_0	toxin concentration in constant-toxin plant	4
\bar{s}	toxin concentration at which food benefit = 0	10
$B(s)$	food benefit to herbivore from feeding on leaf with toxin concentration s	varies
B_{\max}	maximum food benefit of leaf with no toxins = $B(0)$	2
γ	determines concavity of food benefit function, $B(s)$	2.5
$P(s)$	in a variable-toxin plant, the probability a leaf has toxin level s	varies
σ	in variable-toxin plant, determines variance of toxin distribution, $P(s)$	15
D_c	probability of encountering constant-toxin plant	0.6
D_v	probability of encountering variable-toxin plant	0.4
A	determines maximum possible clutch size	40
x_0	determines inflection point of reproduction curve	10
M	exponential probability of mortality for all activities	0.01
$V_{\text{forage}}(x,t)$	fitness value of foraging	varies
$V_{\text{reproduce}}(x,t)$	fitness value of laying eggs	varies

^a When different values are used, they are mentioned in the text.

but cannot discern the precise level of toxin they will encounter if they feed on a variable-toxin plant. This is justified by experimental studies that indicate some generalist herbivores can distinguish between different species of potential host plants, but cannot distinguish high-quality from low-quality hosts within a species (Janz and Nylin, 1997). In the model, herbivores either accept or reject the plant as a whole based on whether it is a constant-toxin or variable-toxin plant.

If a herbivore reproduces, it lays as many eggs as possible given its current state and its energy reserves are reduced to zero. Reproductive and foraging patches are different resources and reproductive patches are not limiting. If the herbivore forages, it either finds one of the two plant types or does not find a plant. The probability of each of these events is determined by the densities of each plant type, D_c and D_v . Whenever a plant of either type is encountered, the herbivore may either feed on that plant or reject it and continue searching (or reproducing) in the next time step. During each step that a herbivore forages, it expends a specific amount of metabolic energy, α , and if it feeds it acquires a metabolic benefit, $B(s)$, determined by the amount of toxin, s , present. The benefit received may be either positive or negative depending on the toxin level. Constant-toxin plants always contain a level of toxin, s_0 , but the toxin level in a variable-toxin plant, s , varies according to a function, $P(s)$:

$$P(s) = \frac{e^{-(s-s_0)^2/2\sigma^2}}{\sum_{s=0}^{s_{\max}} e^{-(s-s_0)^2/2\sigma^2}} \tag{1}$$

with

$$E(s) = \sum_{s=0}^{s_{\max}} sP(s) = s_0 \tag{2}$$

The parameter σ determines the degree of spread. I used a large variance, $\sigma = 15$ for most computations, to mimic the high variation seen in the chemical distribution in most plants.

The benefit function is a concave decreasing curve characterized by the parameters \bar{s} , the point at which the benefit is zero, B_{\max} , the maximum possible benefit to a herbivore, and γ , the degree of concavity. Toxin levels less than the zero benefit toxin level ($\bar{s} = 10$) yield positive benefits, whereas levels greater than this give negative benefits (Fig. 2). For computation, I used

$$B(s) = B_{\max} \left[1 - \left(\frac{s}{\bar{s}} \right)^\gamma \right] \tag{3}$$

with $\gamma = 2.5$ except where noted otherwise. The degree of concavity is determined by

$$\frac{B''(s)}{B'(s)} = \frac{\gamma - 1}{s} \tag{4}$$

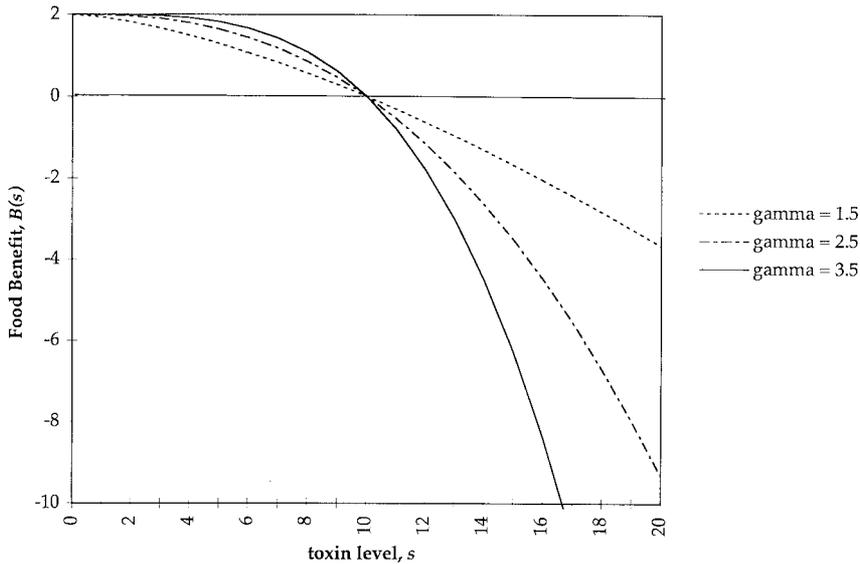


Fig. 2. The benefit, $B(s)$, received by a herbivore from feeding on a plant is assumed to be a strictly concave function of the toxin level. The effect of the toxins is to reduce the food benefit of the plant. The maximum food benefit in this case is 2. The benefit is neutral when $s = 10$, which means the cost of the toxin exactly equals the nutritional benefits of the plant. Benefit decreases rapidly for concentrations of toxins greater than 10. The concavity of the curve is determined by the parameter γ . A value of $\gamma = 2.5$ was used throughout this paper except where explicitly stated otherwise.

In variable-toxin plants, the toxin levels range between 0 and 20, with the probability of each level determined according to the function $P(s)$. The expected value of $B(s)$ for a variable-toxin plant is approximately 0.79, with a standard deviation of 11.5. Since all constant-toxin plants have a fixed toxin level of two, the benefit from a constant-toxin plant is the value $B(2) \approx 1.8$. Given the concavity assumption of the model, the benefit from a constant-toxin plant is always greater than the expected benefit from a variable-toxin plant.

The physiological state of the herbivore is linearly affected by foraging according to the following state dynamics, given $X(t) = x$:

$$\begin{aligned} \text{no plant or rejected plant:} & \quad X(t+1) = x - \alpha \\ \text{constant-toxin plant:} & \quad X(t+1) = x - \alpha + B(s_0) \\ \text{variable-toxin plant:} & \quad X(t+1) = x - \alpha + B(s) \text{ with probability } P(s) \end{aligned} \quad (5)$$

The state variable is constrained so that $0 \leq X(t) \leq 20$, with $X(t) < 0$ corresponding to the death of the herbivore.

The model begins with a terminal fitness function, which corresponds to the end of the season, and fitness is then calculated backwards in time (Mangel and Clark, 1988; Mangel and Ludwig, 1992). This end condition is the expected reproductive success, $F(x, T)$, of a herbivore with state x at the final time T . It is a sigmoid function characterized by metabolic reserves, an inflection point x_0 and an upper limit on the number of eggs laid:

$$F(x, T) = \frac{Ax^2}{(x^2 + x_0^2)} \quad (6)$$

This same function is used to determine the number of eggs laid at other times in the season. I assume eggs have the same reproductive value regardless of the time in the season when they are laid, so that total lifetime fitness is the number of eggs laid on the interval $(0, T)$.

The model operates by computing the value $F(x, t)$:

$$F(x, t) = \text{maximum expected accumulated reproductive success between } t \text{ and } T \text{ for an individual with } X(t) = x \quad (7)$$

The decision rule is to choose the maximum fitness value of either foraging or reproducing; therefore, I calculate the value of each of these activities. The value of reproducing is the sum of current and future reproduction:

$$V_{\text{reproduce}}(x, t) = \frac{Ax^2}{(x^2 + x_0^2)} + e^{-M}F(0, t+1) \quad (8)$$

The first term is the same as the end condition and the second term is the value of future fitness discounted by mortality.

The value of foraging is the sum of each of the three possible foraging results: no plant encountered, constant-toxin plant encountered, variable-toxin plant encountered. The probabilities of encountering constant-toxin and variable-toxin plants are denoted by D_c and D_v respectively, and the probability of not encountering a plant is $1 - D_c - D_v$. Whenever either type of plant is encountered, the herbivore can either accept or reject the plant as a whole based on the expected food benefit of a variable-toxin plant, rather than the actual benefit it would receive, which is determined stochastically. If it accepts the plant, it receives

a food benefit. If it rejects the plant, it continues foraging in the next time period, in which case the effect on fitness is the same as in the case of not encountering a plant. The expected fitness value of foraging is thus:

$$\begin{aligned}
 V_{\text{forage}}(x,t) = & (1 - D_c - D_v)e^{-M}F(x - \alpha, t + 1) \\
 & + D_c e^{-M} \max\{F(x - \alpha + B(s_0), t + 1); F(x - \alpha, t + 1)\} \\
 & + D_v e^{-M} \max\left\{ \sum_{s=0}^{s_{\max}} P(s)F(x - \alpha + B(s), t + 1); F(x - \alpha, t + 1) \right\}
 \end{aligned}
 \tag{9}$$

There is no time cost to feeding on a plant and, therefore, the herbivore will always accept a constant-toxin plant. In this way, the model is similar to classic diet choice models in that one food type is consistently preferred. In addition, mortality is constant for all activities. Differential mortalities for reproduction, searching and feeding can easily be incorporated and do not substantively change the predictions of the model. Equations (8) and (9) are combined to give

$$F(x,t) = \max\{V_{\text{reproduce}}, V_{\text{forage}}\}
 \tag{10}$$

The model is first run backward, beginning with the end condition and then sequentially solving for the optimal decisions for each state x at each previous time (Mangel and Clark, 1988; Mangel and Ludwig, 1992). This backward iteration generates a set of decision rules specifying which behaviours are predicted for specific values of x and t .

RESULTS

Backward iterations

The model predicts that a herbivore with intermediate energy reserves will reject a variable-toxin plant (Fig. 3). Variable-toxin plants present a risk of significantly decreasing a herbivore's state if it encounters a particularly high concentration of toxins. At low

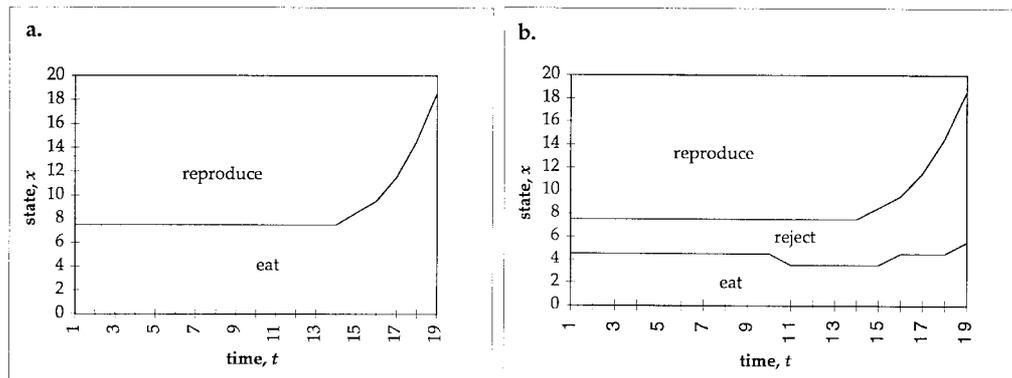


Fig. 3. Plane of backward decisions on a constant-toxin plant (a), or a variable-toxin plant (b). Constant-toxin plants are always accepted, whereas variable-toxin plants are rejected by herbivores with intermediate states.

states, a herbivore is predicted to accept any food source, regardless of risk, to avoid the certain risk of starvation. At high states, a herbivore is predicted to reproduce to gain an immediate fitness benefit and increase the chance for multiple reproductive bouts in the season. Constant-toxin plants are never rejected because they present no risk to the herbivore. Since reproduction is independent of plant type, it is the same for both constant-toxin and variable-toxin plants. It is the existence of these distinct behavioural regions that is important, not the precise values separating the regions.

The rejection region for variable-toxin plants depends on the relative densities of the two plant types in the environment. If the proportions of the two plant types are equal, model herbivores will consistently reject the variable-toxin plants for a narrow range of states (Fig. 4). As the proportion of constant-toxin plants increases, the herbivores are predicted to reject variable-toxin plants over a wider range of states. When variable-toxin plants are more common than constant-toxin plants, the rejection region often disappears entirely. When variable-toxin plants make up less than half the environment, an increase in their densities has a relatively large effect on fitness, but when they make up more than 50%, increasing their densities further has diminishing effects. The presence of constant-toxin plants as a preferred food source is essential for rejection of variable-toxin plants.

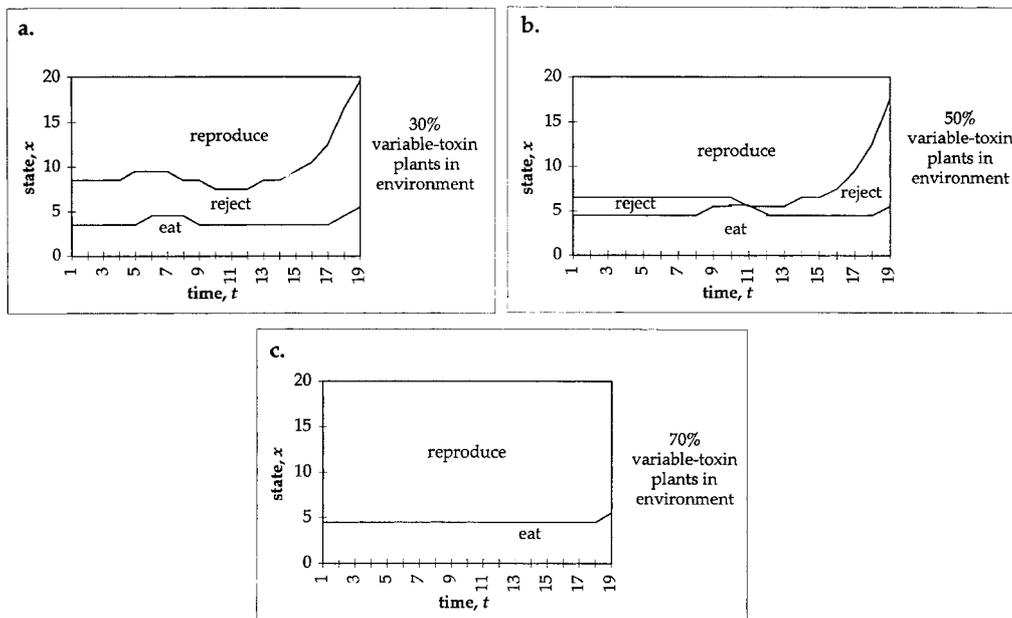


Fig. 4. Plane of backward decisions on variable-toxin plants for different densities of variable-toxin plants. When variable-toxin plants constitute less than half of the environment (a), these plants are rejected over a relatively wide range of states. When variable-toxin plants constitute half of the environment (b), a stable rejection region occurs for a narrow range of intermediate states. When variable-toxin plants constitute the majority of the environment (c), herbivores rarely reject these plants and the rejection region often disappears entirely.

Two other parameters, γ and σ , also affect the rejection region of variable-toxin plants. σ determines the relative probability of encountering a high concentration of toxins or a low concentration of toxins when a herbivore feeds on a variable-toxin plant. When $\sigma = 15$, a herbivore is almost equally likely to encounter a high as a low concentration of toxins, and there is a region of rejection for intermediate states over all time periods (Fig. 3). As σ decreases, the occurrence of rejection decreases, since the probability of encountering a high concentration of toxins decreases. When $\sigma = 11$, the rejection region disappears entirely. When σ is greater than 15, the distribution of different concentrations of toxins approaches a uniform distribution, and the risk increases minimally. There must be a reasonably high probability of encountering a high concentration of toxins for herbivores to reject variable-toxin plants.

The curvature of the benefits function is determined by γ (Table 1). Increasing γ increases the concavity of this function, which means that high concentrations of toxins have a much stronger negative effect. This has a moderate effect on fitness in the backward calculations, but is more apparent in the forward iterations.

Forward iterations

Although the backward calculations determine a set of expected behavioural 'rules' over time and state, the forward iterations use these rules to predict what behaviour is likely to be observed for an individual herbivore in a stochastic environment (Mangel and Clark, 1988; Heimpel *et al.*, 1998). Two parameters have significant effects on the results of the forward iterations: the density of variable-toxin plants, D_v , and the concavity of the benefits function.

The model predicts that γ has a large effect on the time dependence of the rejection of variable-toxin plants (Fig. 5). When γ is small (1.5), there is no rejection of variable-toxin plants until the last few time steps. When γ is intermediate or large (2.5 or 3.5), the rejection rates are relatively high. Whether herbivores accept or reject a plant is determined by their state and this helps explain much of the variation for $\gamma = 2.5$ and $\gamma = 3.5$ in Fig. 5. Herbivores reject at intermediate states and reproduce at high states, and state drops to zero after reproduction. Therefore, we see peaks of rejection immediately before reproduction events and a decline in rejection following this. In Fig. 5, many herbivores reproduced at $t = 1$ and $t = 7$ and, therefore, rejection tends to be lower in the following time steps. Thus, as expected, more toxic plants are rejected more often than less toxic plants. The proportion of variable-toxin plants also has a significant effect on rejection. When variable-toxin plants are rare, they are always rejected because the probability of encountering a constant-toxin plant in the next time step is large. Conversely, when variable-toxin plants are very common, they are never rejected because the probability of encountering the preferred constant-toxin plants is very small.

Survival of herbivores is also significantly affected by the densities of variable-toxin plants (Fig. 6). With 0% variable-toxin plants, there is very little mortality over the course of the season because mortality is due only to predation. With 50% variable-toxin plants, there is a relatively steady decline in survivorship over the season and 80% of the mortality is due to starvation. Mortality is very high when there are 100% variable-toxin plants and all herbivores typically die by $t = 14$. Approximately 95% of this mortality is due to starvation. Survivorship is not significantly affected by γ .

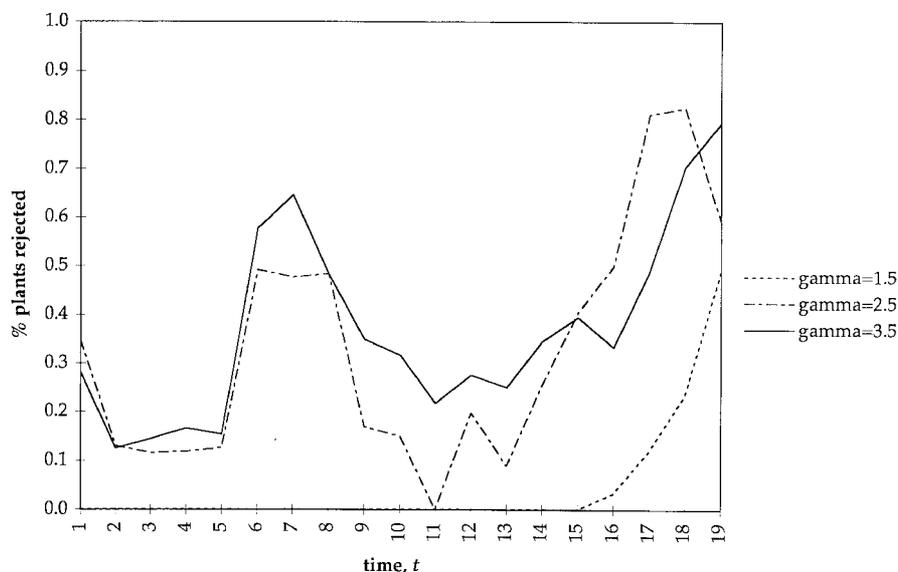


Fig. 5. Percent of encounters with variable plants that result in a decision to reject the plant for different degrees of concavity in the food benefits curve. Increased concavity means increased toxicity of high concentrations of toxins. Concavity of the toxins effect curve is determined by γ ; concavity increases as γ increases. If the standard deviation (computed as the square root of the binomial variance, $p(1-p)$) is used as an estimate of statistical significance, the curves for $\gamma = 2.5$ and $\gamma = 3.5$ appear to differ significantly from $\gamma = 1.5$ only at the highest peaks.

Reproduction is also affected by the density of variable-toxin plants (Fig. 7). When herbivores begin the season with a low state ($x \leq 3$), they do not reproduce until they can increase their state, unless there are very high densities of variable-toxin plants. High densities of variable-toxin plants represent a much higher risk of mortality, because high toxin levels yield negative benefits to the herbivore's energy level, which can reduce it below the minimum level required for survival (Fig. 6). Therefore, when there are high densities of variable-toxin plants, herbivores are willing to reproduce with a low metabolic state, even though this will yield a lower fitness benefit in terms of number of eggs laid. With equal densities of the two plant types, the first reproduction occurs at $t = 3$ if a herbivore's initial state is low ($x \leq 3$) and reproduction continues to occur throughout the season (Fig. 7). In the case where there are no variable-toxin plants, the environment is completely deterministic, so all herbivores increase their states at the same rate and all reproduction occurs in a single peak at the middle of the season.

The interpretation of reproduction is complex. A herbivore is predicted to reproduce whenever its state is high because this yields an immediate increase in fitness. But reproduction can also reflect avoidance of foraging risk. If there is a high probability of encountering a high concentration of toxins that will decrease the herbivore's state, then foraging may be too risky; hence reproduction will be preferred even if the fitness payoffs are low. When interpreting the results of the model related to reproduction, it is important to remember that there are these two possible causes. In addition, the decrease in reproduction as the final

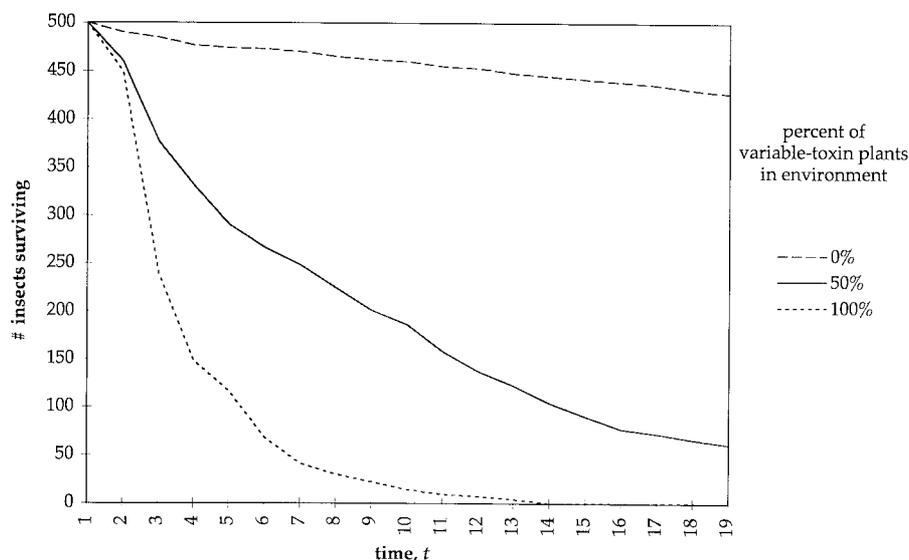


Fig. 6. Different proportions of variable-toxin plants have a significant effect on survival of herbivores. Survivorship is greatly decreased as the proportion of variable-toxin plants is increased.

time period is approached is an artifact of the model, because herbivores are forced to reproduce at the final time period and are therefore less likely to reproduce immediately prior to that.

Another interesting effect of differing proportions of variable-toxin plants is that the number of reproductive events is lowest for 50% variable-toxin plants and increases as the proportion of variable-toxin plants either increases or decreases (Table 2). Reproduction is most common when there are no variable-toxin plants, since there is no risk in the environment. But the number of reproduction events also increases as the proportion of variable-toxin plants increases from 50% to 100%, reflecting a trade-off between increased foraging risk and reduced number of eggs laid per reproductive bout when state is lower. However, reproduction is much more productive with lower proportions of variable-toxin plants, as demonstrated by the average number of eggs laid per herbivore over a season and the average number of eggs laid per reproductive event (Table 2).

Reproduction is also affected by γ . As γ increases and plants become more toxic, reproduction actually increases (Table 3). This is because herbivores reject highly toxic plants more often than less toxic plants. As a result, they experience the negative effects of the toxins less often, and their overall fitness increases as long as there are sufficient numbers of constant-toxin plants to sustain them. Therefore, highly toxic plants may be avoided very effectively, but may also benefit the herbivores if they always avoid the most toxic plants. Although the average number of reproductive events and the average number of eggs per reproduction do not change much, the average number of eggs laid per herbivore increases as γ increases.

The density of variable-toxin plants is also predicted to have an effect on the average state of herbivores. The average state over all time periods is 6.6 ± 3.62 (mean \pm s.d.) when there are 0% variable-toxin plants, 3.3 ± 2.10 with 50% variable-toxin plants, and 1.2 ± 1.16 with

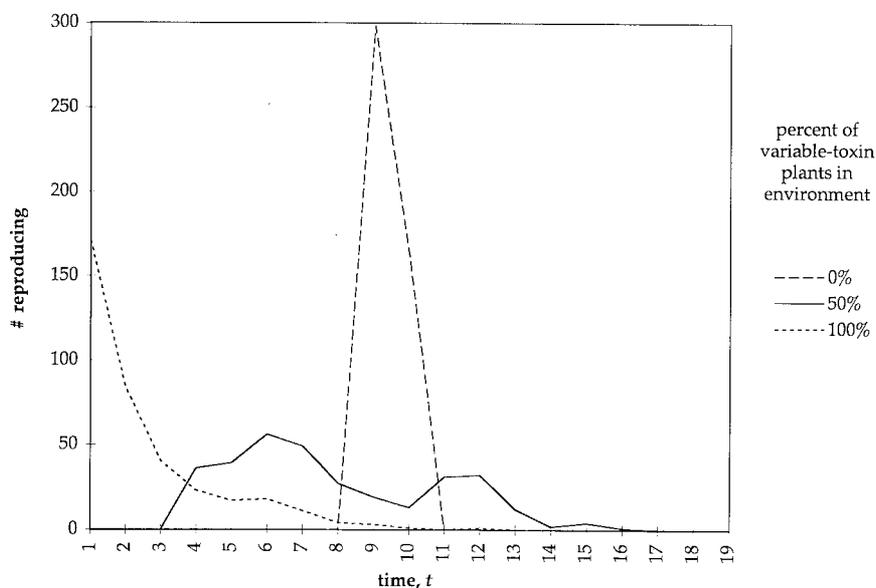


Fig. 7. The density of variable-toxin plants has significant effects on the timing and amount of reproduction. When there are only constant-toxin plants (0% variable-toxin plants), reproduction is synchronous and occurs in a single peak because there is no environmental variability. With 100% variable-toxin plants, reproduction occurs primarily at the beginning of the season due to the high risk of mortality from the variable-toxin plants. With equal proportions of the two plant types, reproduction occurs at low levels throughout most of the season, except at the earliest time periods when states are low.

Table 2. Effects of different proportions of variable-toxin plants on reproduction in forward iterations^a

	Percentage of variable-toxin plants in environment		
	0%	50%	100%
Reproductive events	459	321	373
Total eggs	21331.5	4878.4	1321.4
Average eggs per reproductive event	46.5	15.2	3.5
Average eggs per herbivore	42.7	9.8	2.6

^a Results are for 500 simulated herbivores with initial states $x \leq 3$.

100% variable-toxin plants. The average states fluctuate over the course of the season (Fig. 8), but a consistent pattern of higher states associated with lower proportions of variable-toxin plants is retained across all times. There is a minor effect on average state by γ . As γ increases, the average state increases. This is due to the increasing probability of rejection of variable-toxin plants as toxicity increases (Fig. 6). As a result, as plants become more toxic, the surviving herbivores actually benefit.

Table 3. Effects of γ on reproduction in forward iterations^a

	γ		
	1.5	2.5	3.5
Reproductive events	249	321	322
Total eggs	4302.2	4878.4	5050.5
Average eggs per reproductive event	17.3	15.2	15.7
Average eggs per herbivore	8.6	9.8	10.1

^a Results are for 500 simulated herbivores with initial states $x \leq 3$ and 50% variable-toxin plants in environment.

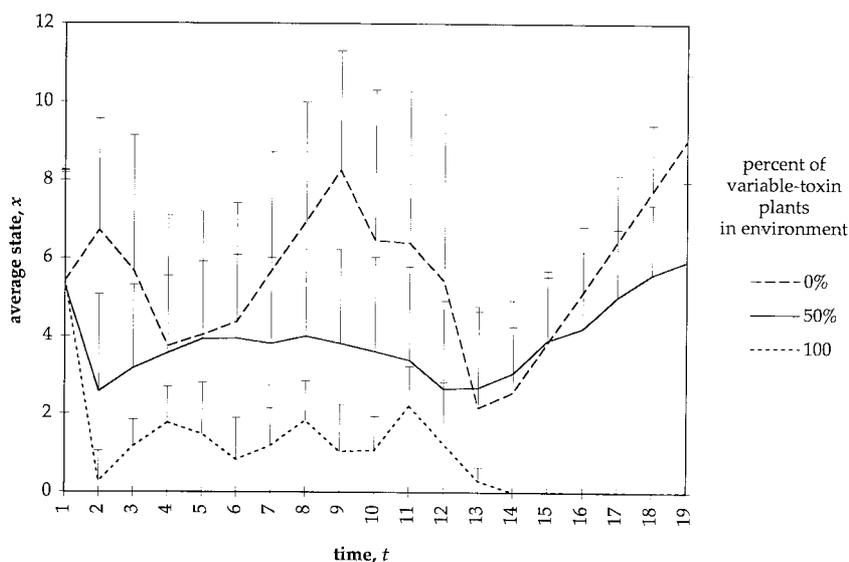


Fig. 8. The proportion of variable-toxin plants affects the average state of herbivores. Average state decreases as the proportion of variable-toxin plants increases. Error bars are 1 standard deviation from the mean.

DISCUSSION

The present results suggest that increasing the toxicity, γ , of the plant to very high levels will actually result in increased fitness and reproduction of the herbivores as long as there is an alternative food source. This assumes that herbivores can discern the quality of different food sources and that they selectively choose their food. Many studies on oviposition have shown that insects can in fact distinguish between different host plants that differ in quality and that they are selective in their preferences (Wasserman, 1986; Singer *et al.*, 1989, 1991). Fewer studies have been conducted on larval food preferences, but the same result is likely (Schultz, 1983). Yet the importance of insect choice has typically been ignored in studies of plant defence.

Herbivore avoidance can, in fact, be a very effective defence. It reduces damage to an individual plant, and might lead to higher herbivory on the plant's neighbours. This could result in indirect benefits for the plant from reduced competition. However, avoidance may or may not be a good long-term defence. If the alternative food source promotes higher fitness and reproduction by the herbivores, then herbivore populations could increase. However, since natural selection acts on individuals and not groups, the defence that provides the best immediate benefit for the individual is more likely to be favoured.

Another implication of the model is that variability might actually increase the effectiveness of plant defences by increasing the uncertainty experienced by herbivores. If herbivores forage to maximize their lifetime fitness, then we might expect them to avoid particularly risky food sources. When toxins have increasingly toxic effects on herbivores as concentrations increase, then plants can gain extra protection, at no extra cost, by producing a few leaves with very high concentrations of toxins and with relatively low concentrations in the rest of the plant. If a herbivore encounters these high toxin leaves often enough to avoid the plant, then the plant benefits.

In addition, other scales of variability could be favoured for the same reasons. In this model, the scale of variation for plants is different from the scale of variation experienced by herbivores. At the plant level, variation is between the two phenotypes – constant-toxin plants and variable-toxin plants. But herbivores experience variation among individual variable-toxin plants, rather than within them, since they only feed on a small portion of an individual plant. From the herbivore's perspective, this is the same as if the plants were variable among individuals but constant within individuals. The predictions of this model are the same in either case. A herbivore in this case might avoid a phenotype with high variability between individuals and, as a result, natural selection could favour plants that produce diverse offspring.

Risk-sensitive behaviour has been widely studied in behavioural ecology (Caraco *et al.*, 1980; Stephens and Krebs, 1986; Harder and Real, 1987; Cartar and Dill, 1990; Cartar, 1991; Kacelnik and Bateson, 1996; Smallwood, 1996). However, herbivory and plant defences have not previously been examined in terms of risk-sensitive foraging. In addition, most studies of risk sensitivity have looked only at a single time in the season and assumed that all the organisms were identical. Thus, they usually predict a single expected behaviour – that individuals are risk-averse, risk-prone or risk-neutral. In some cases, an animal can exhibit more than one of these behaviours, but this is a response to the shape of the benefits curve rather than a result of individual variation. In contrast, dynamic state variable models predict a much wider range of behaviours, which more closely match the individual behavioural variation observed in nature.

Different parameters in the benefit function of this model could lead to significantly different results. For instance, if variable-toxin plants had significantly higher rewards than constant-toxin plants as well as higher penalties, I would expect to see both risk-averse and risk-prone behaviour depending on the state of the forager, the reproductive success and the time in the season. However, the results presented here are likely to apply whenever a benefits curve is concave with respect to the concentration of toxins and the threshold for reproductive success is not extremely high. In addition, since more concave functions result in higher rejection, they may be a better defence and, therefore, we might expect natural selection to favour toxins with this type of effect.

Furthermore, plants might be protected from herbivory by association with less toxic plants that the herbivores prefer. This relies on the ability of the herbivores to make choices

about preferred food sources and assumes they will choose the plants that will lead to the highest possible lifetime fitness. Associational plant refuge (APR) theory suggests the opposite result – that plants will benefit by association with plants more toxic than themselves (Root, 1973; Atsatt and O'Dowd, 1976; Pfister and Hay, 1988). APR theory assumes that plants are difficult for herbivores to find and that a palatable plant hidden among unpalatable plants is either not likely to be detected, or is not worth the effort of attacking if there are large patches of palatable plants nearby. The conflicting results of these two theories are primarily due to different assumptions about herbivore behaviour and scale. The model presented here assumes small costs to switching between plants; in fact, it assumes the herbivores switch plants often. It also assumes that the ability to find a food plant is not limiting. APR theory, on the other hand, assumes that suitable plants are difficult to find when surrounded by less suitable plants. APR theory looks at an entire patch and asks whether a herbivore will forage in that patch based on the overall quality of the plants there. I have considered a finer scale in which the herbivores choose between individual plants.

ACKNOWLEDGEMENTS

I would like to thank Marc Mangel for extensive comments and advice on previous drafts of the manuscript. Mike Sherrill provided invaluable editorial assistance and support. The manuscript was also improved substantially by the comments of Tom Caraco, Carol Boggs, Suzanne H. Alonzo and Melanie Bojanowski. This research was supported by USDA Grant 443080-22463 to M. Mangel and an NSF Graduate Research Fellowship to A.L.S.

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