Plant defence and stochastic risk of herbivory

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Summary

The influence of risk of herbivory and its variation in time on the optimal defence strategy in plants is analysed by a simple optimization model. We contrast two possible defence strategies; a constitutive defence with an invariant defence level in time and an idealized induced defence, that is, a strategy that adjusts the defence level to the prevailing risk of herbivory. We also take into account effects of the efficiency of the defence. If there is no variation in risk of herbivory over years, constitutive and induced defence should have the same expected optimal defence level and both strategies are equally fit. The optimal defence level increases as the maximum fecundity and the adult to juvenile survival ratio of the plants both increase. If the risk of herbivory varies stochastically, the expected optimal level of the constitutive defence is either increased or unaffected by the variation, whereas the induced defence strategy may result in both higher or lower expected optimal defence levels as variance increases. This outcome is dependent on the mean risk of herbivory. It also depends on the defence efficiency, i.e. the shape (convex, concave or linear) of the defence function that relates the probability of survival if encountered by a herbivore to defence level. Thus, the defence level of plants interacting with variable herbivore populations cannot be unambiguously predicted unless the defence strategy (constitutive or induced), mean risk of herbivory, the form of the defence function and plant life history are known.

Keywords: optimal plant defence; constitutive defence; induced defence; stochastic risk; mathematical model

Introduction

Many plants seem to protect themselves against deleterious herbivory by a wide array of chemical and structural defences. The degree to which plants tend to be defended also seems to vary depending on, for instance, the 'apparency' of the plants (Feeny, 1976; Rhoades and Cates, 1976; Chew and Courtney, 1991), resource availability (Coley *et al.*, 1985) and, obviously, the risk of herbivory (Bryant *et al.*, 1989; Edelstein-Keshet and Rausher, 1989; Oksanen, 1990; Augner *et al.*, 1991; Coley and Aide, 1991). As regards the chemical defence, we may distinguish four different principal types. On the one hand, the defence may be either endowed ('constitutive') or induced, i.e. changing in relation to past and present herbivore damage (Haukioja and Neuvonen, 1985; Karban and Myers, 1989). On the other hand, the defence may also be either 'quantitative', i.e. its effects being dosage dependent or 'qualitative', i.e. having more or less full effect if present but without marked improvement as the concentration increases (Rhoades, 1979; Coley *et al.*, 1985).

Antipredator defences are not only confined to plants. There are a number of examples of induced defences among freshwater and marine invertebrates, e.g. spines and crests in bryozoans and cladocerans (Havel, 1987; Harvell, 1990; Clark and Harvell, 1992; Riessen, 1992). Indeed, induced defences, which need a proximate and reliable cue to be triggered, seem to be common to many modular organisms (Harvell, 1990), plants and animals alike. Modular animals and plants may in fact have a lot in common with respect to allocation decisions and inducible

defences, since they both grow by repeated production of modules, which may be subject to grazing.

In this paper we develop a simple optimal defence model focusing explicitly on the role of the risk of herbivory and type of defence according to the above definitions. In particular, we will analyse the effects of a variable risk of herbivory. One of the reasons for this interest is the notion that an occasionally very high herbivore pressure, intervened by periods of low or absent herbivore numbers, e.g. the snowshoe hare 10 year cycle, would select for more heavily defended plants than situations of a more constant and intermediate risk of herbivory (cf. Bryant *et al.*, 1989, for details). The defence problem for an organism facing a variable predation pressure has also been examined in some detail for invertebrates capable of inducing a morphological defence (Harvell, 1990; Clark and Harvell, 1992). Neither theory, nor empirical studies have generally been taken as far by students of plant defences (Karban and Myers, 1989; Zangerl and Bazzaz, 1992). We believe that a more formal treatment of many aspects of plant–animal interactions is still needed since many hypotheses and suggested mechanisms and evolutionary scenarios in this field are not always unequivocally stated (see also Fagerström *et al.*, 1987).

Our approach in this paper is deliberately simple and general and not so much aimed at understanding specific systems, but rather to elucidate the essentials of plant defence in relation to grazing pressure, especially regarding the variability in the risk of herbivory. Therefore we do not consider any frequency dependencies that may influence the optimal defence levels (cf. Lundberg and Åström, 1990), neither do we study the possible evolutionary games between different types of defences. The effects of the level and variability of the risk of herbivory on plant defence are such surprisingly neglected problems in the literature of plant–herbivore interactions. In this paper, we are also interested in the effects of different defence functions, i.e. the shape of the function relating the amount of defence to its efficiency against herbivores. As we shall see, this relationship may not only influence the optimal defence level as such, but also the relative benefit of a constitutive versus an induced defence type.

Models

We have assumed an age-structured plant population with a reproducing adult stage and non-reproducing juvenile one. We further assume that a plant that is potentially subject to herbivory can enhance its expected fitness by allocating resources to a chemical defence. The defence is, however, also assumed to be costly in terms of fitness. We let the expected plant fitness (cf. Schaffer, 1974) be defined as

$$W = S_a + S_j B(D) \tag{1}$$

where S_a is the per capita adult survival rate, S_j is the per capita juvenile survival rate and $B(D)$ is fecundity as a decreasing function of the defence level of the plant ($0 \leqslant D \leqslant 1$). If $D = 0$, the plant allocates none of its resources to defence, whereas if $D = 1$ all available resources (constrained by some minimum maintenance and growth) are allocated to defence. We may regard D as the concentration of some defence compound, scaled such that $D = 0$ means zero concentration and $D = 1$ maximum concentration of that particular compound (cf. Fagerström *et al.*, 1987).

For simplicity, we assume that the defence cost only affects fecundity and that this cost is linear, i.e.

$$B(D) = b - cD \tag{2}$$

where b is the maximum fecundity (in the absence of defence allocation) and c is a cost constant

$(0 < c \leqslant b/D)$ determining the rate of the fecundity reduction as more resources are allocated to defence. We are aware of the fact that the allocation of resources to defence may affect other components of the life history of a plant as well, e.g. growth and competitive ability (Gulmon and Mooney, 1986; Fagerström *et al.*, 1987; Crawley, 1988; Simms, 1992). However, we have chosen a simple, but still meaningful, effect on fitness (Briggs and Schultz, 1990). If we also assume that fecundity generally is somehow proportional to growth and adult size (Harper, 1977), a defence reducing growth may also reduce fecundity (see also Louda *et al.*, (1990) for a review).

During each suitable time interval (e.g. a year) a plant may or may not be encountered by a herbivore. Thus, we introduce the following probabilities: p is the probability that a plant is encountered by a herbivore during this time interval and $q(D)$ is the probability that a plant survives a herbivore encounter as a function of D. We assume that p is somehow positively related to herbivore density and initially that p is constant in time. We also let

$$q(D) = D^\mu \quad (\mu > 0) \tag{3}$$

We will call Equation 3 the defence function. If $\mu < 1$ then the defence function is a monotonically increasing but decelerating (concave) function of D, if $\mu > 1$ then the defence function is an exponential one (convex) and if $\mu = 1$ it is a straight line. In the following analyses, the three μ-cases will be exemplified by values of 0.5, 1 and 2. The mortality risk if encountered $(1 - q(D))$ will be positive for all $D < 1$ and will be zero if $D = 1$. The defence may either lower the risk of being attacked upon encounter or reduce the damage of an attack.

We may now write fitness as

$$W = (1 - p)(S_a + S_j B(D)) + p(S_a + S_j B(D))D^\mu \tag{4}$$

which simplifies to

$$W = (S_a + S_j(b - cD))(1 - p + pD^\mu) \tag{5}$$

after inserting Equation 2 into Equation 4. Thus, fitness in the absence of herbivory $(S_a + S_j (b - cD))$, is reduced by the term $1 - p + pD^\mu$ if $p > 0$, i.e. if the risk of herbivory is larger than zero. Any defence level $D < 1$ decreases the survival probability of the plant if encountered compared to $D = 1$, which ensures the herbivore-independent survival given by S_a and S_j.

Equation 5 is the function to be maximized and we may now find the optimal defence level by setting $W'(D)$ equal to zero, solving for D^* and checking that $W''(D) < 0$. After some rearrangements we have

$$D^* = \left(\sqrt{\left(\frac{1-p}{3p}\right)^2 + \frac{A}{3}} - \frac{1-p}{3p} \right)^2 \text{ for } \mu = 0.5 \tag{6a}$$

$$D^* = \frac{A}{2} - \frac{1-p}{2p} \qquad \text{for } \mu = 1 \tag{6b}$$

$$D^* = \frac{A}{3} + \sqrt{\left(\frac{A}{3}\right)^2 - \frac{1-p}{3p}} \qquad \text{for } \mu = 2 \tag{6c}$$

for the three μ-cases, respectively, where $A = (S_a/S_j + b)/c$. These solutions represent the optimal defence levels as long as $0 \leqslant D^* \leqslant 1$, otherwise $D^* = 0$ or $D^* = 1$. Note also, that Equation 6c gives the optimal solution only if

$$\left(\frac{A}{3}\right)^2 > \frac{1-p}{3p} \tag{7}$$

i.e. if S_j and c are sufficiently small and S_a, b and p are relatively large. Otherwise, the square root

in Equation 6c is undefined. When that is the case the fitness function has no extreme points and one of the boundary solutions ($D^* = 0$ or $D^* = 1$) must represent the optimal solution.

In the absence of variation in the risk of herbivory we conclude for all three cases that the optimal defence level quite intuitively decreases as the defence cost (c) and the probability of escape from herbivory ($1 - p$) both increase. On the other hand, note that the optimal defence level increases as maximum fecundity (b) and the adult to juvenile survival ratio (S_a/S_j) both increase. When Inequality 7 is not fulfilled, the boundary solutions ($D^* = 0$ or 1) prevail and the change in D^* is stepwise.

Variable risk of herbivory

We now assume that the probability of herbivore attack (p) varies stochastically between years. We will analyse the simplest case when p only take two different values, p_1 and p_2 with probabilities k and $1 - k$, respectively. Using Equation 5 and the above assumptions, we may now calculate the expected fitness over a large number of years as the geometrical mean (Schaffer, 1974),

$$\begin{aligned} E[W] &= \left[(S_a + S_j(b - cD))(1 - p_1 + p_1 D^\mu) \right]^k \\ &\quad \left[(S_a + S_j(b - cD))(1 - p_2 + p_2 D^\mu) \right]^{(1-k)} \\ &= (S_a + S_j(b - cD))(1 - p_1 + p_1 D^\mu)^k (1 - p_2 + p_2 D^\mu)^{(1-k)} \end{aligned} \tag{8}$$

In the following, we will focus on two different strategies a plant may adopt in order to maximize fitness when the risk of herbivory varies stochastically among years. The first, which we call 'constitutive' defence is a strategy with a constant optimal defence level with respect to the expected fitness $E[W]$ over all years. The second will be called 'induced' defence, which is an idealized flexible defence strategy. It means that the plant adopts an optimal defence level for each year's level of herbivory, i.e. D_{p1}^* and D_{p2}^*, respectively.

Constitutive defence

Analogous to the deterministic case, we can now find the optimal defence level for the constitutive strategy, D_c^*, by putting $E[W]'(D)$ equal to zero, solving for the optimal D and checking that $E[W]''(D) < 0$. As $\mu = 0.5$ and $\mu = 2$ D_c^* cannot be analytically solved therefore we have to rely on numerical solutions. The expected fitness can then be found by inserting these solutions into Equation 8.

Induced defence

First, we are interested in the optimal defence level for each level of herbivory, i.e. D_{p1}^* and D_{p2}^*. These can be obtained by inserting each herbivory risk level, p_1 and p_2 respectively, into Equations 6a–6c. To be able to compare the defence levels of the induced defence strategy with that of the constitutive defence strategy we calculate the mean optimal defence level for the induced strategy over several years. This is represented by the arithmetic mean of D_{p1}^* and D_{p2}^*

$$E\left[D_i^* \right] = k D_{p_1}^* + (1 - k) D_{p_2}^* \tag{9}$$

where the subscript i denotes the induced defence strategy. Using Equations 6 and 8, we may calculate the expected fitness of the induced defence strategy as

$$\begin{aligned} E\left[W(D_{p_1}^*, D_{p_2}^*) \right] &= \left((S_a + S_j(b - cD_{p_1}^*))(1 - p_1 + p_1(D_{p_1}^*)^\mu \right)^k \\ &\quad \left((S_a + S_j(b - cD_{p_2}^*))(1 - p_2 + p_2(D_{p_2}^*)^\mu \right)^{(1-k)} \end{aligned} \tag{10}$$

Results

In Fig. 1 the optimal defence level is plotted as a function of the risk of herbivory for $\mu = 0.5$, 1 and 2 when p does not vary ($k = 1$). As mentioned previously, the optimal defence level increases as p increases, but differently so for different values of μ. The higher μ is, the steeper the optimal defence function will be. If μ is sufficiently large ($\mu = 2$ in Fig. 1) D^* will be a step function, i.e. at a certain p-value the optimal defence level abruptly changes from zero to one. Increasing S_j or c or decreasing S_a or b would decrease the optimal defence level but also make the curves smoother.

What is then the effect of introducing variation in the risk of herbivory? To be able to deal with a variable risk of herbivory we define the mean and variance of the binomially distributed random variable p as $\bar{p} = kp_1 + (1 - k)p_2$ and $\text{Var}[p] = k(1-k)(p_1 - p_2)^2$, respectively. In Fig. 2 the optimal defence level is plotted as a function of the variation in the risk of herbivory (with $k = 0.5$) for a given mean risk (note that the maximum possible variance in p is $\text{Var}[p] = 0.25$). The optimal defence level for the constitutive defence strategy is either increasing or unaffected as variation in the risk of herbivory increases. Both $\bar{p}$ and μ also influence the optimal defence level (D_c^*). In contrast, the optimal defence level for the induced defence strategy can be differently affected by $\text{Var}[p]$, so that it increases with increasing variation if $\bar{p}$ is low (0.25, Fig. 2a and b), and decreases if $\bar{p}$ is high (0.75, Fig. 2c), except when $\mu = 2$. When the induced defence is increasing with increasing variance the level of the induced defence also exceeds that of the constitutive defence. The opposite is true when the induced defence decreases. In addition to the general patterns in Fig. 2 it is also possible for the optimal defence function of the induced defence strategy to change the direction of the response as the variance in risk of herbivory increases. As shown in Fig. 3 the optimal induced defence first decreases for increasing low variance and then starts to increase as the variance of risk of herbivory further increases. We thus conclude that there is no unambiguous effect of variation in the risk of herbivory on the optimal defence solution without considering mean herbivore pressure ($\bar{p}$), defence efficiency (μ), type of
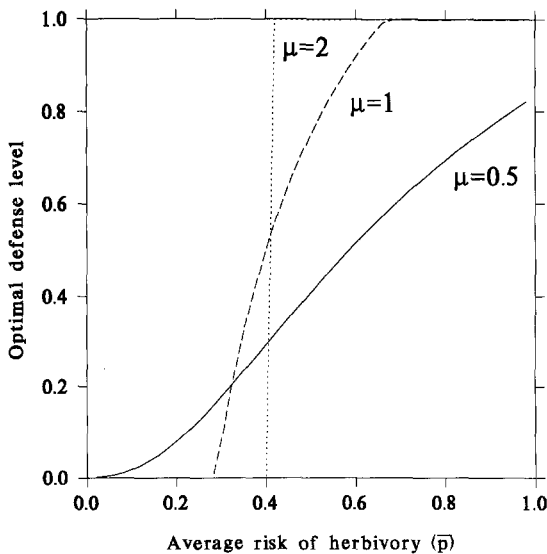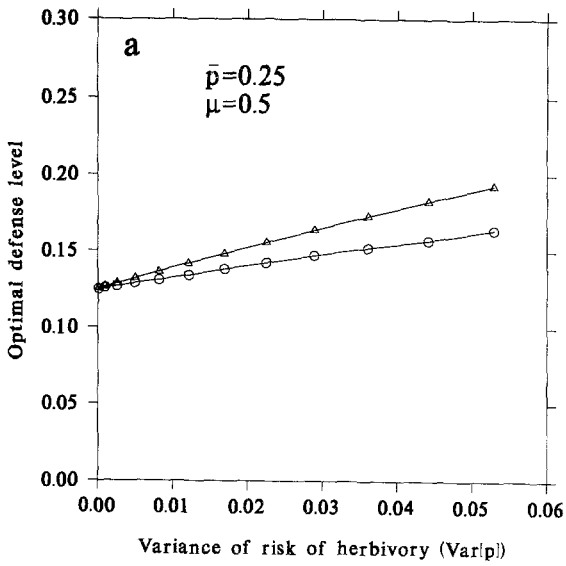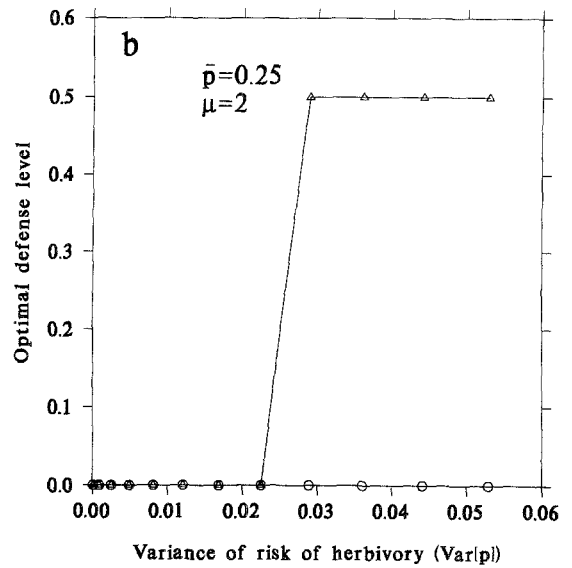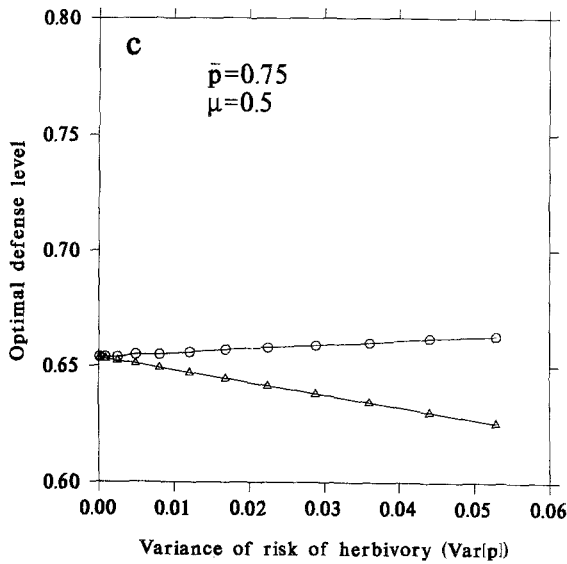

Figure 1. The optimal defence level as a function of $\bar{p}$, the mean risk of herbivory for $\mu = 0.5$, 1 and 2 with $c = 4$, $b = 5$, $S_a = 0.5$, $S_j = 0.1$ and $\text{Var}[p] = 0$, i.e. no variation in risk of herbivory between years. Since $\text{Var}[p] = 0$ the constitutive and induced defence strategies coincide.
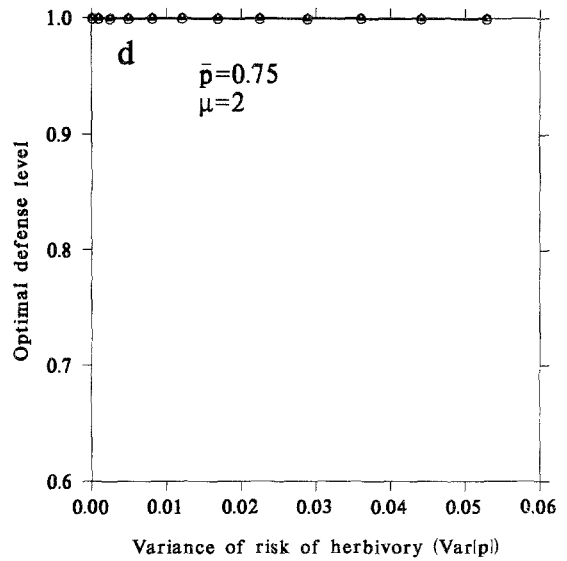
(a)

(b)

(c)

(d)

Figure 2. The optimal defence level as a function of Var[p], the variance in risk of herbivory for(a) $\mu = 0.5$ and (b) $\mu = 2$ when the mean risk of herbivory $\bar{p} = 0.25$ and (c) $\mu = 0.5$ and (d) $\mu = 2$ when the mean risk of herbivory $\bar{p} = 0.75$. Other parameter values as in Fig. 1. (○) constitutive defence strategy. (△) induced defence strategy.

defence strategy (constitutive versus induced) and plant life history (especially juvenile and adult survival).

Not only does the optimal defence level vary with the mean and variance of the risk of herbivory, but also the expected fitness when the defence is optimized. It follows from Equations 8 and 10 that the expected fitness decreases as $\bar{p}$ increases for both the constitutive and the induced strategy. As shown in Fig. 4 the difference in expected fitness between the two strategies increases as the variance in the risk of herbivory increases, the induced defence increasing its
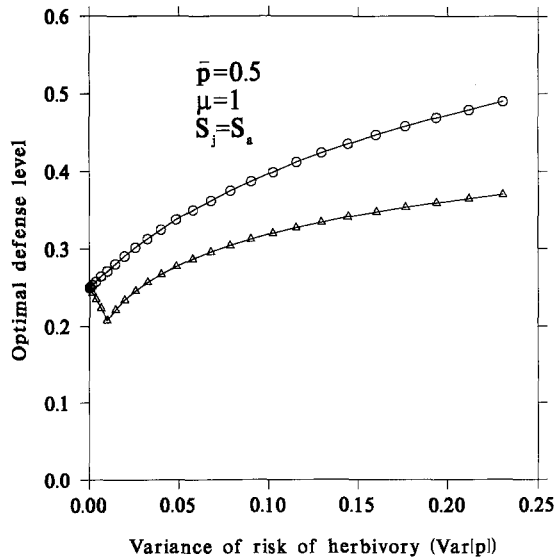

Figure 3. As Fig. 2, but with $\mu = 1.0$, $\bar{p} = 0.5$ and higher juvenile survival, $(S_j = 0.5)$.
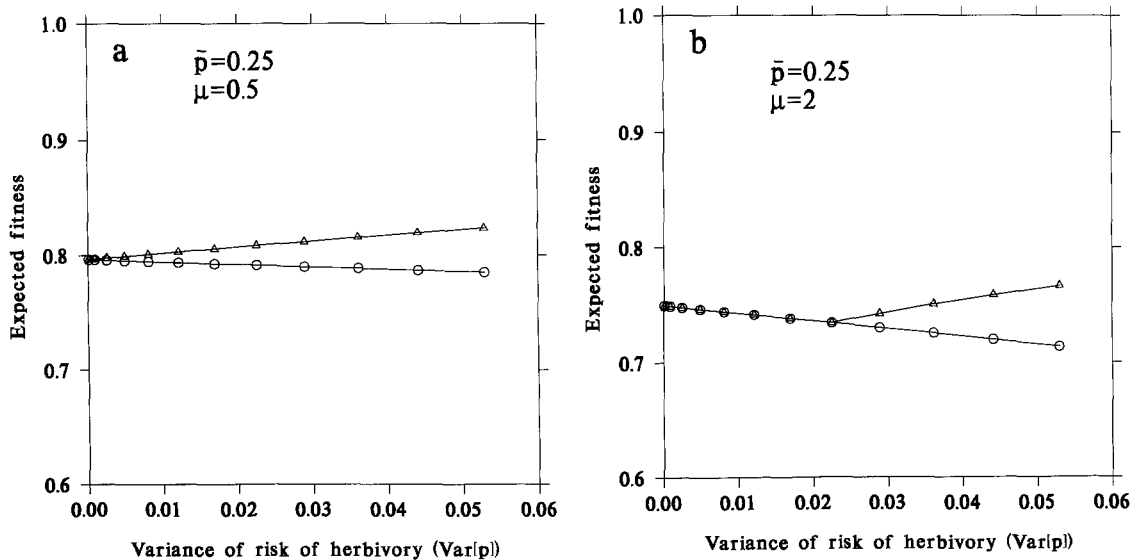

Figure 4. The expected fitness of the constitutive ($\bigcirc$) and induced ($\triangle$) defence strategies as a function of the variance in the risk of herbivory, Var[p], for (a) $\mu = 0.5$ and (b) $\mu = 2$. $\bar{p} = 0.25$. Other parameter values as in Fig. 1.

superiority. Generally the expected fitness of the induced defence strategy increases as the variance of the risk of herbivory increases, while the opposite generally is true for the constitutive defence.

Discussion

The general result that the optimal defence level increases as the risk of deleterious herbivory increases is rather obvious. What is of note and may be considered as counter-intuitive is the effect of μ on the shape of the optimal defence function. If we allow $\mu < 1$ to represent a 'qualitative' defence type, i.e. being efficient if present, but without further strong dosage dependence, then the optimal defence response will be smooth with respect to the risk of herbivory. This is because the qualitative defence is a relatively cost-effective defence, since a small allocation into defence results in a faster than linear increase in the benefit of defence (the survival when encountered by a herbivore), while the cost of the defence only increases linearly. Thus, the qualitative defence is relatively effective when the defence is at a low concentration and should accordingly be produced at relatively lower levels of risk of herbivory. The slope of this optimal defence curve is shallow because the rate of increase in the efficiency decreases as the allocation to defence increases. On the other hand, the 'quantitative' defence ($\mu > 1$) is effective at higher concentrations, making it relatively more expensive to deploy, since the cost is assumed to be linear. Therefore, a quantitative defence should not be deployed unless the risk of herbivory is relatively high. If the risk is sufficiently high to warrant deployment of a defence, a large allocation should be made because the quantitative defence is relatively inefficient at low concentrations. Thus, the plot of D^* for $\mu > 1$ in Fig. 1 is a step function.

In this model we have not considered the possibility that different defences with respect to μ may also be associated with different costs (Coley *et al.*, 1985). However, if we assume that a defence type with $\mu < 1$ is still linear but more costly (i.e. have a higher c) than a defence type with $\mu \geq 1$, that would only reinforce the results discussed above. The optimal defence function for $\mu = 0.5$ in Fig. 1 would then be pushed downwards but retain its smooth shape. For $\mu = 2$ (Fig. 1) the threshold risk of herbivory (when D^* goes from 0 to 1) would be pushed to the left but remain as a step function. This stepwise pattern may, however, be smoothed out if a non-linear cost of defence is assumed. More precisely, if the cost of the quantative defence ($\mu > 1$) is increasing in a convex manner as the allocation to defence increases, then the optimal defence function would be less stepwise. Likewise, for the qualitative defence the optimal defence function would be steeper if the associated cost increased in a concave manner as the allocation to defence increases, thus decreasing the difference between the optimal defence for the quantitative and the qualitative defence types.

The response to variations in the risk of herbivory is markedly different for the constitutive and induced defence strategies. While the constitutive defence strategy always increases or is indifferent to variation, the induced defence strategy may result in both an increase (if the mean risk is low) or decrease (if the mean risk is high) in the optimal defence level as the variation increases. The direction of the response in relation to the mean risk is dependent on the position of the mean risk in relation to the convex and concave parts of $D^*(p)$ (Fig. 1). If $\bar{p}$ is below the inflection point, i.e. in the convex region of the function, then the induced defence will increase as variation increases due to variation in non-linear functions (Jensen's inequality; cf. also Welsh *et al.*, 1988). If $\bar{p}$ is above the inflection point, i.e. in the concave region of the function, the opposite is true. Now, only $\mu = 0.5$ produces a truly sigmoidal function with a mathematically defined inflection point, but the above reasoning will also hold true if the function is more or less stepwise (Fig. 1).

Thus, it is obvious that to predict differences in defence levels between different populations, information about mean herbivore pressure, defence efficiency (approximately qualitative versus quantitative defence), type of defence strategy (constitutive versus induced) and plant life history is necessary. Bryant *et al.* (1989) suggested a co-evolutionary response of North American willows and birches to the strongly cyclic snowshoe hare herbivory, as opposed to the weakly defended shrubs and trees in Finland with no hare cycles. Since cyclicity entails either increased variance in the risk of herbivory, increased mean risk or both, one cannot unambiguously infer the response in defence level.

The life history of a plant may also have an important influence on its optimal defence level. For instance, Loehle (1988) suggested that increased adult longevity in woody plants should be associated with chemical and structural defences. This is exactly what our model predicts (Equations 6a–6c). In fact, increasing adult survival rate (S_a) for a constant juvenile survival (S_j) should lead to an increased optimal defence level for all types of defence strategies. Conversely, plants with high juvenile survival rate in relation to adult survival should generally invest less in a chemical defence. For such plants, the fitness benefit of a defence does not outweigh the fecundity cost since juvenile survival is already relatively high and some contribution to future generations is secured. The most extreme case of this is when $S_a = 0$, i.e. when the plant is annual. Thus, annual plants can be expected generally to have lower defence levels than perennial plants (cf. Herms and Mattson, 1992). This actually corresponds very well with the observations by Feeny (1976) about the apparency of the plants, where perennial plants may be regarded as more apparent than annuals. Zangerl and Bazzaz (1992) have also suggested that plants with a low root : shoot ratio (as is the case for many annual vascular plants) should have less defence per unit weight than those with a high root : shoot ratio. Also, the maximum fecundity (b) affects the optimal level of defence. Increased b compensates for the fecundity costs of defence and, thus, allows an increased optimal defence level.

From Fig. 2b it is clear that if a defence is quantitative $(\mu > 1)$, the mean risk of herbivory is low $(\bar{p} = 0.25)$ and the variation in the risk of herbivory is high, the only defence strategy that can be realized is the induced one. This is because a quantitative defence is less cost-effective. When evaluating the expected fitness of the two different defence strategies one has to note that the constitutive defence is predicted to be less fit than the induced one whenever there is a variation in the risk of herbivory, regardless of the defence efficiency (Fig. 4). The superiority of the inducible defence is, however, exaggerated in our model since we implicitly impose a perfect induction (i.e. perfect knowledge of the changes in the risk of herbivory, without any costly sampling or triggering and without delays in the changes of defence levels when the risk of herbivory changes). If the induced defence is less perfect, the constitutive defence would probably have a selective advantage, at least when the variation in the risk of herbivory is low.

Our model gives qualitative predictions about the level of defence allocation in plants as a result of the mean level and variation in the risk of herbivory. Unfortunately, this risk, and particularly its variation over time is rarely quantified in studies of plant defences. This is also true for recent reviews in the field (e.g. Karban and Myers, 1989; Herms and Mattson, 1992; Zangerl and Bazzaz, 1992; but see Lubchenco and Gains 1981). However, for example, Zangerl and Bazzaz (1992) suggested that the chemical defence in wild parsnip (*Pastinaca sativa*) will be under the direct influence of the probability of attack from herbivores. Lubchenco and Cubit (1980) found strong induced morphological changes in marine annual algae when subjected to a high risk of herbivory. This is in conformity with our predictions, in the sense that plants with induced defence should respond strongly to a high risk of herbivory within that season, although annual plants are generally predicted to have lower defence levels than perennial plants. Moreover, the root : shoot argument of Zangerl and Bazzaz (1992) and the general problem of

resource allocation in plants depending upon environmental resources (Herms and Mattson, 1992) may modify the processes in the simplified world we have modelled. Studies of freshwater and marine invertebrates give strong support for the conclusion that induced defences are expected when the risk of predation is unpredictable and the cost of defence is high (e.g. Clark and Harvall, 1992). For invertebrates both theory and data unambigously point in the same direction. For plants, on the other hand, we still lack good data on the risk of herbviory and its distribution over time, in relation to defence strategies.

In this paper we have outlined an analytical framework to these questions by explicitly considering plant defence in relation to fitness. Many of the predictions remain to be tested and more elaborate and specific models to be developed. Plant life history and adequate fitness measures should be more closely considered in order to understand both the evolution, as well as the dynamic consequences of the myriad of chemical defences found among plants. Our knowledge about plant defence in relation to available resources and individual plant growth is fairly detailed. However, we still do not fully understand how the risk of herbivory, which is fundamental to defence theory in the first place, may influence plant defence and life-history solutions.

Acknowledgements

References

Augner, M., Fagerström, T. and Tuomi, J. (1991) Competition, defense and games between plants. *Behav. Ecol. Sociobiol.* **29**, 231–4.

Briggs, M.A. and Schultz, J.C. (1990) Chemical defense production in *Lotus corniculatus* L. II. Trade-offs among growth, reproduction and defense. *Oecologia* **83**, 32–7.

Bryant, J.P., Tahvanainen, J., Sulkinoja, M., Julkunen-Tiitto, R., Reichardt, P. and Green, T. (1989) Biogeographic evidence for the evolution of chemical defense by boreal birch and willow against mammalian browsing. *Am. Nat.* **134**, 20–34.

Chew, F.S. and Courtney, S.P. (1991) Plant apparency and evolutionary escape from insect herbivory. *Am. Nat.* **138**, 729–50.

Clark, C.W. and Harvell, C.D. (1992) Inducible defenses and the allocation of resources: a minimal model. *Am. Nat.* **139**, 521–39.

Coley, P.D. and Aide, T.M. (1991) Comparison of herbivory and plant defenses in temperate and tropical broad-leaved forests. In *Plant–animal interactions: evolutionary ecology in tropical and temperate regions* (P.W. Price, T.M. Lewinsohn, G.W. Fernandez and W.W. Benson, eds), pp. 25–49. John Wiley & Sons, Inc., New York.

Coley, P.D., Bryant, J.P. and Chapin, F.S., III (1985) Resource availability and plant antiherbivore defense. *Science* **230**, 895–9.

Crawley, M.J. (1988) Herbivores and plant population dynamics. In *Plant population ecology* (A.J. Davy, M.J. Hutchings and A.R. Watkinson, eds), pp. 367–92. Blackwell Scientific Publications, Oxford.

Edelstein-Keshet, L. and Rausher, M.D. (1989) The effects of inducible plant defenses on herbivore populations. 1. Mobile herbivores in continuous time. *Am. Nat.* **133**, 787–810.

Fagerström, T., Larsson, S. and Tenow, O. (1987) On optimal defense in plants. *Funct. Ecol.* **1**, 73–81.

Feeny, P.P. (1976) Plant apparency and chemical defense. Biochemical interactions between plants and insects. In *Recent advances in phytochemistry* (J.W. Wallace and R.L. Mansell, eds) Vol. 10, pp. 1–40. Plenum Publishing, New York.

Gulmon, S.L. and Mooney, H.A. (1986) Costs of defense and their effects on plant productivity. In *On the economy of plant form and function* (T.J. Givnish, ed.), pp. 681–98. Cambridge University Press, Cambridge.

Harper, J.L. (1977) *Population Biology of Plants*. Academic Press, Oxford.

Harvell, C.D. (1990) The ecology and evolution of inducible defenses. *Q. Rev. Biol.* **65**, 323–40.

Haukioja, E. and Neuvonen, S. (1985). Induced long-term resistance of birch foliage against defoliators: defensive or incidental? *Ecology* **66**, 1303–8.

Havel, J.E. (1987) Predator-induced defenses: a review. In *Predation: direct and indirect impacts on aquatic communities* (W.C. Kerfoot and A. Sih, eds), pp. 263–78. University Press of New England, Hanover, NH.

Herms, D.A. and Mattson, W.J. (1992) The dilemma of plants: to grow or defend. *Q. Rev. Biol.* **67**, 283–335.

Karban, R. and Myers, J.H. (1989) Induced plant responses to herbivory. *Ann. Rev. Ecol. Syst.* **20**, 331–48.

Loehle, C. (1988) Tree life history strategies: the role of defenses. *Can. J. Forest Res.* **18**, 209–22.

Louda, S.M., Keeler, K.H. and Holt, R.D. (1990) Herbivore influences on plant performance and competitive interactions. In *Perspectives on plant competition* (J.B. Grace and D. Tilman, eds), pp. 413–44. Academic Press, San Diego.

Lubchenco, J. and Cubit, J. (1980) Heteromorphic life histories of certain marine algae as adaptations to variations in herbivory. *Ecology* **61**, 676–87.

Lubchenco, J. and Gains, S.D. (1981) A unified approach to marine plant-herbivore interactions. I. Populations and communities. *Ann. Rev. Ecol. Syst.* **12**, 405–37.

Lundberg, P. and Åström, M. (1990) Low nutritive quality as a defense against optimally foraging herbivores. *Am. Nat.* **135**, 547–62.

Oksanen, L. (1990) Predation, herbivory, and plant strategies along gradients of primary productivity. In *Perspectives on plant competition* (J.B. Grace and D. Tilman, eds), pp. 445–74. Academic Press, San Diego.

Rhoades, D.F. (1979) Evolution of plant chemical defense against herbivores. In *Herbivores. Their interactions with secondary plant metabolites* (G.A. Rosenthal and D.H. Janzen, eds), pp. 3–54. Academic Press, New York.

Rhoades, D.F. and Cates R.G., (1976) Toward a general theory of plant antiherbivore chemistry. In *Biochemical interactions between plants and insects. Recent advances in phytochemistry* (J.W. Wallace and R. Mansell, eds), Vol. 10, pp. 205–38, Plenum Publishing, New York.

Riessen, H.P. (1992) Cost–benefit model for the induction of an antipredator defense. *Am. Nat.* **140**, 349–62.

Schaffer, W.M. (1974) Optimal reproductive effort in fluctuating environments. *Am. Nat.* **108**, 783–90.

Simms, E.L. (1992) Costs of plant resistance to herbivory. In *Plant resistance to herbivores and pathogenes. Ecology, evolution and genetics* (R.S. Fritz and E.L. Simms, eds), pp. 392–425. University of Chicago Press, Chicago.

Welsh, A.H., Peterson, A. T and Altmann, S.A. (1988) The fallacy of averages. *Am. Nat.* **132**, 277–88.

Zangerl, A.R. and Bazzaz, F.A. (1992) Theory and pattern in plant defense allocation. *Am. Nat.* **132**, 363–91.