

Competition, defense and games between plants

Magnus Augner, Torbjörn Fagerström, and Juha Tuomi

Department of Ecology, Theoretical Ecology, University of Lund, Ecology Building, S-223 62 Lund, Sweden

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Summary. Coexistence of defended and undefended plants may be maintained by herbivory. In the present paper this phenomenon is analyzed by means of evolutionary game theory. The plants in the model play either a defensive or a non-defensive strategy and they interact indirectly: when a plant is grazed its competitive ability decreases, because of this a neighboring plant makes a profit. The solution to the game leads to three qualitatively different cases depending on whether the profit is equal for the two strategies, defended and undefended, or if the profit is higher for one type than for the other. When the results are applied to intra-specific interactions, the model predicts that polymorphic populations should be expected only under certain specific conditions. When the results are applied to inter-specific interactions, the model predicts either stable coexistence, i.e., increased diversity, or a paradoxical situation without increased diversity.

Introduction. Herbivory is often considered to be an important factor governing the dynamics of plant populations and communities (e.g., Rosenthal and Janzen 1979; Crawley 1983; Brown and Allen 1989). One aspect of this is that herbivory can lead to increased species diversity, allowing species with, e.g., different levels of defense or different competitive abilities to coexist (e.g., Harper 1977; McNaughton 1979; Belsky 1986). Many field studies and experiments (reviewed in, e.g., Crawley 1983) support this notion.

A related phenomenon on the intraspecific level is found in plant populations where individuals with different kinds, or levels, of anti-herbivore defenses coexist. One of the most well-known examples is *Trifolium repens*, where a cyanogenic morph coexists with an undefended one (e.g., Dirzo and Harper 1982; Burgess and Ennos 1987). Other examples are *Cecropia peltata*, where individuals have different levels of tannins (Coley 1986),

Pinus ponderosa, which has various concentrations of terpenes (Edmunds and Alstad 1978), and *Rubus bogotensis*, which has two types of individuals with different kinds of defenses, hardened cuticle and trichomes, respectively (Björkman and Andersson 1990).

In the present paper we attempt a game theoretical approach to the coexistence of plants with different levels of defense. We analyze conditions for stable coexistence in a game where the plants are physiologically independent and where individuals are endowed with given levels of defense. We assume that individuals compete for the same limited resources (e.g., mineral nutrients, space) and that herbivory reduces the competitive capacity of the attacked plants. Thus, herbivory triggers indirect interactions between physiologically independent individuals, in that it leads to benefits to a grazed plant's neighbors (see e.g., White 1973; Harper 1977; Bentley and Whittaker 1979; Fowler and Rausher 1985; Rai and Tripathi 1985).

Theory

We consider a game played between two units, a player and its opponent. Each unit always plays either of two strategies, defensive or non-defensive. The proportions of the two strategies in the population are p and $(1-p)$, respectively. The pay-off matrix (Fig. 1) prescribes that defense against herbivory confers an expenditure (C) and so does herbivory (H). When an opponent is grazed, and the player is not, the latter will make a profit because of the opponent's decreased competitive ability. V_D and V_{ND} are the profits made by defensive and non-defensive players, respectively; m stands for the probability of herbivory. The parameters of the game can assume the following values:

$$0 \leq C, H, V_D, V_{ND} \quad (1a)$$

$$V_{ND} \leq H \quad (1b)$$

$$0 \leq m, p \leq 1 \quad (1c)$$

The reason why the profit made by a non-defensive player (V_{ND}) has to be smaller than, or equal to, the cost of herbivory (H) is that these two components are coupled (without H , no V_{ND}) since both affect the same strategy. The cost for herbivory can be divided into two parts: a direct loss of biomass and an indirect loss, in the form of decreased competitive capacity. The profit

		Opponent	
		D	ND
Player	D	-C	$mV_D - C$
	ND	-mH	$mV_{ND} - mH$

Fig. 1. Pay-off matrix for a game between two units always playing either of the two strategies defensive (D) and non-defensive (ND). The matrix shows the player's pay-off. C =cost of defense; H =cost of herbivory; m =probability of herbivory; V_D =profit made by a defensive player when a non-defensive opponent is grazed; V_{ND} =profit made by a non-defensive player when a non-defensive opponent is grazed

(V_{ND}) stems from the latter component, the indirect loss, and, therefore, cannot be larger than that part of the cost for herbivory.

Let W represent the player's fitness. Then, from Fig. 1 we have

$$W_D = p(-C) + (1-p)(mV_D - C) \quad (2a)$$

$$W_{ND} = p(-mH) + (1-p)(mV_{ND} - mH) \quad (2b)$$

If we treat W as a function of p , Eqs. 2a, b can be graphically visualized as straight lines, representing the fitness of defenders and non-defenders, respectively (Fig. 2). If the two lines intersect, there is a value of p where the two strategies enjoy the same fitness, i.e., $W_D = W_{ND}$.

There are three qualitatively different cases depending on whether $V_{ND} = V_D$, $V_{ND} < V_D$, or $V_D < V_{ND}$. The derivatives of Eqs. 2a, b show that when $V_{ND} = V_D$, the lines representing fitness do not intersect (Fig. 2a), whereas they do if $V_{ND} \neq V_D$. When $V_{ND} < V_D$ the line representing the fitness of defensive players (W_D) will have a steeper negative slope than the line representing the fitness of non-defensive players (W_{ND} ; Fig. 2b). Thus, in this case the intersection of the lines represents a point of stable equilibrium. The reverse prevails when $V_D < V_{ND}$. In that case the intersection of the lines represents a point of unstable equilibrium (Fig. 2c).

Here, we introduce a new parameter

$$\Delta V = V_D - V_{ND} \quad (3)$$

When $\Delta V = 0$ the population does not have any polymorphic state. From Eqs. 2a, b; 3 we get the solution to this case:

$$m = \frac{C}{H} \quad (4)$$

From Eqs. 2a, b; 3 we also find that when $\Delta V \neq 0$, the equilibrium point is given by

$$p^* = \frac{m(H + \Delta V) - C}{m\Delta V} \quad (5)$$

which is stable if $0 < \Delta V$ and biologically feasible (i.e., satisfying $0 < p^* < 1$) for

$$\frac{C}{H + \Delta V} < m < \frac{C}{H} \quad (6)$$

When $\Delta V < 0$ the equilibrium point is unstable. Moreover, because ΔV is now a negative quantity, the condition 6 is transformed into two conditions defining areas in parameter space that can never overlap:

$$\frac{C}{H + \Delta V} < m \quad (7a)$$

$$m < \frac{C}{H} \quad (7b)$$

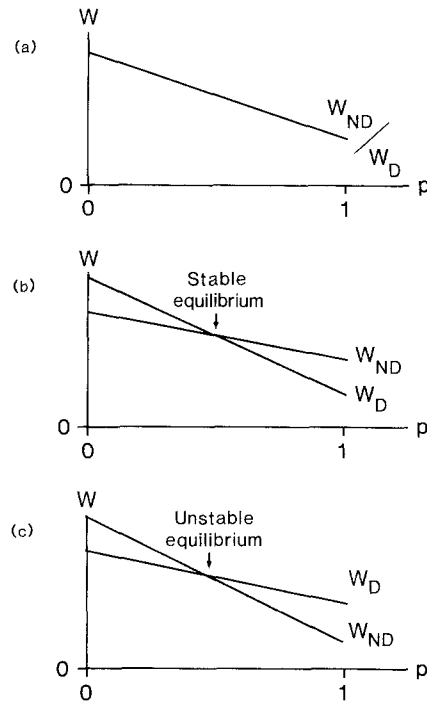


Fig. 2a-c. Fitness (W) of the defensive and non-defensive strategies, W_D and W_{ND} , as functions of the proportion of defenders in the population (p). Other symbols as in Fig. 1. Three cases are shown, (a) $0 = \Delta V$, (b) $0 < \Delta V$, (c) $\Delta V < 0$, where $\Delta V = V_D - V_{ND}$

Interpretation and discussion

The solution to our model gives us three qualitatively different cases (Fig. 3a-c). Which case we get depends on whether there is any difference or not between defended and undefended individuals with respect to the value of the profit they enjoy when a neighbor is grazed.

The assumption that the value of the profit may be different for the two strategies requires that they have different abilities in transforming the resources gained into the appropriate fitness currency (Fig. 4). When there is no such difference between them, i.e., they respond in exactly the same way, we find that no coexistence between defended and undefended individuals is possible (Fig. 3a). Thus, the solution to this case is a pure ESS, evolutionarily stable strategy (Maynard Smith 1982). Which of the two strategies that will be the ESS is independent of the initial frequencies of the strategies in the population (Fig. 2a).

If the profit is more valuable to defenders than to non-defenders, a stable coexistence between the two types is possible (Fig. 2b). This means that the solution can be an evolutionarily stable population, ESP (sensu Cresswell and Sayre 1991). However, if the probability of herbivory lies above or below the critical values defined by the i - and ii -isoclines, then defensive and non-defensive, respectively, will be pure ESS's (Fig. 3b). No ESP is possible in the last case, i.e., when the profit is more valuable to non-defenders than to defenders (Fig. 2c). The biologically feasible solution here is a pure ESS, just as in the first case. However, the solution in this case is a paradoxical one. It is paradoxical in the sense that the parameter space for the non-defensive

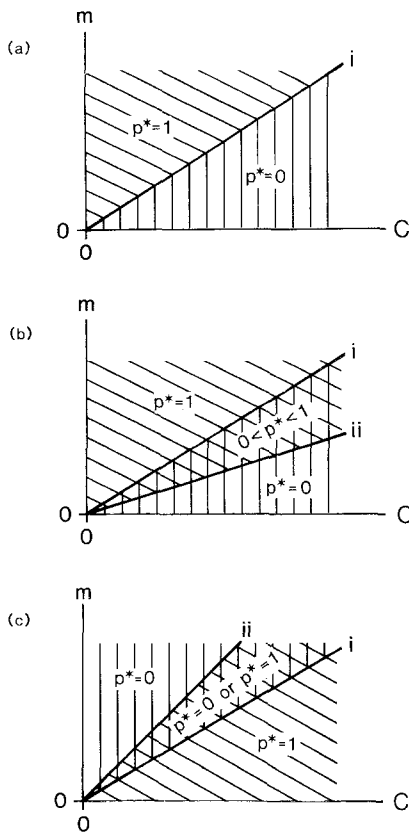


Fig. 3a-c. The graphical solutions in the $m-C$ plane to the game for the three cases (a) $0 = \Delta V$, (b) $0 < \Delta V$, (c) $\Delta V < 0$. Symbols as in Fig. 1. The values of p in the figures are truncated to fulfill the biological condition that the proportion of a phenotype in the population can not be larger than 1 or smaller than 0. The i - and ii -isoclines correspond to $m = C/H$ and $m = C/(H + \Delta V)$, respectively

strategy increases with increasing probability of herbivory and the parameter space for the defensive strategy increases with increasing cost of defense (Fig. 3c). For sufficiently high and sufficiently small probabilities of herbivory, the ESS is independent of initial frequencies. However, for intermediate levels of herbivory, which of the strategies that will be the ESS depends on the initial frequencies of the two strategies in the population (Fig. 2c).

Our approach does not require that the two types, defenders and non-defenders, are of the same species but only that they compete for the same limited resources and that they are potentially attacked by the same herbivores. However, if our model is to be applied to interspecific interactions, it is required that the two types are exchangeable, such that an increase in the frequency of one type results in a corresponding decrease in the other, since the sum of the two frequencies has to be one.

The biological interpretations of our results do depend, however, on whether we envisage intra- or interspecific interactions (Fig. 5). In the case of intraspecific interactions, one question is whether the model predicts an evolutionarily stable polymorphic state and if so, under what conditions? It follows from Ineq 6 that an ESP is possible only if $0 < \Delta V$, i.e., if the defended morph

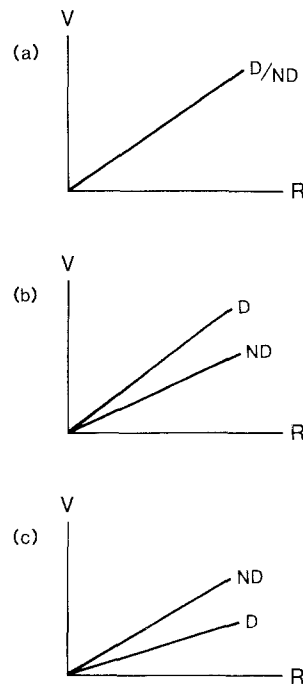


Fig. 4a-c. Three possible relations between the two strategies with respect to their abilities to use resources gained when a neighbor is grazed. R is the amount of resources gained by the plant while V is the fitness-related profit. Three cases are shown, (a) $0 = \Delta V$, (b) $0 < \Delta V$, (c) $\Delta V < 0$. Symbols as in Fig. 1

enjoys a higher profit than the undefended one when a neighbor is grazed. This would be the case, e.g., if the defense system itself is genotypically or phenotypically coupled with other components of the plant's physiology such that a defended individual is also better at utilizing, e.g., an increased amount of available nitrogen in the soil. If there is no such within-species difference with respect to indirect responses to grazing, then our model does not allow an ESP, the prediction being that the population should then be monomorphic (Fig. 5). However, if the grazing pressure is different in different areas, the population may still be polymorphic on a regional scale. This can be seen from Fig. 3a: to a given cost of defense there are two corresponding pure ESS's, viz., all individuals being defended (which will prevail at a high grazing pressure) and all being undefended (which will prevail at a low grazing pressure).

In the case of interspecific interactions, the question is whether the model predicts stable situations with high diversity. In contrast to the intraspecific case, the basic assumption here must be that it is very likely that the two types, being different species, do not have the same physiological requirements. Thus, we consider it likely that the general condition $\Delta V \neq 0$ holds in the interspecific case. Moreover, we see no reason why the specific condition required for stable coexistence, i.e., $0 < \Delta V$, should not hold in many cases. Accordingly, our prediction is that herbivory should often enhance interspecific diversity, the condition being that defended species are better than undefended ones in utilizing resources that are released subsequent to a grazing episode (Fig. 5). The biological explanation for this is that part of the defender's cost of defense is compensated for by the profit made when a neighbor is grazed. Thus, the defensive strategy can "invade" part of parameter space of the non-defensive strategy (Fig. 3b). If the profit did

	INTRA	INTER
$\Delta V = 0$	Monomorphy	Low diversity
$0 < \Delta V$	Polymorphy (stable)	High diversity (stable)
$\Delta V < 0$	Monomorphy (polymorphic state unstable)	Low diversity (coexistence unstable)

Fig. 5. Summary of predictions of the present model to intra- and interspecific interactions. Symbols as in Fig. 1

not exist, defenders would be outcompeted by non-defenders in this region.

The other possible case of interspecific interactions, $\Delta V < 0$, is unstable and would render lower diversity (Fig. 5). It is quite interesting that this case, with a paradoxical solution, is not only *a priori* possible, but as probable as the previous one. The biological interpretation of this case is that the profit made by non-defenders compensates for part of their cost of herbivory. This allows non-defenders to "invade" the region of parameter space where the cost of defense is lower than the cost of herbivory ($C < mH$). When m is sufficiently small we have a situation where the profit is too small to compensate for the cost of herbivory, and since $C < mH$ the defense strategy is the pure ESS. When m is sufficiently large, the defense strategy cannot outcompete the non-defense strategy, because of the profit. Then, non-defensive is the pure ESS (Fig. 3c). The paradox arises because the grazed strategy (non-defensive) enjoys a larger grazing-mediated profit than the non-grazed strategy (defensive).

In conclusion we have shown that stable coexistence of different defense strategies may be maintained by indirect responses to grazing. Such a coexistence is possible even without any specific assumptions concerning the behavior of herbivores or their population dynamics.

Obviously these factors do influence the defense strategies of plants and they are highly interesting areas for further analyses.

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