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The Shape of the Curve of Tolerance to Herbivory

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ABSTRACT

Perhaps the most questioned aspect of defoliation experiments that fail to detect negative effects of damage is whether the amount of tissue removed was appropriate. Despite this implicit acknowledgment that low levels of damage may not cause a detectable change in plant fitness, many studies of plant-herbivore interactions assume that plant fitness decreases with damage following a simple linear relation. However, the (apparently accepted) absence of a fitness effect of herbivory at low levels of damage implies that the reduction in fitness either starts at a damage threshold greater than zero (a truncated fitness function), or follows a convex (inverted J-shaped), curvilinear function. The possibility of a convex tolerance function is highly relevant to herbivory studies because it modifies the expectation that damage should invariably cause a decrease in fitness, and opens the possibility that damage could have positive or null effects on plant fitness depending on the exact shape of the function for a particular plant-herbivore system. Here, we expand on a previously published model to show that the tolerance function is more likely to be curvilinear because of the way in which the relative growth rate changes with damage. Finally, we argue that a convex tolerance function would favour the evolutionary stability of a mixed defence system, characterized by simultaneous allocation of resources to resistance and tolerance traits.

Keywords: biomass, compensation, costs of damage, over-compensation, relative growth rate

INTRODUCTION

Tolerance to herbivory has been defined as the capacity of plants to reduce the negative effects of herbivory on fitness (Strauss and Agrawal 1999; Stowe *et al*. 2000). The concept of tolerance is tightly linked to that of compensation, which can be defined as the physiological capacity to recover from damage and continue to perform vegetative and reproductive functions (McNaughton 1983). Depending on whether individuals damaged by herbivores (D) perform better or worse than those in the undamaged state (U), compensation has been divided into under-compensation ($W_D<W_U$), equal compensation ($W_D=W_U$), and over-compensation ($W_D>W_U$) (where W is a measurement of performance; Maschinski and Whitham 1989; Strauss and Agrawal 1999). For evolutionary biologists, the most interesting measure of performance is individual fitness. Evidently, it is impossible to measure compensation to a range of damage levels on a single individual. Thus, the response to different levels of damage must be measured as a norm of reaction, and if the main variable of interest is fitness, the measurement becomes, indeed, tolerance (Strauss and Agrawal 1999; Simms 2000).

In general, herbivory is expected to have a detrimental effect on plant fitness (Crawley 1983; Belsky 1986; Marquis and Fritz 1992). However, the actual effect of herbivory on plant fitness depends on a variety of factors including resource availability, the amount and kind of tissue removed, the timing of damage with respect to plant development, the pattern of damage with respect to vascular connections, and growth form (Whitham *et al*. 1991; Hawkes and Sullivan 2001; Avila-Sakar *et al*. 2003; Avila-Sakar and Stephenson 2006; Wise 2007). Still, the magnitude of the effect of damage on plant fitness is usually attributed to the amount of tissue removed (intensity of damage) in a rather simplistic fashion: the more the damage, the greater the detrimental effect. The assumption of a simple linear decrease of fitness with damage has appeal not only because of its simplicity, but more importantly because it is difficult to imagine how a certain genotype could achieve the same or greater fitness when it incurs the direct costs of tissue damage than when it does not (Bloom *et al*. 1985; Belsky 1986, Juenger and Bergelson 2000).

Curiously, experiments that fail to detect negative effects of damage on fitness-related traits frequently elicit questions about whether the amount of tissue removed was appropriate, as though there is an implicit acceptance that a small amount of damage has no negative fitness consequences. However, if the tolerance function (the relation between fitness and the intensity of damage) is a simple linear decreasing function, then detecting the presumably small negative fitness changes that occur in response to small amounts of damage should simply be a matter of achieving the appropriate statistical power. On the other hand, if the true fitness function is truncated or convex (inverted J-shaped or characterized by a decreasing slope), the likelihood of detecting negative fitness changes in response to damage should increase with the intensity of damage. Moreover, positive effects of damage are not expected under a simple linear, decreasing fitness function, but positive or null effects of damage on plant fitness are likely to occur under a convex tolerance function, depending on its exact shape. The possibility of a convex tolerance function is highly relevant to studies of the evolutionary ecology of plant-herbivore interactions because it modifies the main expectation that damage, even in small amounts, should invariably cause a decrease in fitness, and consequently, it has implications for the stability of a mixed defence system (see below).

Of the few studies that explicitly acknowledge that the tolerance function may be curvilinear (e.g., Dyer 1975; Hilbert *et al*. 1981; McNaughton 1983; Pedigo *et al*. 1986; Dyer *et al*. 1993; Pilson 2000; Fornoni *et al*. 2004), only Hilbert *et al*. (1981) provide a detailed model of the physiological mechanisms occurring at the individual plant level that underlie such curvilinear response: plant growth is allometric, and tolerance is tightly linked to the capacity of plants to regrow after tissue loss. Here we revisit the model developed by Hilbert *et al*. (1981) to show that the tolerance function is not necessarily a simple, straight, declining linear function.

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Original Research Paper

THE GROWTH RATE MODEL

Hilbert *et al.* (1981) provide a model (hereafter, the growth rate model or GRM, after Hicks and Turkington 2000) that explores the circumstances under which net primary productivity of grazed plants may surpass or equate that of ungrazed ones. The model is set up through the formulation of mathematical expressions for biomass production on an ungrazed plant:

$$P = S_1\left(e^{\bar{R}\Delta t} - 1\right) \tag{1}$$

and on a grazed plant:

$$\tilde{P} = S_1\left(1 - G\right)\left(e^{\bar{R}_g\Delta t} - 1\right) \tag{2}$$

where S_1 is the shoot mass at time t_1, $\bar{R}$ is the mean relative growth rate (RGR) of an ungrazed plant over the time period $\Delta t = t_2 - t_1$, $\bar{R}_g$ is the mean RGR of a grazed plant over the same period, and G is the proportion of shoot mass removed by grazers ($0 < G < 1$).

These equations can be used to find the changes in relative growth rate that allow these two quantities to be equal. The only parameter allowed to differ between the production of grazed and ungrazed plants for these quantities to be equal is $\bar{R}_g$, which is a function of G. Following the same logic as Hilbert *et al.* (1981), we solve for $\bar{R}_g$ in order to obtain the RGR needed by the grazed plant to attain equal production to that of an ungrazed plant, and we call this quantity $\hat{\bar{R}}_g$ because it is a special case of $\bar{R}_g$:

$$\hat{\bar{R}}_g = \frac{1}{\Delta t}\ln\left(\frac{e^{\bar{R}\Delta t} - G}{1 - G}\right) \tag{3}$$

In other words, $\hat{\bar{R}}_g$ is the relative growth rate needed by a grazed plant to achieve equal compensation, but rather than a single value, $\hat{\bar{R}}_g$ is a production isoline in three dimensions because it is a function of Δt, G and $\bar{R}$. It must be noted that $\hat{\bar{R}}_g$ is a curvilinear function of the grazing intensity because the term $1 - G$ appears in the denominator (Fig. 2 in Hilbert *et al.* 1981). For this same reason, (3) has no real solution for $G = 1$, which means that a completely grazed plant has no way of achieving equal compensation — a biologically realistic premise.

Hilbert *et al.* (1981) proceeded to explore the change in RGR needed for production of a grazed plant to remain equal to that of an ungrazed plant ($\Delta\bar{R} = \hat{\bar{R}}_g - \bar{R}$, which is a special case of the more general equation $\Delta\bar{R} = \hat{\bar{R}}_g - \bar{R}_g$), and they also examined the consequences for biomass production of other possible changes in growth rate that plants could have in response to grazing (see below). An analysis of the changes in production (ΔP) that result from damage is particularly relevant to the study of the shape of the tolerance function because final biomass (equivalent to production) can been used as a surrogate of fitness in studies of compensation and tolerance (McNaughton 1983). While final biomass is not equivalent to individual fitness, it has been shown to be positively, and sometimes strongly correlated with other more direct measures of fitness such as fruit or seed production (Solbrig 1981; Aarssen and Taylor 1992; Weiner *et al.* 2009 and references therein).

Here, we use (1) and (2) to calculate ΔP for the same three possible changes in growth rate examined by Hilbert *et al.* (1981) so as to explore the different shapes that this function can take using the first and second derivatives where necessary. The calculation of ΔP from (1) and (2) provides a comparison of the production of grazed and ungrazed plants subjected to a certain grazing intensity. If P is a reasonably good estimate of fitness, when applied to a group of related plants, the relationship between ΔP and G is, in essence, a tolerance curve where $\Delta P = 0$, $\Delta P > 0$, and $\Delta P < 0$ indicate, respectively, equal compensation, over-compensation, and under-compensation. The three cases examined by Hilbert *et al.* (1981) correspond to three possible ways in which the RGR can change in response to varying intensities of damage. In order to simplify the equations, we have taken $\Delta t = 1$, so these particular equations indicate the change in production over one time unit. Also, for simplicity we have chosen very simple functions of G for $\bar{R}_g$ that correspond to the three cases shown in Fig. 3 of Hilbert *et al.* (1981).

For all three cases, $\Delta P = \tilde{P} - P$.

(a) ΔP for $\bar{R}_g = \bar{R} + G$: the growth rate changes positively in response to damage.

$$\begin{aligned}\Delta P &= S_1\left(1 - G\right)\left(e^{\bar{R}+G} - 1\right) - S_1\left(e^{\bar{R}} - 1\right)\\ &= S_1\left[G + \left(1 - G\right)\left(e^{\bar{R}+G}\right) - e^{\bar{R}}\right]\end{aligned} \tag{4}$$

$$\Delta P' = -S_1\left(-1 + Ge^{\bar{R}+G}\right)$$
$$\Delta P'' = -S_1 e^{\bar{R}+G}(G+1)$$

(b) ΔP for $\bar{R}_g = \bar{R}$: the growth rate does not change in response to damage.

$$\begin{aligned}\Delta P &= S_1(1-G)\left(e^{\bar{R}}-1\right) - S_1\left(e^{\bar{R}}-1\right)\\ &= -S_1 G\left(e^{\bar{R}}-1\right)\end{aligned} \tag{5}$$

(c) ΔP for $\bar{R}_g = \bar{R} - G$: the growth rate changes negatively in response to damage.

$$\begin{aligned}\Delta P &= S_1(1-G)\left(e^{\bar{R}-G}-1\right) - S_1\left(e^{\bar{R}}-1\right)\\ &= S_1\left[G + (1-G)\left(e^{\bar{R}-G}\right) - e^{\bar{R}}\right]\end{aligned} \tag{6}$$

$$\Delta P' = S_1\left[1 + e^{\bar{R}-G}(G-2)\right]$$
$$\Delta P'' = -S_1 e^{\bar{R}-G}(G-3)$$

In (a), the second derivative is always negative, so the function is convex (**Fig. 1**). Positive values of ΔP occur for a larger range of values of G at small $\bar{R}$'s (**Fig. 2**). For case (b), ΔP is clearly a simple linear function with slope $-S_1\left(e^{\bar{R}}-1\right)$, because both S_1 and the term in brackets are constants with respect to G. Thus, the maximum value of ΔP is zero, at $G = 0$ (**Fig. 1**). For (c), the second derivative will always be positive because G–3 is always negative for $0 < G < 1$. Therefore, ΔP is a concave function (**Fig. 1**).

The three cases of $\bar{R}_g$ used for the above calculations are particular cases of the more general equation: $\bar{R}_g = \bar{R} + KG$. It can be shown that for $K > 0$, as K increases, the range of G for which overcompensation occurs ($\Delta P > 0$) increases too, as the $\bar{R}_g$ line will be above the isoline for most values of G (**Fig. 3**). Increasing K also changes the shape of the function, making it sigmoid as it approaches its maximum point (**Fig. 3**). Whether we see a predominance of the effect of K or R depends on the relative value of these two parameters (data not shown). For $K \leq 0$, there are no qualitative changes compared to the particular cases (b) and (c) analysed above.

We can also calculate ΔP as the difference between the production of a grazed plant (with a given $\bar{R}_g$) and that of a grazed plant that compensates equally: $\Delta P = \tilde{P} - \hat{\tilde{P}}$

where $\tilde{P}$ is the production of a plant that compensates equally.

(a') ΔP for $\bar{R}_g = \bar{R} + G$

$$\begin{aligned}\Delta P &= S_1(1-G)\left(e^{\bar{R}+G}-1\right) - S_1(1-G)\left(e^{\hat{\bar{R}}_g}-1\right)\\ &= S_1(1-G)\left(e^{\bar{R}+G} - e^{\hat{\bar{R}}_g}\right)\end{aligned} \tag{7}$$

(b') ΔP for $\bar{R}_g = \bar{R}$

$$\begin{aligned}\Delta P &= S_1(1-G)\left(e^{\bar{R}}-1\right) - S_1(1-G)\left(e^{\hat{\bar{R}}_g}-1\right)\\ &= S_1(1-G)\left(e^{\bar{R}} - e^{\hat{\bar{R}}_g}\right)\end{aligned} \tag{8}$$

(c') ΔP for $\bar{R}_g = \bar{R} - G$

$$\begin{aligned}\Delta P &= S_1(1-G)\left(e^{\bar{R}-G}-1\right) - S_1(1-G)\left(e^{\hat{\bar{R}}_g}-1\right)\\ &= S_1(1-G)\left(e^{\bar{R}-G} - e^{\hat{\bar{R}}_g}\right)\end{aligned} \tag{9}$$

Numerically, both calculations of ΔP are equivalent because a plant that compensates equally has, by definition, the same production as an ungrazed plant regardless of the intensity of grazing experienced by the grazed plant ($0 \leq G < 1$). However, the plant that compensates equally is incurring a cost of compensation. This cost is reflected in $\Delta\bar{R}$, which increases disproportionately with grazing intensity (Hilbert *et al.* 1981). Calculating $\Delta\bar{R}$ for the three cases above gives:

(A) $\Delta\bar{R}$ for $\bar{R}_g = \bar{R} + G$

$$\Delta\bar{R} = \ln\left(\frac{e^{\bar{R}\Delta t} - G}{1-G}\right) - \bar{R} - G \tag{10}$$

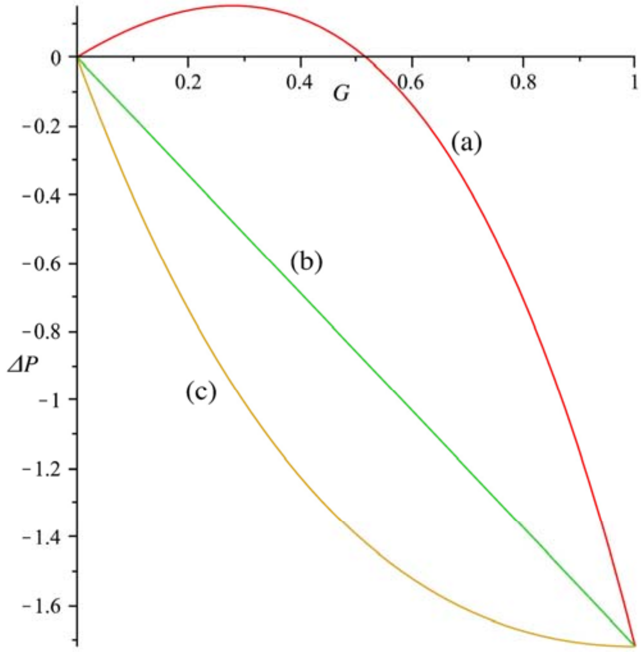

Fig. 1 Change in biomass production in response to grazing intensity (Δ*P*) for plants in three cases. (**A**) Adjust their relative growth rate in direct proportion to the intensity of grazing; (**B**) do not change their relative growth rate in response to grazing; and (**C**) suffer a decrease in relative growth rate proportional to the intensity of grazing ($S_1 = 1, \bar{R} = 1$).

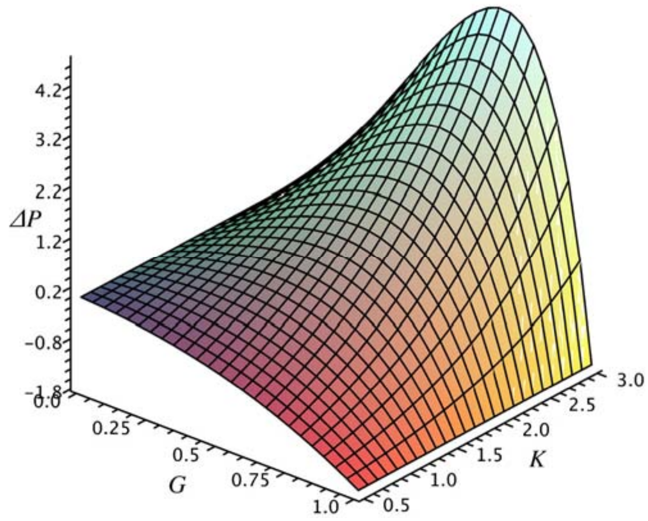

Fig. 3 Change in biomass production in response to grazing intensity for several positive slopes in the response of growth rate to grazing (*K* = 0.5 to 3), and $\bar{R}$ = 1. Greater values of *K* signify greater increases in RGR in direct proportion to grazing intensity ($S_1 = 1$).

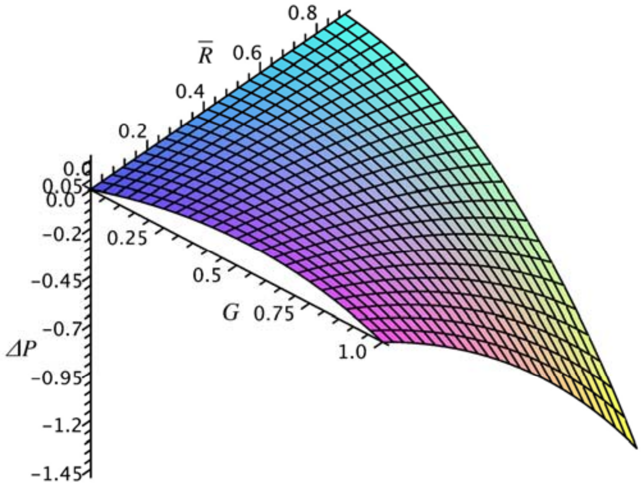

Fig. 2 Change in biomass production in response to grazing intensity for several values of mean relative growth rate ($\bar{R}$ = 0.1 to 0.9), and *K* = 0.5. Greater values of $\bar{R}$ signify faster overall RGR for a given period. ($S_1 = 1$).

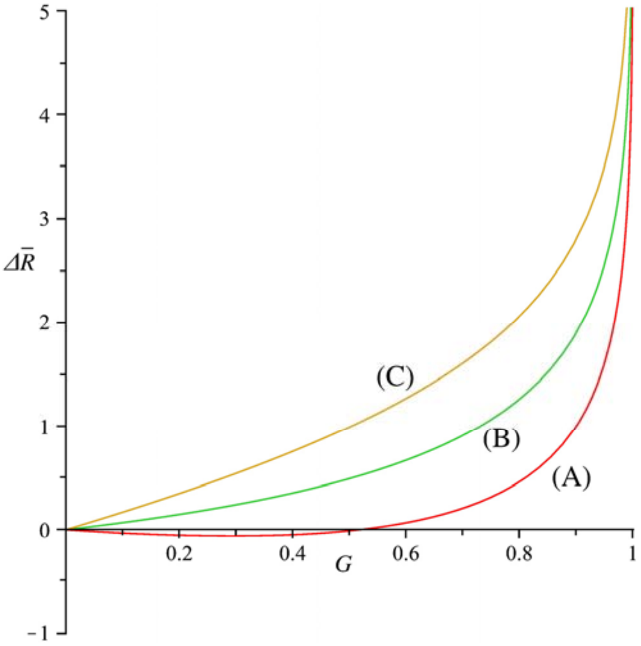

Fig. 4 The difference between the mean relative growth rate needed by a grazed plant to achieve the same production as an ungrazed plant ($\hat{\bar{R}}_g$) and the mean relative growth rate of a grazed plant for three possible functions of $\hat{\bar{R}}_g$: (A) $\bar{R}_g = \bar{R} + G$, (**B**) $\bar{R}_g = \bar{R}$, and (**C**) $\bar{R}_g = \bar{R} - G$; ($\bar{R} = 1$).

(B)$\Delta\bar{R}$ for $\bar{R}_g = \bar{R}$

$$\Delta\bar{R} = \ln\left(\frac{e^{\bar{R}\Delta t} - G}{1 - G}\right) - \bar{R} \qquad (11)$$

(C) $\Delta\bar{R}$ for $\bar{R}_g = \bar{R} - G$

$$\Delta\bar{R} = \ln\left(\frac{e^{\bar{R}\Delta t} - G}{1 - G}\right) - \bar{R} + G \qquad (12)$$

For cases (B) and (C), $\Delta\bar{R} = \hat{\bar{R}}_g - \bar{R}_g$, is positive for all values of *G*, with its minimum being $\bar{R}$, when *G* = 0 (**Fig. 4**; Hilbert *et al*. 1981 show case (B) for three values of $\bar{R}$ shown also in their Fig. 4). However, in (A), $\Delta\bar{R}$ may take negative values, indicating that the growth rate of a plant that compensates equally is lower than that of a plant responding positively to damage.

It must be noted that our calculations of ΔP for the three cases analysed differ from those shown in Fig. 3B of Hilbert *et al.* (1981) labeled "change in NPP", which is another name for ΔP. The curves shown in their figure are convex (a and b), or simple linear (c). In contrast, our figure shows that the shape of the function is different for each case: (A) convex, (B) simple linear, and (C) concave. In fact, their statement that the change in production of the grazed plant relative to production of the ungrazed plant "is a function of the distance between the plant's response curve and the [production] isoline" is imprecise since ΔP is a function of the difference between $e^{\bar{R}_g}$ (an exponential function of G), and the constant $e^{\bar{R}}$. In working through our calculations for $\Delta\bar{R}$, we realized that Hilbert *et al.*'s Fig. 3B seems to show the difference between $\bar{R}_g$ and $\hat{\bar{R}}_g$, which is precisely the distance between the plant's response curve and the isoline, and is equivalent to $-\Delta\bar{R}$, rather than ΔP (**Fig. 4**). All three curves of $-\Delta\bar{R}$ are convex although with different degrees of curvature (**Fig. 4**).

DISCUSSION

We have shown that the shape of the function for the change in production (ΔP) with regards to the intensity of grazing depends on the particular response of plants to herbivory in terms of their relative growth rate $\bar{R}_g$: for a positive response, ΔP is a convex function that may include positive values (overcompensation); for a null response, ΔP takes a simple linear, decreasing function, with its maximum value of zero when no grazing occurs; for a negative response, ΔP is concave. In reality, it is unlikely that the relation between growth rate and grazing intensity is as simple as any of the three cases analysed here. It is quite possible that RGR increases in response to low to moderate amounts of damage, but decreases at greater intensities of damage (Huhta *et al.* 2003; Zhao *et al.* 2008). In going from a positive to a negative response, there is necessarily a range of grazing intensities at which the growth rate does not change in response to damage intensity. Consequently, the ΔP curve would be a combination of the three responses analysed above, with a convex shape at low grazing intensities, followed by a simple linear portion, and a concave segment at high grazing intensities. A similar general response curve for plant yield in relation to insect injury level has been proposed and tested in some crop plants (Pedigo *et al.* 1986; Sanchez *et al.* 2007).

As mentioned above, ΔP is not a tolerance function *sensu stricto* because tolerance is defined in terms of fitness. Therefore, the above analysis applies directly to the shape of the tolerance curve only to the degree that production reflects individual fitness. While reproductive variables such as seed production or seed siring success may be better estimators of individual fitness, and therefore, more appropriate for tolerance studies, a recent review has found that the relationship between production and fitness is generally strong, and usually linear for short-lived species or log-log allometric with a slope less than one for longer-lived species (Weiner *et al.* 2009). Consequently, the fact that ΔP is most likely a curvilinear function makes it very unlikely for the true tolerance function to be simple linear, as it would require a relation between fitness and production mathematically opposite to ΔP in order to cancel out its curvilinearity and produce a simple linear function.

How does the analysis of the effects of a single damage event apply to species with long life spans, whether herbaceous or woody? It is important to note that the ΔP curve does not portray a dynamic response to damage, i.e., it is not a change in time, but a collection of responses from individual plants subjected to different amounts of damage. However, we must keep in mind that RGR changes throughout the life of an individual, so even though the model does not consider this, $\bar{R}_g$ is expected to vary with ontogeny. For example, in the annual *Arabidopsis thaliana*, tolerance to herbivory decreases from the four-leaf to the first-flower ontogenetic stage, a variation that is at least partly related to a decrease in RGR (Barto and Cipollini 2005; Tucker and Avila-Sakar 2010). In addition, plants are likely to experience more than one grazing event throughout their lives: the longer their life cycle, the more herbivory events. Therefore, the tolerance curve for perennial plants will be determined by the particular changes in RGR corresponding to damage events experienced at different ontogenetic stages.

There are important implications of the curvilinearity of the tolerance function for the stability of a mixed defence strategy, where neither tolerance nor resistance (the avoidance of herbivore attack) is selected to be maximal, but the highest fitness peak is at a combination of allocation to both defence strategies (Fornoni *et al.* 2004; Núñez *et al.* 2007). If tolerance curves generally have an important degree of convexity, this means that there is a certain intensity of damage for which there are no significant negative fitness consequences. So, in practical terms this amount of damage can be considered a threshold below which, there are no negative fitness consequences. Therefore, plants would not benefit from investing any resources in traits that decrease damage below that threshold. In other words, a convex tolerance curve favours the stability of a mixed defence strategy because the benefit function of increased resistance is curvilinear (Tiffin and Rauscher 1999; Fornoni *et al.* 2004; Núñez *et al.* 2007).

CONCLUSIONS

Given that the change in biomass production in response to damage follows most likely a curvilinear function, it is also more likely that the shape of the function of tolerance to herbivory is also curvilinear. Therefore, studies of tolerance to herbivory should use more than two levels of damage (with appropriate sample sizes) or continuous variation in damage intensity so as to be able to detect curvilinearity in the tolerance function either through analysis of variance, regression or analysis of covariance (Pilson 2000). Moreover, further studies of tolerance must consider a variety of interrelated factors that may influence the shape of the tolerance function, including how much the plants can change their RGR after damage, the ontogenetic stage at which damage occurs, the availability of meristems, growth form, and resource availability (Oesterheld 1992; Vinton and Hartnett 1992; Wandera *et al.* 1992; Rooney and Waller 2001; Anten *et al.* 2003; Mediavilla and Escudero 2003; van Staalduinen and Anten 2005; Myers and Kitajima 2007; Hodar *et al.* 2008; Zhao *et al.* 2008). Failure to control these factors, or to account for their effects in statistical analyses, may obscure the non-linearity of an estimated tolerance function.

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