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MEASURING TOLERANCE TO HERBIVORY: ACCURACY AND PRECISION OF ESTIMATES MADE USING NATURAL VERSUS IMPOSED DAMAGE

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Abstract.—Tolerance to herbivory (the ability of a plant to incur herbivore damage without a corresponding reduction in fitness) can be measured using either naturally occurring or imposed herbivore damage. After briefly reviewing some of the advantages and disadvantages of these approaches, we present calculations describing the degree to which estimates of tolerance will be biased by environmental variables that affect both herbivory and fitness. With naturally occurring herbivory the presence of environmental variables that are correlated with herbivory and fitness will result in biased estimates of tolerance. In contrast, estimates obtained from experiments in which herbivory is artificially imposed will be unbiased; however, under a wide range of parameter values these estimates will be less precise than estimates obtained from experiments in which herbivory is not manipulated.

Key words.—Artificial damage, herbivory, measurement error, natural damage, tolerance.

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Understanding the evolution of plants in response to the selective pressure imposed by herbivores has been a major focus of evolutionary biologists for more than thirty-five years. The vast majority of studies in this area have concentrated on mechanisms plants have evolved that reduce the amount of herbivory experienced (i.e., resistance; reviewed in Denno and McClure 1983; Fritz and Simms 1992; Karban and Baldwin 1997). However, resistance is not the only mechanism by which plants may minimize the potentially detrimental effects of herbivores on fitness. Plants may also evolve to tolerate or compensate for tissue lost to herbivores (Painter 1958). Tolerance, defined as the ability of a plant to incur herbivore damage without a corresponding reduction in fitness, may result in very different evolutionary and ecological dynamics between plants and herbivores than plant resistance (van der Meijden et al. 1988; Fineblum and Rausher 1995; Tiffin 2000). Thus, understanding tolerance is necessary to understand plant-herbivore interactions (reviewed in Rosenthal and Kotenian 1994; Strauss and Agrawal 1999).

Recent studies on tolerance have focused on environmental conditions that affect the expression of tolerance (Mashinski and Whitham 1989; Hjalten et al. 1993; Fay et al. 1996; Juenger and Bergelson 1997); mechanisms of tolerance (reviewed in Strauss and Agrawal 1999), the presence of costs, including trade-offs with resistance and trade-offs with fitness in the absence of herbivores (Fineblum and Rausher 1995; Mauricio et al. 1997; Stowe 1998; Tiffin and Rausher 1999); and the pattern of selection acting on tolerance (Mauricio et al. 1997; Tiffin and Rausher 1999). In these studies, researchers have employed naturally occurring (Paige and Whitham 1987; van der Meijden et al. 1988; Mashinski and Whitham 1989; Mauricio et al. 1997; Tiffin and Rausher 1999)

as well as artificial or manipulated (imposed) herbivory (Mashinski and Whitham 1989; Doak 1991; Hjalten et al. 1993; Fineblum and Rausher 1995; Rosenthal and Welter 1995; Fay et al. 1996; Juenger and Bergelson 1997; Lennartsson et al. 1997; Stowe 1998; Agrawal et al. 1999) to estimate values of tolerance. However, the majority of studies have relied on imposed herbivory (Strauss and Agrawal 1999), presumably because of an implicit assumption that naturally occurring herbivore damage will result in poor estimates of tolerance. In fact, there are advantages and disadvantages associated with both natural and imposed damage. The main focus of this paper is to compare the accuracy and precision of the estimates of tolerance obtained with natural versus imposed herbivory. Before addressing these issues, we briefly review the standard operational definition of tolerance and some of the advantages and disadvantages of using natural versus imposed damage.

Advantages and Disadvantages of Natural and Imposed Damage

For herbivore damage that can be measured as a continuous variable, e.g., proportion leaf area removed by leaf feeding insects, the standard operational definition of tolerance for a genetic family is the slope of a linear regression of fitness on the level of damage sustained by each individual within that family (Simms and Triplett 1994; Mauricio et al. 1997; Tiffin and Rausher 1999). For types of damage that are measured categorically, for example, removal of apical of floral meristems, the standard operational definition of tolerance is simply the difference in fitness between damaged and undamaged plants (Simms and Triplett 1994). Empirically, these operational definitions are employed using data collected on both the herbivore damage experienced by and the fitness of a group of related individuals. Tolerance is measured on a group of related individuals that experience different amounts of herbivore damage because a single plant will only experience a single level of damage (Rausher 1992a). As stated above, the measured herbivore damage can

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be natural damage that occurs in a field setting or imposed damage that has been manipulated by caging herbivores or mimicking herbivore damage using scissors, hole-punches, or other mechanical devices.

The primary advantage of estimating tolerance from experiments in which herbivores are not manipulated is that plants experience the timing, distribution, and pattern of damage that they would experience in a natural population. However, there are two potential problems with using natural damage. The first is that if resistance to herbivory varies among genetic families, then those families will experience different amounts of damage. In extreme cases, the range of damage experienced by individuals in one family may not even overlap with the range of damage experienced by individuals in a second family. Unequal amounts of damage are not a problem for estimating tolerance if the relationship between fitness and herbivory is linear across the range of damage experienced by all individuals (the slope of the regression line will not change due to changes in the amount of herbivore damage). If, however, the effect of an increment of herbivory on fitness changes as the amount of herbivory increases, then it is possible that differences in resistance will lead to erroneous conclusions regarding the relative tolerance of different genotypes (see below).

The second potential problem with using naturally occurring damage is a bias resulting from an unmeasured biotic or abiotic microenvironmental variable that affects both plant fitness and herbivore density or preference (Mitchell-Olds and Shaw 1987; Rausher 1992b). For example, if both plant fitness and herbivore abundance are greater in wetter microclimates, then estimates of tolerance may be artificially inflated, possibly even leading to a situation in which plants receiving more damage have higher fitness than less damaged plants, or apparent overcompensation (Paige and Whitham 1987; Hoopes 1999). For some traits, the bias caused by the microenvironment can be eliminated by analyzing breeding values, that is, family means, rather than phenotypic values (Rausher 1992b). Because tolerance is generally measured on genetic families, breeding values cannot be used easily to remove bias in estimates of tolerance.

An alternative to naturally occurring herbivory is to measure tolerance to imposed herbivory. Assuming that experiments are properly randomized, imposed damage avoids the problem of different genetic families receiving unequal amounts of herbivory as well as the problem of environmental factors that may bias estimates of tolerance (see below). However, imposed herbivore damage is problematic for several reasons. First, plants may respond differently to simulated versus natural herbivory (Dyer and Bokhari 1976; Capinera and Roltsch 1980; Baldwin 1988, 1990; Karban and Baldwin 1997), although it may be possible to partially avoid this problem by applying saliva of herbivores or using caged herbivores (Dyer and Bokhari 1976; Agrawal et al. 1999). Second, replicating the natural distribution and intensity of herbivory is likely to be difficult if not impossible for at least some types of herbivores. This is especially true for herbivores that attack the inside of plant parts, for example, leaf miners, gall makers, and stem borers. Third, the labor necessary for imposing damage in experiments involving a large number of plants may be prohibitive, and thus using imposed

damage may limit the scope of experiments and the types of questions that can be addressed. Fourth, if plants are grown in natural settings, methods of excluding or containing herbivores (e.g., pesticides or cages) may alter plant physiology and thus the expression of tolerance. If, alternatively, plants are grown in a greenhouse or growth chamber, the novel environment (e.g., pot effects and unnatural lighting and watering) may alter plant growth producing results that do not represent what happens in a natural environment (Service and Rose 1985). Finally, as shown below, under a wide range of conditions, manipulated herbivory results in less precise estimates of tolerance than estimates based on natural herbivory.

Estimates of Tolerance

Here we compare estimates of tolerance from natural versus manipulated herbivory. Regardless of the type of herbivory, we assume that measurements are made on plants that have been planted in a randomized experimental design in a relatively uniform environment. After presenting general equations for fitness, herbivory, and tolerance, we calculate the magnitude of the bias that may result from using natural damage and compare the precision of estimates from natural and artificial damage. Finally, we discuss the effects of the bias and precision on calculating costs of tolerance and the pattern of selection acting on tolerance. We assume that the relationship between herbivory and fitness is linear throughout the range of damage experienced by individual plants and we use a continuous measure of herbivory in calculating tolerance. The importance of this assumption and tests of this assumption are discussed below. Our arguments also apply to categorical measures of herbivory, for example, apical meristem damage; however, because categorical measures are a special case of continuous traits (plants have damage values of zero or one), we present the continuous case for generality.

Following the general model of Simms and Rausher (1987), the fitness of an individual plant i of genotype j , W_{ij} , can be expressed as

$$W_{ij} = W_{0j} + SE_i + T_j H_{ij} + \epsilon_i. \quad (1)$$

In this equation W_{0j} is the mean fitness of genotype j in the absence of either herbivory or microenvironmental variables that affect W ; S is the effect of microenvironmental variables on fitness; E_i is the level of the microenvironmental factor experienced by individual i ; T_j is the effect of herbivory on fitness, which is equivalent to the tolerance of genotype j ; H_{ij} is the amount of herbivore damage experienced by individual i of genotype j , and ϵ_i is an error term for factors not included in H or E . By omitting a subscript for S we assume that the effect of the environment on fitness is the same for all genotypes (discussed below). The environmental factor E_i and the error term ϵ_i are not subscripted for genotype because we assume that the randomization of plants results in identical distributions of E_i and ϵ_i for all genotypes. Genotype is used loosely and is meant to designate a group of individuals, those within genotype j , that are more closely related to one another than they are to individuals within other genotypes. Thus, j could represent populations or spe-

cies in studies designed to compare the tolerance of these groups.

The herbivory experienced by an individual is a result of genetic factors, random movement of the herbivores, and in some cases, environmental factors. H_{ij} can be defined as

$$H_{ij} = H_{R_{ij}} + BE_i. \quad (2)$$

In equation (2) $H_{R_{ij}}$ represents herbivory resulting from the resistance of family j (i.e., genetic factors, with higher resistance leading to less herbivore damage) and random herbivore activity, or the amount of imposed damage in experiments using manipulated damage; and B is the effect of the environmental factor on H . The parameter B is equivalent to the coefficient from the regression of H on E . Because we assume that tolerance is linear throughout the range of damage, we ignore the effects of resistance on the mean amount of damage experienced by individuals within j . By omitting a subscript on B we assume that there are no genotype-by-environment ($G \times E$) interactions, that is, the covariance between E_i and H_{ij} is the same for all genotypes (discussed below). This assumption is similar to the assumption that was made for S above.

The standard operational definition of tolerance is the regression coefficient of W_{ij} on H_{ij}

$$T_j = \frac{\sum_i^n (H_{ij} - \bar{H})(W_{ij} - \bar{W})}{\sum_i^n (H_{ij} - \bar{H})^2}. \quad (3)$$

The numerator of equation (3) is simply the covariance between H_{ij} and W_{ij} (σ_{HW}^2); whereas, the denominator is simply the variance of H_{ij} (σ_H^2). The variable S can be defined similarly by substituting E for H in equation (3). In equation (3) a bar above a variable indicates the mean of that variable. For simplicity, we assume that H , E , and W have been scaled to have a mean of zero and variance of one. Estimates of T_j can be obtained by substituting equations (1) and (2) into equation (3) resulting in

$$T_j = \sum_i^n (H_{R_{ij}} + BE_i)(W_{ij}), \quad (4)$$

which is equivalent to the covariance between $H_{R_{ij}}$ and W_{ij} plus B times the covariance between E_i and W_{ij} (i.e., $\sigma_{HRW}^2 + B \sigma_{EW}^2$). Imposing herbivory in a randomized fashion means that $B = 0$ and $T_j = \sigma_{HRW}^2$. In other words, using naturally occurring damage rather than artificially imposed damage will result in a bias in the estimate of tolerance equal to $B\sigma_{EW}^2$. Thus, as stated above, estimating tolerance from experiments in which damage is imposed will result in more accurate estimates of tolerance (assuming that manipulated damage is a good proxy for natural damage). The magnitude of $B\sigma_{EW}^2$ will depend on the magnitude by which microenvironmental factors (e.g., sun, water, nitrogen) affect herbivory and fitness as well as the uniformity of the environment in which a study is conducted. The more uniform the environment in which the study is conducted, the smaller the expected bias.

Precision of Estimates of Tolerance

Although using imposed herbivory results in more accurate estimates of tolerance, those estimates are not necessarily more precise. Tolerance is equivalent to the slope from a linear regression of fitness on herbivory; thus, the precision of an estimate of tolerance can be expressed as the proportion of the total variation in fitness that is explained by herbivory, or the r^2 of the regression equation (Zar 1996, p. 324). The precision of estimates obtained from natural damage are greater than or equal to the precision obtained from imposed damage when the r^2 obtained with natural herbivory is greater than or equal to the r^2 obtained from manipulated herbivory, or

$$\frac{\sigma_{HRW}^2 + 2B\sigma_{HRW}\sigma_{EW} + B^2\sigma_{EW}^2}{\sigma_{HRW}^2 + \sigma_{EW}^2 + 2B\sigma_{HRW}\sigma_{EW} + B^2\sigma_{EW}^2} \geq \frac{\sigma_{HRW}^2}{\sigma_{HRW}^2 + \sigma_{EW}^2}, \quad (5)$$

which can be simplified to

$$B^2\sigma_{EW}^2 + 2B\sigma_{HRW}\sigma_{EW} \geq 0. \quad (6)$$

Under a wide range of parameter values, equation (6) is true and thus greater precision is obtained with natural than imposed herbivory (Fig. 1). In general, the precision with which tolerance is estimated using natural damage is greater than or equal to the precision of estimates made using imposed damage whenever two of the three terms B , σ_{HRW} , and σ_{EW} are negative, all of the terms are greater than zero, or one of these terms is equal to zero. Only when one or all three of these terms are negative is there a possibility of obtaining less precise estimates from using natural damage. It is probably safe to assume that herbivory will nearly always have no effect, or a negative effect on plant fitness ($\sigma_{HRW} \leq 0$; but see Paige and Whitham 1987; Lennartsson et al. 1997). Thus, only when the effects of the environmental variable(s) on herbivory (B) and fitness (σ_{EW}) have the same sign (e.g., increased amounts of available nitrogen increase plant fitness but also attractiveness to herbivores, thereby resulting in greater herbivore damage; Coley et al. 1985) are less precise estimates of tolerance expected from using natural damage. Unfortunately it is difficult to make generalizations about the magnitude or sign of these relationships (reviewed in Tingey and Singh 1980; Herms and Mattson 1992).

Consequences of Biased and Imprecise Estimates

Bias is a problem if the goal of an experiment is to estimate the true relationships between herbivory and fitness. If, however, one is interested in detecting the presence of genetic variation for tolerance, the presence of costs, or the pattern of selection acting on tolerance, bias that affects all genotypes equally is not a problem, but precision is a problem. The reason that the precision of estimates is of more concern than the bias of estimates is because of the way in which genetic variation, costs, and selection are detected. The presence of genetic variation for tolerance is tested for by examining the genotype-by-damage interaction term in an analysis of variance (Simms and Triplett 1994; Mauricio et al. 1997; Stowe

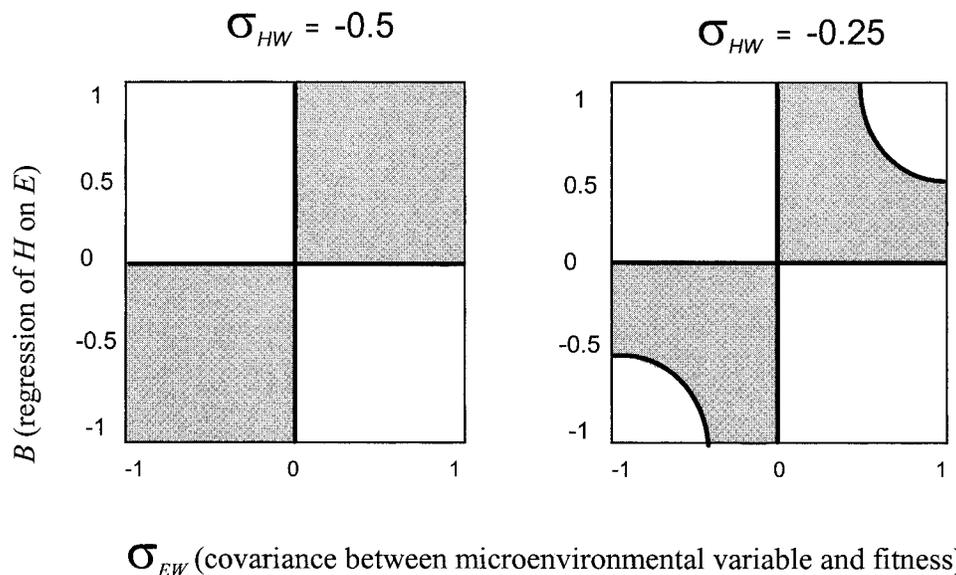


FIG. 1. Comparison of the precision of tolerance estimates made using natural versus imposed damage at two values of σ_{HW} (the covariance between herbivory and fitness). Estimates are equally precise at values on the lines, less precise with natural damage in the shaded areas, more precise with natural damage in the unshaded areas. When $\sigma_{EW} = 0$, estimates obtained from natural and imposed damage are equally precise. When $\sigma_{HW} = 0$, the precision of estimates obtained from natural damage are always greater than or equal to those obtained from manipulated damage.

1998; Tiffin and Rausher 1999). The overall mean value of a trait will not affect the power of ANOVA to detect a significant effect, but the magnitude of the residuals around the mean value of different families will. The power to detect significant genetic variation for tolerance thus depends on the precision with which tolerance is measured in each family. Costs of tolerance are generally detected by testing for significant genetic covariance between tolerance and another trait of interest. Because calculating a covariance involves subtracting the mean values of a trait from the individual values of that trait, a bias in individual estimates is removed and will not affect the magnitude or significance of costs. A similar argument applies to estimating the pattern of selection acting on tolerance because the mean values of tolerance are subtracted from individual values when calculating the regression coefficient that describes the pattern of selection acting on tolerance (Lande and Arnold 1983; Mitchell-Olds and Shaw 1987).

Tests of Assumptions

In deriving the estimates of tolerance, we made two assumptions. The first assumption was that tolerance can be estimated using a linear relationship between fitness and herbivore damage. We know of no studies that found tolerance to be nonlinear over the range of natural damage experienced within a population. Nevertheless, tolerance is likely to be nonlinear in some systems. The assumption of nonlinearity can be tested by including second-order terms in a regression of fitness on herbivory (Tiffin and Rausher 1999). Significant second-order terms in such an analysis indicate that tolerance should not be estimated using only linear terms. For categorical types of herbivore damage, nonlinearities cannot be calculated; thus, the assumption of a linear measure of tol-

erance applies only to continual measures of herbivore damage.

If the means and variances of damage experienced by different genotypes are similar, then the arguments we make for estimating linear regression coefficients (linear definition of tolerance) apply to nonlinear regression coefficients. If, however, there are large differences in the amount of damage experienced by different genotypes (significant genetic variation for resistance) and the analysis does not account for a nonlinear relationship between fitness and herbivore damage may lead to spurious conclusions regarding tolerance. For example, assume that two genotypes have equal tolerance and tolerance is expressed by a function between fitness and herbivory that is concave down. Moreover, assume that one genotype experiences significantly greater amounts of herbivory than the other genotype and that tolerance is described using a linear function. In this situation, the estimate of tolerance for the genotype that experiences significantly greater damage (less resistant) will be more negative than the estimate for the genotype that experienced less damage even though these two genotypes are equally tolerant (Fig. 2). Moreover, the data will indicate a positive correlation between tolerance and resistance even though these traits are, in fact, not correlated. Thus, if there is (1) significant genetic variation for resistance; (2) a positive correlation between tolerance and resistance; and (3) the relationship between fitness and herbivory is nonlinear (a significant herbivory² term in an ANOVA in which fitness is the response variable), then it may be necessary to use imposed damage in order to obtain accurate estimates of tolerance.

We also assume the absence of genotype by environment interactions (GxE) between the microenvironmental variable

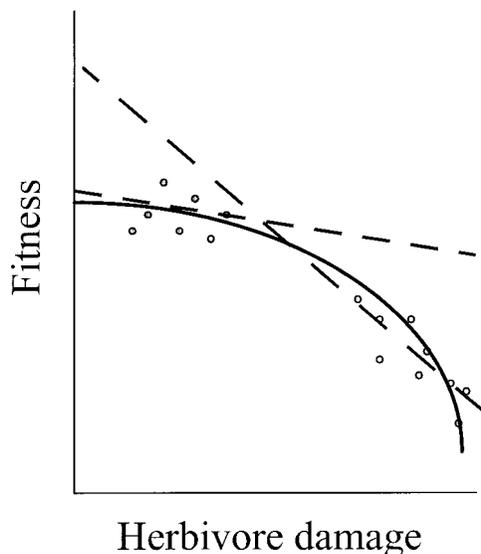


FIG. 2. Differences in the range of herbivore damage experienced by individuals within families, as well as a nonlinear tolerance function, may lead to inaccurate estimates of tolerance. In the figure, individuals from family A (open circles) and family B (shaded circles) have the same true tolerance to herbivory (solid line). Tolerance of family A is measured only using individuals that experienced large amounts of damage (low resistance) and tolerance of family B is measured using individuals that experienced large amounts of damage (high resistance). In this case, linear estimates of tolerance (dashed lines) for families A and B are erroneous.

and herbivory (all B_j are equal) and between the microenvironmental variable and fitness (all σ_{jEW}^2 are equal). If these assumptions are violated, then the bias in estimates of tolerance made from naturally damaged plants will not be equal for all genotypes ($B_j\sigma_{jEW}^2 \neq B_k\sigma_{kEW}^2$ for all j). Studies showing significant $G \times E$ interactions for plant fitness response to environmental variables (e.g., Sultan and Bazzaz 1993; Stratton 1994; Galloway 1995) suggest this assumption will not be true in at least some systems. However, as long as the magnitude of $G \times E$ interactions is small in relation to the effects of herbivory on fitness, then the presence of $G \times E$ interactions should not have large effects on estimates of tolerance. Note that the accuracy of tolerance estimates obtained from experiments using imposed herbivory will not be affected by $G \times E$ interactions between the microenvironmental variable and herbivory ($B_j = 0$ for all j), although the precision of the estimates will vary among genotypes. To test for the presence of $G \times E$ interactions, it is necessary to conduct replicated field experiments in which multiple individuals of multiple genotypes are exposed to different levels of an environmental variable (e.g., water availability is manipulated for some plants in a randomized block design that includes multiple replicated genotypes; Bright 1998). Analysis of variance can then be used to test for genotypic differences in the effects of the environmental variable on herbivory and the environmental variable on plant fitness.

Conclusions

Unmeasured environmental variables have the potential to alter estimates of tolerance made using either natural or im-

posed herbivore damage. Estimates of tolerance using natural herbivory may be biased; however, in the absence of genotype-by-microenvironment interactions, the estimates for each genotype will be biased equally and thus not affect estimates of genetic variation for tolerance, costs of tolerance, or selection acting on tolerance. Manipulated herbivore damage removes the bias in tolerance estimates, but under some conditions will inflate the error around estimates of tolerance, making it more difficult to detect genetic variation, costs, and selection. Moreover, imposing damage will not always remove the problems associated with unmeasured environmental factors. In particular, if damage makes plants more or less susceptible to infection by pathogens (Clay 1996; Clay and Brown-Valerie 1997) or attack by other herbivores (Pilson 1992; Hougren-Eitzman and Rausher 1994 and references therein) that are not also controlled, then even imposed damage may result in biased estimates of tolerance (in eq. 4, $B \neq 0$).

In conclusion, experimental manipulation of herbivory is preferable to naturally occurring herbivory when the aim of the investigation is to obtain true, rather than relative, estimates of tolerance. By comparison, natural herbivory offers several advantages including: (1) the ability to obtain estimates of tolerance and resistance from a single experiment using the same set of plants, thereby allowing one to estimate trade-offs between tolerance and resistance; (2) experiments that are logistically easier to perform; and (3) in some cases greater power to detect genetic variation for tolerance.

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