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MINI-REVIEW

Minireviews provides an opportunity to summarize existing knowledge of selected ecological areas, with special emphasis on current topics where rapid and significant advances are occurring. Reviews should be concise and not too wide-ranging. All key references should be cited. A summary is required.

A meta-analysis of tradeoffs between plant tolerance and resistance to herbivores: combining the evidence from ecological and agricultural studies

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Resistance and tolerance represent two general strategies of plant defence against herbivores. Since resources available for allocation to defence are limited and resistance and tolerance are likely to serve the same functions for plants, the occurrence of trade offs between these two strategies has been assumed. We review the empirical evidence for tolerance–resistance tradeoffs by means of meta-analysis of genetic correlations between resistance and tolerance obtained from 31 ecological and agricultural studies published during 1980–2003 and conducted on 17 different plant species. The sign of the relationship between tolerance and resistance differed depending on the type of plants examined. Tolerance and resistance tended to be positively correlated in crops and negatively correlated in wild plants, but the mean correlation coefficients in both plant types were not significantly different from zero. The magnitude of correlations was affected neither by the tolerance measure (reduction in growth or in fitness in damaged plants) nor by the resistance measure used (inverse of damage, antibiosis, antixenosis, or specific resistance trait). In wild plants correlations between resistance and tolerance were significantly negative ($r = -0.069$) only in studies where resistance was assessed as a specific chemical or mechanical resistance trait, but this correlation is based only on two studies. No difference in the mean resistance–tolerance correlations was found between studies conducted in the field and in the greenhouse; in both cases mean correlations tended to be positive. The results of our analysis indicate that conditions under which a negative association between resistance and tolerance occurs and, thus, the evolution of multiple defensive strategies in plants is constrained, are much more restrictive than previously assumed. However, the currently available studies are still scarce and taxonomically skewed to allow a thorough analysis of sources of variation in resistance–tolerance relationship. Specifically, we need more studies examining the relationship between specific resistance and tolerance traits, studies on perennial plants and under different environmental conditions.

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Plants may employ two general defensive strategies against herbivores: reduction of the amount of herbivore damage (resistance) and/or reduction of the impact of herbivory on plant fitness (tolerance) (Crawley 1983, Rausher 1992, Stowe et al. 2000). Resistance traits include mechanical and chemical characters that reduce herbivore performance (antibiosis) or preference (antixenosis). Tolerance mechanisms include increased photosynthetic activity, compensatory regrowth, utilization of stored resources, phenological changes, and mechanisms related to physiology and morphology at the time of damage (Tiffin 2000a).

While tolerance has been traditionally considered as an alternative to plant resistance in plant breeding (Painter 1958), ecological and evolutionary studies of plant responses to attack by herbivores have until recently largely focused on the mechanisms of resistance. The joint evolution of tolerance and resistance as plant defences has received considerable attention among ecologists only during the last decade, after several studies have suggested the existence of a tradeoff between these two mechanisms (van der Meijden et al. 1988, Fineblum and Rausher 1995). This tradeoff is expected to occur if plant resources are limited and both defensive strategies have allocation costs. Under these conditions, high investment in resistance reduces the resources available to compensate for herbivore damage, resulting in a negative association between resistance and tolerance (Rosenthal and Kotanen 1994, de Jong and van der Meijden 2000). Moreover, if resistance and tolerance are functionally redundant, highly tolerant genotypes are unlikely to benefit from increased resistance, while genotypes with high levels of resistance will not benefit from increased tolerance (Tiffin and Rausher 1999). If exists, a tradeoff between resistance and tolerance would have important evolutionary consequences because it can result in selection leading either to maximal resistance or maximal tolerance, but not both (Fineblum and Rausher 1995).

A number of ecological studies have tested for a tradeoff between resistance and tolerance to herbivores in wild plants by assessing genetic correlations between resistance and tolerance traits. These correlations reflect the extent to which the two traits share a common genetic basis due to pleiotropy or linkage disequilibrum (Falconer 1981). A negative correlation between resistance and tolerance has been found in some studies (Fineblum and Rausher 1995, Stowe 1998), but not in others (Mauricio et al. 1997, Stinchcombe and Rausher 2002, Valverde et al. 2003). The frequent failure to detect a tolerance-resistance tradeoff has led to a questioning of the generality of the assumptions behind the tradeoff hypothesis (Strauss and Agrawal 1999, de Jong and van der Meijden 2000, Stowe et al. 2000). It has been suggested that a stable coexistence of the two strategies may actually be quite common (Mauricio et al. 1997, de Jong and van der Meijden 2000, Valverde et al. 2003, Restif and Koella 2004), and that the conditions under which a negative correlation occurs may be more restrictive than previously thought (de Jong and van der Meijden 2000). Moreover, some recent models predict that selection could actually favour intermediate levels of both resistance and tolerance (Tiffin 2000b, Fornoni et al. 2004, Restif and Koella 2004). For instance, Tiffin's (2000b) model predicts that both resistance and tolerance will be maintained at intermediate levels if the costs of these strategies are independent and unequal. The outcome of a recent model by Fornoni et al. (2004), on the other hand, suggests that the variation in costs of tolerance and resistance is an important key factor in the maintenance of intermediate levels of resistance and tolerance. The model by Restif and Koella (2004) predicts that mixed defence strategies can be favoured over pure strategies if the costs of defences are non-linear. Thus, the arguments and evidence both for and against the tradeoffs between plant resistance and tolerance to herbivores exists.

Here, we undertake the first quantitative review of studies that examined the relationship between resistance and tolerance with the aim to evaluate the empirical evidence for the tradeoff hypothesis. In our review, we combine the evidence for tradeoffs between plant resistance and tolerance from both ecological and agricultural studies. The strength and the direction of the relationship between tolerance and resistance to herbivores may differ between crops and wild species for at least two reasons. First, selection for increased yield often leads to reduced levels of resistance and tolerance in crops as compared to their wild relatives (Welter and Steggall 1993, Rosenthal and Welter 1995, Rosenthal and Dirzo 1997), and this may affect the magnitude of the tradeoffs between resistance and tolerance in crops as compared to wild species. Second, different strengths and signs of correlations between tolerance and resistance in ecological and agricultural studies may be due to publication bias. Under-reporting or delayed publication of results that contradict the predictions of the prevailing theories or hypotheses has been found in ecology especially at the initial stage of theory development (Leimu and Koricheva 2004). Ecological studies conducted on wild plants have aimed mainly at testing for the presence of the predicted tradeoff between resistance and tolerance, and, since the theoretical justification for the lack of the above tradeoff has been suggested only recently (Tiffin 2000b, Fornoni et al. 2004, Restif and Koella 2004), studies reporting negative correlations may have been more likely to be published. In contrast, since selection for both resistance and tolerance to herbivory is an important goal of many crop breeding programs, agricultural studies are more likely to report positive correlations between resistance and tolerance. We therefore hypothesized that agricultural studies would provide weaker evidence of tradeoffs between resistance and tolerance. Furthermore, if there exists a publication bias against studies reporting results that do not support a prevailing hypothesis or assumption, we can expect a resistance–tolerance tradeoff in wild plants and a positive correlation between resistance and tolerance in crops.

We used meta-analysis to review the results of published studies that examine the relationship between tolerance and resistance. Meta-analysis represents a set of statistical methods which allows combining the results from independent studies addressing the same research question, in order to estimate the mean effect size and to identify the factors which influence the magnitude and direction of the effect (Gurevitch et al. 2001). This method is particularly useful for summarizing the evidence in areas where empirical results provide no clear "consensus" (Arnqvist and Wooster 1995) and has previously been applied to an examination of tradeoffs between plant growth and defense (Koricheva 2002) and among different types of plant resistance to herbivores (Koricheva et al. 2004). In addition, meta-analysis provides methods for detection of publication bias (Light and Pillemer 1984, Palmer 1999).

Our analysis addresses the following questions: 1) is there a tradeoff between tolerance and resistance to herbivores? 2) Are there differences in the direction or strength of this relationship between crop species and non-crop species? 3) If so, are these differences likely to be caused by publication bias? 4) Does the relationship between tolerance and resistance differ depending on whether resistance is measured as the inverse of damage, antixenosis, antibiosis, or as a specified resistance trait?

Methods

We conducted key word searches in the Web of Science (ISI) electronic bibliographic database (1975–2003) to find studies that had examined the relationship between resistance and tolerance or offered data on the covariation of these defensive strategies. We used different combinations of the keywords "tradeoff", "defense", "resistance", "tolerance", "antibiosis", and "antixenosis". We also searched for articles citing some of the key papers on resistance–tolerance tradeoffs (van der Meijden et al. 1988, Fineblum and Rausher 1995). We restricted our analysis of tradeoffs between resistance and tolerance to genetic correlations (among family means, clones or cultivars), since these have clearer evolutionary significance than phenotypic or among-species correlations (Roff 1992). The final dataset consisted of 46 correlations from 31 studies published during 1980–2003 in 20 different ecological and agricultural journals or books (Table 1). The studies selected had been conducted on 17 different plant species, including 9 crop and 8 non-crop species.

In most studies tolerance was measured as a proportional difference between damaged and undamaged plants in plant height, dry mass or mean fitness or as the slope of regression of fitness on damage. We therefore classified tolerance measures into those assessing difference in growth (height and biomass) and those assessing differences in fitness. The lesser is the difference in growth or fitness between damaged and undamaged plants, the more tolerant is the plant genotype. Resistance was measured either as 1- relative herbivore damage received by a particular genetic family, clone or cultivar (= total resistance), antibiosis (= the inverse of herbivore performance on plants), antixenosis (= non-preference, i.e. the inverse of herbivore densities on plants), or as specified resistance traits (chemical or structural).

We used the Pearson product-moment correlation coefficient r as a measure of effect size in our analysis, since most studies reported the association between resistance and tolerance as correlation coefficients. If correlation coefficients were not reported in a study, we calculated them from the mean values for resistance and tolerance given in tables or figures. When data were presented in figures, the graphs were enlarged and digitized manually. In cases where correlation coefficients were not given and no data were presented allowing the calculation of a correlation, we asked the authors of these papers to provide us with the necessary correlations (Tiffin 2002, Prittinen et al. 2003). If regression analysis was used to assess the relationship between tolerance and resistance, we took the square root of the coefficient of the determination (R^2).

Many of the studies selected presented measurements of resistance and tolerance for several sampling dates or for different initial numbers of herbivores. In these cases we calculated the means of the values given and used them to calculate the correlation between tolerance and resistance. If a range between the lowest and the highest correlation coefficients was reported instead of individual correlations (Stinchombe and Rausher 2002, Valverde et al. 2003), we used the highest correlation coefficient in our analyses. If different studies examined the same plant species, these were included in our analyses only if they dealt with different herbivore species. We found only few studies on crops that examined same plant species and same herbivore species. From these studies we selected the ones with the highest sample sizes.

The meta-analysis was carried out by using the Meta Win 2.0 statistical program (Rosenberg et al. 2000). Individual correlation coefficients were z-transformed and weighted by their sample size. The transformed coefficients were combined across studies using the mixed effects model, which assumes that differences

Table 1. Characteristics of studies included in the meta-analysis on correlations among tolerance and different types of resistance.

	Species	Resistance measure	Tolerance measure	Type of experiment	Source	Correlation coefficient	Sample size	Reference
Crop species	*Citrus* sp.	Antibiosis	Growth	Greenhouse	Fig. 1, 3	−0.073	8	Shapiro and Gottwald 1995
	Hordeum vulgare	Antixenosis	Growth	.	Table 2	0.394	23	Assad et al. 1999
	Hordeum vulgare	Antibiosis	Growth	.	Table 2	−0.111	23	Assad et al. 1999
	Hordeum vulgare	Antixenosis	Growth	Greenhouse	Table 2	0.897	4	Robinson et al. 1991
	Hordeum vulgare	Antibiosis	Growth	Greenhouse	Table 2	0.986	4	Robinson et al. 1991
	Hordeum vulgare	1-damage	Growth	Greenhouse	Table 3	0.817	10	Webster et al. 1991
	Hordeum vulgare	Antixenosis	Growth	Greenhouse	Table 3, 4	0.089	10	Webster et al. 1991
	Hordeum vulgare	Antibiosis	Growth	Greenhouse	Table 3, 4	0.832	10	Webster et al. 1991
	Oryza sativa	Antibiosis	Growth	Greenhouse	Fig. 2	0.782	5	Cohen et al. 1997
	Oryza sativa	Antibiosis	Growth	Greenhouse	Fig. 1	0.200	6	Lye and Smith 1988
	Oryza sativa	1-damage	Fitness	Field	Fig. 1, Table 3	−0.423	14	N'Guessan and Quisenberry 1994
	Oryza sativa	1-damage	Fitness	Greenhouse	Fig. 1, Table 3	−0.218	7	N'Guessan et al. 1994
	Oryza sativa	Antixenosis	Fitness	Greenhouse	Table 1, 2, 3	0.241	7	N'Guessan et al. 1994
	Oryza sativa	Antibiosis	Fitness	Greenhouse/field	Table 7	−0.807	9	Panda and Heinrichs 1983
	Pisum sativum	Antibiosis	Growth	Greenhouse	Table 3, 4	0.328	6	Soroka and Mackay 1991
	Sorghum bicolour	Antibiosis	Growth	Greenhouse	Fig. 3	−0.409	10	Dixon et al. 1990
	Sorghum bicolour	1-damage	Fitness	Field	Fig. 1	0.608	60	Van den Berg et al. 1994
	Sorghum bicolour	1-damage	Growth	Greenhouse	Table 2	−0.785	5	Webster 1990
	Sorghum bicolour	Antixenosis	Growth	Greenhouse	Table 1, 2	0.371	5	Webster 1990
	Sorghum bicolour	Antibiosis	Growth	Greenhouse	Table 1, 2	−0.110	5	Webster 1990
	Stenotaphrum secundatum	Antixenosis	Growth	Greenhouse	Table 1	−0.274	7	Busey et al. 1993
	Saccharum officinarum	Antibiosis	Fitness	Greenhouse	Table 12, 13	0.477	25	Allsopp and Cox 2002
	Triticum aestivum	Antixenosis	Growth	Greenhouse	Table 1, 4	−0.760	7	Budak et al. 1999
	Triticum aestivum	Antibiosis	Growth	Greenhouse	Table 2, 4	−0.750	7	Budak et al. 1999
	Triticum aestivum	Antixenosis	Growth	Greenhouse/field	p. 135	0.055	13	Havlickova 1993
	Triticum aestivum	Antibiosis	Growth	Greenhouse/field	p. 135	0.425	13	Havlickova 1993
	Zea mays	1-damage	Fitness	.	Table 2	−0.137	10	Butrón et al. 1998
	Zea mays	1-damage	Fitness	.	Table 2	−0.579	10	Butrón et al. 1998
	Zea mays	1-damage	Fitness	.	Fig. 2	0.572	25	Ortega et al. 1980
Non-crop species	*Arabidopsis thaliana*	Specific resistance trait	Fitness	Field	p. 1306	−0.080	144	Mauricio et al. 1997
	Arabidopsis thaliana	Specific resistance trait	Fitness	Field	p. 1306	0.040	144	Mauricio et al. 1997
	Arabidopsis thaliana	1-damage	Fitness	Field	p. 1274	−0.130	98	Weinig et al. 2003
	Betula pendula	1-damage	Growth	Field	Pers. comm.	−0.004	20	Prittinen et al. 2003
	Brassica rapa	1-damage	Fitness	Field	Table 3C	0.004	40	Pilson 2000
	Brassica rapa	1-damage	Fitness	Field	Table 3C	−0.380	40	Pilson 2000
	Datura stramonium	1-damage	Growth	Field	p. 131	0.160	39	Valverde et al. 2003
	Datura stramonium	1-damage	Fitness	Field	p. 1056	−0.41	25	Fornoni et al. 2003
	Datura stramonium	1-damage	Fitness	Field	p. 1056	−0.15	23	Fornoni et al. 2003
	Ipomoea hederacea	1-damage	Fitness	Field	p. 1243	0.220	16	Stinchcombe and Rausher 2002
	Ipomoea purpurea	1-damage	Fitness	Greenhouse/field	p. 518	−0.943	6	Fineblum and Rausher 1995
	Ipomoea purpurea	1-damage	Fitness	Field	Pers. comm.	0.138	24	Tiffin 2002
	Ipomoea purpurea	1-damage	Fitness	Field	Pers. comm.	0.153	24	Tiffin 2002
	Ipomoea purpurea	1-damage	Fitness	Field	Table 5	0.065	35	Tiffin and Rausher 1999
	Ipomoea purpurea	1-damage	Fitness	Field	Table 5	−0.151	35	Tiffin and Rausher 1999
	Raphanus raphanistrum	Specific resistance trait	Fitness	Greenhouse	Fig. 1	−0.542	10	Strauss et al. 2003
	Salix cordata	Antixenosis	Growth	Greenhouse/field	p. 339	−0.033	9	Shen and Bach 1997

among studies within a class are due to both sampling error and random variation. In ecological data synthesis the assumptions of mixed models are more likely to be met than those of fixed effects models, and the former are thus preferred (Gurevitch and Hedges 2001). We used bias-corrected 95% bootstrap confidence intervals (Adams et al. 1997) of the mean z-transformed correlation coefficients to define the significance of the relationship between different defence strategies. The bias-corrected 95% bootstrap confidence intervals were generated from 4999 iterations. A relationship was considered significant if the confidence interval did not include zero. To test the importance of different sources of variation in determining the sign and magnitude of the correlation between tolerance and resistance, we subdivided studies in terms of various study characteristics and examined between-group heterogeneity using a chi-square test statistic, Q_b. The following sources of variation were examined: plant type (crop vs non-crop), tolerance measure (reduction in growth vs reduction in fitness in damaged plants as compared to the control), resistance measure (1- damage, antibiosis or antixenosis for crop species; 1- damage or a specified resistance trait for non-crop species) and study environment (greenhouse vs field study). Since these study characteristics may be not independent from each other, we first conducted chi-square tests of independence to examine the associations between them (Sokal and Rohlf 1995).

Possible publication bias in ecological and agricultural studies was examined using the funnel plot technique (Light and Pillemer 1984, Palmer 1999). Effect sizes from studies conducted on wild plants and crops were plotted against their sample sizes. In the absence of bias, the resulting plots should be symmetrical around the mean effect size for each group and no correlation between effect size and sample size should occur. Bias against studies with nonsignificant results (i.e. those that did not find significant correlation between resistance and tolerance) would manifest as a gap in the inner area of the funnel as only extreme values in studies with small sample sizes would reach statistical significance. Bias against results in a particular direction (i.e. negative or positive correlations between resistance and tolerance) would manifest as a significant correlation (either positive or negative depending on the direction of the bias) between the effects size and the sample size. We thus calculated Spearman's rank correlations between effect sizes and sample sizes for crops and wild plants.

Results

The relationship between tolerance and resistance was highly variable across studies, with correlation coefficients ranging from -0.943 to 0.986 (Fig. 1). The magnitude and sign of the correlations sometimes varied even for the same plant species (Table 1). When correlations from all the studies were analyzed together ($N = 46$), the mean correlation coefficient was positive ($r_+ = 0.018$) but not significantly different from zero (95% CI = -0.1185 to 0.1581). When the studies were divided into those conducted on crop and non-crop species, the mean correlation coefficients were not significant in either crops or wild species (Table 2), but the difference between the two groups was significant ($Q_b = 3.851$, df = 1, $P = 0.049$). The sign of the correlations differed between the groups; in crops the correlations tended to be positive, in wild species negative. Funnel plots did not reveal any marked asymmetry in the distribution of effect sizes in relation to sample sizes in either ecological or agricultural studies (Fig. 1). In addition, we found no correlation between the effect sizes and sample sizes in either group (crop species: $r = 0.022$, $P = 0.908$; wild: $r = 0.159$, $P = 0.540$). Thus, the difference between crops and wild species in the direction and magnitude of the resistance–tolerance correlations was not due to publication bias.

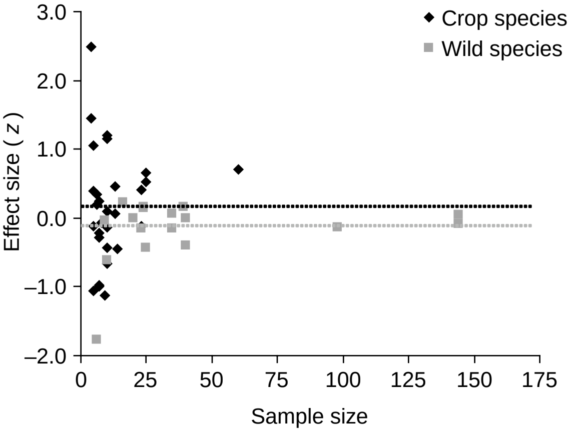

Fig. 1. A funnel plot of effect sizes (Z) and sample sizes. The black dots denote crop species and the grey dots denote wild species. Horizontal lines denote mean effect sizes for crops (black) and wild (grey) studies.

In crop species, there was a significant association between the measures of tolerance and resistance used ($\chi^2 = 9.99$, df = 2, $P = 0.007$). In studies where resistance was assessed as antibiosis or antixenosis, tolerance was usually measured as the difference in growth between damaged and undamaged plants. In contrast, when resistance was measured as 1- damage, tolerance was mainly measured as the difference in fitness between damaged and undamaged plants. The effects of resistance and tolerances measures thus cannot be distinguished in the analysis. The magnitude of the correlation coefficient between tolerance and resistance in crops, however, was not affected either by the measure of resistance ($Q_b = 0.037$, df = 2, $P = 0.981$, Table 2) or by the tolerance measure ($Q_b = 0.373$, df = 1, $P = 0.541$).

Table 2. Mean correlations (r_+) between tolerance and resistance. Resistance 1 = resistance measured as 1- damage; resistance 2 = resistance measured as a specific defensive trait. Correlations that differ significantly from zero are shown in bold.

Category of studies	N	r_+	Bias-corrected bootstrap 95% CI
Crop species	29	0.148	−0.100 to 0.378
Tolerance vs resistance 1	8	0.116	−0.368 to 0.566
Tolerance vs antibiosis	13	0.143	−0.266 to 0.549
Tolerance vs antixenosis	8	0.083	−0.307 to 0.374
Non-crop species	17	−0.076	−0.178 to 0.009
Tolerance vs resistance 1	11	−0.083	−0.218 to 0.027
Tolerance vs resistance 2	3	**−0.069**	−0.608 to −0.000

In non-crop species, the mean correlation coefficient between tolerance and resistance was not significant when resistance was measured as 1- damage (Table 2). When resistance was measured as a specific resistance trait, the mean correlation coefficient was significantly negative, although its magnitude was very low and was based on three correlations from two studies only (Table 2). There were no significant differences between the mean correlation coefficients when resistance was measured as 1- damage or as a specific resistance trait ($Q_b = 0.010$, df = 1, p = 0.919). The impact of the tolerance measure could not be tested for non-crop species because almost all studies used fitness differences to assess tolerance.

No differences were found in the mean correlation coefficient (calculated over all plant types and resistance and tolerance measures) between studies conducted in the greenhouse ($r_+ = 0.139$, 95% CI = −0.190 to 0.459) and in common garden/ field ($r_+ = 0.009$, 95% CI = −0.135 to 0.140; $Q_b = 0.946$, df = 1, P = 0.331).

Discussion

Our survey is the first quantitative review of studies on resistance–tolerance tradeoffs that combines evidence from both the ecological and the agricultural literature. Given that the interest of ecologists in this topic has emerged relatively recently and the diversity of plant species for which the relationship between resistance and tolerance has been examined is still limited, the conclusions of our study should be considered as provisional rather than definite. However, since research in this field is currently quite active, we believe that review of the available studies at the present stage is still very useful because it allows to reveal the gaps in our knowledge and to identify the useful directions for future research.

The main result of our study is that there is no overall trade off in plants between tolerance and resistance to herbivores. The only significant negative correlation found between tolerance and specific resistance traits was very low. The results of our meta-analysis thus contradict the hypothesis that tradeoffs between resistance and tolerance significantly constrain the evolution of different defensive strategies in plants; rather, they support recently suggested models, which predict the coexistence of resistance and tolerance as defense strategies if their allocation costs are unequal (Tiffin 2000b) or non-linear (Restif and Koella 2004).

Our results indicate that the relationship between tolerance and resistance is stronger and more positive in crop species than in non-crop species. This agrees with our prediction that agricultural studies would provide weaker evidence of tradeoffs between resistance and tolerance. This could be either because the absolute levels of resistance and tolerance are often lower in crops than in non-crops (Welter and Steggall 1993, Rosenthal and Welter 1995, Rosenthal and Dirzo 1997) or because artificial selection favored genotypes with high levels of both defense strategies and discarded genotypes which expressed only one strategy. We also found that in crop species the relationship between tolerance and resistance tends to be positive irrespective of the type of resistance. The lack of a tradeoff between tolerance and resistance in crops indicates that selective breeding has succeeded in creating cultivars and varieties that may express several defense strategies simultaneously, although often at lower absolute levels than in wild plants.

In contrast to agricultural studies, studies published in ecological or evolutionary journals usually aim at testing the hypothesis of a tradeoff between resistance and tolerance. If a publication bias against results not supporting a prevailing hypothesis exists (Leimu and Koricheva 2004), published studies can be expected to be more likely to report negative correlations between the two defense strategies. However, we found no evidence of such bias; the mean correlation coefficient between resistance and tolerance for non-crop plants was not significantly different from zero and there was no marked asymmetry in the distribution of the effect sizes in relation to the sample sizes or any significant correlation between the effect sizes and sample sizes. This indicates that the differences between crops and wild species in the magnitude and direction of the correlation between herbivore resistance and tolerance are due to biological reasons (i.e. due to allocation of larger proportion of resources to resistance and tolerance in wild species as compared to crops) rather than to publication bias.

Another possible reason for differences in the magnitude and sign of correlations between crops and wild species could be the fact that most of the studies on crops were conducted in the greenhouse whereas most studies on wild plants were carried out in the field (Table 1). It has been suggested that genetic correlations between tolerance and resistance expressed in the greenhouse may be different from those measured in the field (Tiffin and Rausher 1999) because the novel environment of the greenhouse may result in the expression of positive genetic correlations that are not expressed in the field (Service and Rose 1985). In our meta-analysis, however, we found no differences between studies conducted in the greenhouse or in a common garden or experimental field; in both cases the sign of the correlation was positive.

In wild species, a significant negative correlation between resistance and tolerance was found when a specific defensive trait (chemical or mechanical) was used as a measure of resistance. Stowe (1998) argued that the defensive trait under consideration should be specified in studying possible tradeoffs between tolerance and resistance. This is because the inverse of damage as a measure of resistance can be a composite of a number of traits that may have different relationships with tolerance (Stowe 1998). However, most ecological studies examining the tolerance–resistance tradeoff used the inverse of damage as a measure of plant resistance. Thus, even though the results of our meta-analysis do not support the tradeoff hypothesis, individual resistance traits may exhibit negative correlations with plant tolerance.

Given the relatively small number of studies which have so far examined the relationship between resistance and tolerance in wild plants, we were unable to test other potentially important sources of variation in the magnitude of resistance–tolerance tradeoffs, such as the degree of resource limitation, the type and level of herbivory or plant longevity (Mole 1994). It has been suggested that a tolerance–resistance tradeoff is more likely to be found under strong resource limitation or heavy herbivore damage (Valverde et al. 2003). However, most of the studies examining tolerance–resistance tradeoffs were conducted in more or less controlled environments and under conditions less stressful than in nature. Moreover, many of the studies included in our meta-analysis used natural herbivores or natural damage levels in their experiments. It has recently been debated whether simulated or natural herbivory should be used in tolerance experiments in order to obtain true estimates of tolerance given that the distribution of damage in nature is erratic, and resistance may vary among genotypes, leading to variation in damage levels (Tiffin and Inouye 2000, Lehtilä 2003). In future studies, it would therefore be interesting to examine the relationship between resistance and tolerance under different levels of resource limitation and using natural and simulated herbivory.

Another bias among the available ecological studies assessing the relationship between resistance and tolerance is that almost all of them use annual plants, and data on long-lived species are scarce. Dealing with longlived plants is much more difficult than studying annual plants, for many reasons. For example, the creation of genetic families or lines is much more time-consuming than in annual plants. Moreover, the prediction and estimation of fitness differences between damaged and undamaged plants, i.e. the measurement of tolerance, cannot be reliably performed by means of short-term experiments. Determining the consequences of herbivory for the lifetime fitness of perennial plants requires a modeling approach that is based on demographic data (Doak 1992, Ehrlén 1999). Despite these difficulties, studies assessing the relationship between resistance and tolerance in long-lived plants should be encouraged, since tolerance of herbivory may be a very important defense strategy in such plants; their susceptibility to herbivory is high due to their large size and long life span, and their resistance traits cannot completely exclude herbivory (Haukioja and Koricheva 2000).

To conclude: the results of our meta-analysis provide little evidence of negative genetic correlations between tolerance and resistance, which would indicate a tradeoff between these defensive strategies. It thus seems that tolerance and resistance are not mutually exclusive responses of plants to herbivory, and that plants can evolve and maintain multiple defensive strategies against herbivores. However, tradeoffs between tolerance and individual resistance traits may exist. More empirical studies examining the relationship between tolerance and resistance in different environments are needed, in order to understand the circumstances under which a tradeoff might arise.

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