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Meta-analysis of Trade-offs among Plant Antiherbivore Defenses: Are Plants Jacks-of-All-Trades, Masters of All?

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ABSTRACT: On the basis of physiological and ecological costs of defense allocation, most plant defense theories predict the occurrence of trade-offs between resource investment in different types of antiherbivore defenses. To test this prediction, we conducted a meta-analysis of 31 studies published in 1976–2002 that provided data on covariation of different defensive traits in plant genotypes. We found no overall negative association between different defensive traits in plants; instead, the relationship between defensive traits varied from positive to negative depending on the types of co-occurring defenses. Evidence of trade-off was found only between constitutive and induced defenses. Therefore, to a large extent, plants appear to be jacks-of-all-trades, masters of all and may successfully produce several types of defense without paying considerable trade-offs. Our survey thus provides little evidence that genetic trade-offs between defensive traits significantly constrain the evolution of multiple defenses in plants.

Keywords: meta-analysis, trade-off, plant defense, publication bias.

Plants display different types of defenses against herbivores, including the constitutive and inducible production of various chemical compounds and structural traits. These various defense types often co-occur in the same plant species, genotypes, or individuals. It appears, in fact, that plants seldom, if ever, rely on a single defense mechanism, for example, the production of a single toxin (Schoonhoven 1982); multiple defensive mechanisms are by far more common (Paul and Hay 1986; Hartmann and

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Dierich 1998; Romeo 1998). The possession of several defensive mechanisms may be costly for a plant, since investment in antiherbivore defenses is assumed to reduce the resources available for growth and reproduction (reviewed in Bergelson and Purrington 1996; Koricheva 2002; Strauss et al. 2002). Several authors have therefore suggested the existence of constraints on simultaneous resource allocation to multiple defensive strategies, resulting in negative associations between different types of defenses. Such trade-offs have been predicted to occur among different types of chemical defenses (Lebreton 1982), between chemical and mechanical defenses (Steward and Keeler 1988), and between constitutive and induced defenses (Mattson et al. 1988; Karban and Myers 1989). The concept of trade-offs between antiherbivore defenses is also inherent in most of the plant defense theories, such as the apparency theory (Feeny 1976), the optimal defense theory (Rhoades 1979), the resource availability hypothesis (Coley et al. 1985), and the growth-differentiation balance hypothesis (Herms and Mattson 1992).

However, in some situations, plants may produce several types of defense without paying considerable trade-offs. This may be the case when the benefits of possessing several defenses outweigh the costs. For example, multiple defenses may help to avoid damage by a wider range of attacking organisms as compared with individual defensive mechanisms. Chemical defenses, for instance, are often effective against generalist herbivores but can be circumvented by specialists (van Dam et al. 1995; Hägele and Rowell-Rahier 2000; Wittstock and Gershenzon 2002), whereas mechanical defenses may protect plants against specialized enemies as well (Mauricio 1998). The presence of several defensive mechanisms may also be required for efficient defense against the same herbivore. For instance, plant defenses may interact synergistically, as has been reported for several plant toxins (Berenbaum and Neal 1985; Hummelbrunner and Isman 2001; Calcagno et al. 2002) and for chemical and mechanical defenses in seaweeds (Hay et al. 1994). Finally, under some conditions, defenses may not be costly for plants (van Noordwijk and de Jong 1986; Mole 1994; Koricheva 2002). A functional

multiplicity of defensive traits, including both wide-spectrum resistance against various herbivores and pathogens and physiological roles in plants (e.g., Langenheim 1994; Romeo 1998; Close and McArthur 2002), may also reduce their allocation costs. In the absence of costs, there are no constraints on resource allocation, and selection may favor the maintenance of multiple defenses because it enhances the probability of possessing a trait that confers resistance against organisms with which the plant interacts (Jones and Firn 1991). Thus, the arguments both for and against the trade-offs between the production of different types of antiherbivore defenses by plants exist. No attempt has yet been made, however, to combine the results of different studies examining the covariation of defensive characters in plants in order to assess the magnitude and significance of trade-offs among plant defenses and to understand to what extent these trade-offs may constrain the evolution of multiple defensive traits.

In this article, we review by means of meta-analysis published studies that have examined the relationship between different defensive traits in plants. Since it is based on a formal set of statistical procedures, meta-analysis is less subjective than narrative reviews; it is particularly useful for summarizing the evidence in areas where empirical results provide no clear "consensus" (Arnqvist and Wooster 1995). The critical assumption of meta-analysis (as of all other types of research synthesis) is that the published studies included in the review are representative of all the studies conducted on a subject. This assumption may be violated if statistically nonsignificant results and/or results that contradict widely accepted hypotheses are less likely to be published. When such publication biases occur, meta-analysis based solely on published studies may considerably overestimate the magnitude of the effect (Kotiaho and Tomkins 2002). This problem may be solved by including in the analysis data that are suitable for testing the hypothesis of interest but that were gathered for other purposes. The results of these studies are less affected by publication bias, since the bias toward significant results or toward results in the predicted direction probably does not extend much beyond the primary hypothesis (Cooper 1998). Therefore, in addition to studies specifically testing the existence of trade-offs between plant defenses, we also included in our analysis studies that provided data on the covariation of different defensive traits in plants but did not aim at assessing trade-offs and/or did not report measures of association between defensive traits.

Our analysis addressed the following questions. First, is there a trade-off between different defensive traits in plants? If so, then we would expect a negative correlation between estimates of different defense types within species. Second, does the strength of this relationship depend on the types of co-occurring defenses (e.g., chemical and me-

chanical, or constitutive and induced)? If so, the magnitude of correlations would differ among the above defense types. Third, is there a publication bias against studies that do not support the trade-off hypothesis? Our prediction was that, if such a bias exists, studies that specifically aimed at measuring trade-offs between plant defenses would report stronger negative correlations between defensive traits than studies with other aims. Fourth, is there a bias against nonsignificant results? If so, the magnitude of correlations in studies that report the relationship between defensive measures would be larger than in studies that provide data on the covariation of different defensive traits in plants but do not report measures of association between defensive traits.

Methods

Studies aimed at assessing trade-offs between plant defenses were found by conducting searches in the Web of Science (ISI) electronic bibliographic database (1975–2002). We used different combinations of keywords "trade-off*," "defen?e," "constitutive," "induced," "chemical," "structural," and "mechanical" and searched for articles citing key papers on among-defense trade-offs (Steward and Keeler 1988; Björkman and Anderson 1990; Brody and Karban 1992). In order to retrieve studies that provide data on covariation of different defensive traits in plants but do not aim at assessing trade-offs, we also examined issues of *Biochemical Systematics and Ecology*, *Ecology*, *Journal of Chemical Ecology*, *Oecologia*, *Oikos*, and *Phytochemistry* published between 1990 and 2002. Older studies were found by searching the reference sections of the articles obtained. Altogether, we located 31 suitable studies published during 1976–2002 and conducted on 22 different plant species (see "Studies Included in the Meta-analysis").

For the purpose of this review, we define antiherbivore defense as any plant trait (chemical or mechanical, constitutive or induced) that is known to reduce the preference or performance of herbivores. We restricted our analysis of trade-offs between plant defensive traits to correlations expressed among different plant genotypes (family-mean correlations or correlations among clones or cultivars), because these have clearer evolutionary significance than phenotypic correlations (Roff 1992). In order to be included in the analysis, a study had to provide data on the covariation of defensive characters in the same plant parts and during the same ontogenetic stage. Thus, studies that addressed the between-defense trade-off hypothesis by comparing the expression of various defense types in different plant organs (e.g., Zangerl and Rutledge 1996) or by examining seasonal patterns of allocation to different antiherbivore compounds (e.g., Prudhomme 1983) were not included in the survey.

Measures of chemical defenses were usually expressed as concentrations of secondary metabolites per unit weight of tissue. We excluded studies in which chemical data were expressed as percentages of total yield of compounds in a group (e.g., the percentage of total terpenes), since spurious negative correlations are likely to occur in this case (White 1983; Birks and Kanowski 1988). Measures of mechanical defenses included trichome density and leaf toughness. Induced defenses were measured either as concentrations of defensive secondary metabolites in induced plants or as the inverse of herbivore densities on or damage of induced plants. When both measures were available, we chose concentrations of secondary metabolites over herbivore variables. Measures of induced defenses were included in the analysis only when there was evidence of induction for at least some of the genotypes within a study.

Induced defenses were expressed in original studies either in absolute terms (as the sum of the constitutive defense level and induction response) or in relation to control plants (as a ratio between defenses of damaged and control plants). Since only relative induction response is hypothesized to be negatively correlated with constitutive defenses, we converted absolute measures of induced defenses into induction ratios and used the latter to assess the relationship between constitutive and induced defenses. The trade-off between induced and constitutive defenses was thus assessed by calculating a correlation between the induction ratio of a defensive trait and the absolute level of the same trait in control plants. This approach, however, may produce spurious negative correlations because the ratio is correlated with its own denominator. Recently, a bias-free method of testing for the trade-offs between constitutive and induced defenses has been suggested (Gianoli 2002; Traw 2002). This method is based on the calculation of the slope of the linear regression of absolute values of induced resistance on those of constitutive resistance. If the induction response decreases with increasing constitutive defense, as predicted by the trade-off hypothesis, the slope of the regression line (m) will be <1. Therefore, in addition to analyzing the correlations between induction ratios and constitutive defenses, we also conducted a bias-free analysis by examining the slopes of the regression of induced defense on constitutive defense. A one-tailed t-test was applied to test the hypothesis that the slope is <1, using the formula $t = (m - 1)/SE_m$, where SE_m is the standard error of m and $df = N - 2$ (Zar 1996).

We examined the following three types of trade-offs: between different types of chemical defenses, between chemical and mechanical defenses, and between constitutive and induced defenses. The first category of trade-offs was further subdivided into three types: between individual compounds belonging to the same biochemical group and synthesized in the same pathway (e.g., individual monoterpenes, phenolic glycosides, iridoid glycosides, furanocoumarins), between compounds belonging to different biochemical groups produced in different branches of the same pathway (e.g., phenolic glycosides and tannins, condensed tannins and hydrolysable tannins), and between compounds belonging to different biochemical classes and produced in different pathways (e.g., terpenoids and phenolics). In addition, we distinguished between studies that specifically aimed at measuring trade-offs between plant defenses (as stated in the introductions of the original articles) and those that had other aims.

In many cases, several measures of association between different defensive traits could be retrieved from a single study. To reduce the statistical problems associated with the inclusion of such nonindependent comparisons (Gurevitch et al. 2001), we applied certain rules in selecting the data from each study. First, when data on several chemical defenses of the same plant species were reported, we included a maximum of three individual compounds per each biochemical group. Compounds were chosen on the basis of their concentrations, with the three most abundant ones included. Second, when the association between different defensive traits was examined in different years, we chose the year in which the largest correlation was observed. Third, when data were available for different plant parts or different ontogenetic stages of plant organs, foliage was always preferred to other plant parts (e.g., buds and stems), and young foliage was always preferred to mature one. Fourth, when associations between defensive traits were examined for several plant species, we included the data for each species. Fifth, when different induction treatments were applied to plants, natural damage was preferred over mechanical damage and the latter over chemical elicitors; in the case of different levels of the same induction treatment, the treatment resulting in the highest magnitude of induced responses was chosen. Our final database consisted of 54 measures of association between different defensive characters (appendix).

We used the Pearson's product-moment correlation coefficient r as a common measure of association between different defensive traits because in many studies the results are reported in the form of correlation coefficients. The advantages of r as a measure of the effect size are the simplicity of interpretation (the absolute value of r varies from −1 to +1, and its squared value represents the amount of variance explained by the predictor variable) and the possibility of obtaining it from most of the commonly used test statistics (Rosenthal 1994). When the results of studies were expressed in the form of correlation coefficients, the latter were included into the database directly. The F values from statistical tests were converted into r by using the formula $r = [F/(F + df)]^{1/2}$ (Rosenthal

Table 1: Mean correlations (r_+) among different types of antiherbivore defenses

Category of studies	N	r_+	Bias-corrected bootstrap 95% CI
Chemical defenses	34	.235	−.072 to .465
Individual compounds within a group	19	.481*	.077 to .694
Groups of compounds within a class	10	−.119	−.384 to .187
Classes of compounds	5	−.234	−.798 to .401
Mechanical vs. chemical defenses	5	.033	−.200 to .255
Constitutive vs. induced defenses	15	−.453*	−.589 to −.322

   * Correlations significantly different from 0.

1994). When quantitative data on the co-occurrence of different defensive measures in plant genotypes were presented in the form of tables or graphs but correlation coefficients were not reported, we calculated Pearson's product-moment correlation coefficient by using PROC CORR (SAS Institute 1996). Data from graphs were obtained by digital enlargement and analysis of the figures using SigmaScan.

Meta-analysis was carried out using the MetaWin 2.0 statistical program (Rosenberg et al. 2000). Individual correlation coefficients were z transformed, weighed by their sample size, and combined across studies using the mixed effects model, which assumes that differences among studies within class are due to both sampling error and random variation. Mixed models are preferable to fixed effect models in ecological data synthesis because the assumptions of the former are more likely to be satisfied (Gurevitch and Hedges 2001). The relationship between the measures of plant defenses was considered significant if the 95% confidence interval (CI) of the mean z-transformed correlation coefficient did not include 0. To be conservative, we used bias-corrected 95% bootstrap CIs (Adams et al. 1997) generated from 4,999 iterations. Between-group heterogeneity was examined using a χ^2 test statistic, Q_b, calculated as

$$Q_b = \sum_{i=1}^{m} w_{i_+} z_{i_+}^2 - \frac{\left(\sum_{i=1}^{m} w_{i_+} z_{i_+}\right)^2}{\sum_{i=1}^{m} w_{i_+}},$$

where m is the number of groups, w_{i_+} is the sum of the mixed model weights for the ith group, and z_{i_+} is the cumulative effect size for the ith group (Gurevitch and Hedges 2001). The resulting statistic can be tested against a χ^2 distribution with $m - 1$ df. A significant Q_b implies that there are differences in cumulative effect sizes among the groups. At the end of the analysis, the mean z values for each group and their 95% CIs were back transformed to the Pearson's correlation coefficient for ease of interpretation.

To combine the probabilities of one-tailed t-tests of slopes of the linear regression of induced defense on constitutive defense being <1, we used the sum of Z's method (Rosenthal 1979). The statistic Z is defined as $Z = \sum_{i=1}^{N} Z_i/N^{1/2}$, where N is the number of studies and Z_i is the standard normal deviate for the probability from the ith study. The resulting Z value is then tested against the critical value on the basis of the normal distribution. One of the advantages of the sum of Z's method is that it allows the calculation of a fail-safe number (Rosenthal 1979). The fail-safe number provides an estimate of the number of undiscovered studies with a mean effect size of 0 needed to reduce the combined significance to the critical level (.05) and is calculated as $N_{FS} = (\sum_{i=1}^{N} Z_i/1.645)^2 - N$, where 1.645 is the standard normal deviate associated with $P = .05$ and all other quantities are defined as above. Large fail-safe numbers suggest that a finding is resistant to unretrieved null results.

Results

When all types of chemical defenses were considered together, the mean correlation coefficient between different chemical defensive traits was not significantly different from 0 (table 1). However, there were significant differences in mean correlations between individual compounds belonging to the same biochemical group, different groups within the same class, and different classes of chemical compounds ($Q_b = 7.11$, df $= 2$, $P = .029$). The mean correlation coefficient between individual compounds belonging to the same group was significantly positive, whereas the mean correlation coefficients between concentrations of compounds belonging to different groups within a class and between different classes of chemical compounds were not significantly different from 0 (table 1). However, significant positive correlations between individual compounds within a group were found only in articles that self-reported the relationship ($r_+ = 0.666$, 95% CI $= 0.529$ to 0.775, $n = 11$), whereas correlations calculated as a part of this study were not significantly different from 0 ($r_+ = 0.006$, 95% CI $= -0.717$ to 0.710,

$n = 8$; $Q_b = 5.93$, df $= 1$, $P = .015$). A comparison of correlations between studies with different aims could not be conducted because only one of the studies reporting correlations among individual compounds has aimed specifically at assessing trade-offs between defenses.

Only two studies have examined genetic association between mechanical and chemical defenses providing five correlations for the meta-analysis (appendix). The mean correlation coefficient between mechanical and chemical defenses was not significantly different from 0 (table 1).

The mean correlation coefficient between constitutive and induced defenses was significantly negative (table 1). The fail-safe number for the above correlation was 153, indicating high tolerance for the unretrieved null results. The magnitude of correlations was not affected by the aim of the study (studies aiming at detection of trade-offs: $r_+ = -0.446$, 95% CI $= -0.608$ to -0.284, $n = 8$; studies with other aims: $r_+ = -0.452$, 95% CI $= -0.653$ to -0.206, $n = 7$; $Q_b = 0.002$, df $= 1$, $P = .968$). The difference between reported and calculated correlations between measures of constitutive and induced defenses was not significant (reported correlations: $r_+ = -0.475$, 95% CI $= -0.640$ to -0.319, $n = 6$; calculated correlations: $r_+ = -0.394$, 95% CI $= -0.589$ to -0.192, $n = 9$; $Q_b = 0.304$, df $= 1$, $P = .582$).

The slopes of the regression of induced defenses on constitutive defenses were significantly <1 in four out of 14 tests (appendix). Combining the one-tailed probabilities from individual t-tests of $m < 1$ by the sum of Z's method resulted in $Z = 3.9394$, which corresponds to the overall $P < .00005$. The fail-safe number (the number of additional studies averaging null results required to bring the overall P value to .05 level) was 66.

Discussion

The main findings of this work are that there is no overall negative association between different defensive traits in plants and that the relationship between defensive traits varies from positive to negative depending on the types of co-occurring defenses. Significant positive correlations were found between individual compounds belonging to the same biochemical group, for example, between individual monoterpenes, phenolic glycosides, iridoid glycosides, and furanocoumarins (appendix). Positive correlations between two compounds may indicate linkage of genes or linkage of biosynthetic reaction sequences (Zavarin 1970; White 1983). For instance, all furanocoumarins share a common precursor, umbelliferone (Zangerl and Berenbaum 1990). Thus, any genetic or environmental variation affecting the abundance of umbelliferone is also likely to affect the abundance of all the furanocoumarins, resulting in highly significant positive correlations between

their concentrations. A negative correlation may, however, emerge between two biosynthetically closely related compounds if they share the same precursor and the amount of the precursor is limiting, as is the case for α-pinene and 3-carene in Scots pine (Hiltunen 1976).

Interestingly, correlations between individual compounds reported in the original studies were significantly higher than those calculated as a part of this study. A similar tendency was found in another recent meta-analysis (Reed and Frankham 2001): correlations between the molecular and quantitative measures of genetic variation were higher in articles that reported the relationship than in articles where the correlation was not reported but calculated as part of the meta-analysis. This pattern indicates the presence of publication bias against nonsignificant results. As a result, the magnitude of positive correlation between individual compounds within a group obtained in our meta-analysis may be overestimated and should be used only as an estimate of the upper limit of the true effect size (Kotiaho and Tomkins 2002).

No significant among-genotype correlations were found between concentrations of compounds belonging to different groups within a class, between different classes of chemical compounds, and between chemical and mechanical defenses (table 1). These patterns suggest that there are no genetic constraints on the evolution of multiple chemical and mechanical defensive traits, and hence these traits may exhibit independent evolutionary responses to selection. This finding agrees with the results of several recent studies that have specifically examined the responses of different defensive traits to selection (e.g., Mauricio and Rausher 1997; Siemens and Mitchell-Olds 1998; Tiffin 2002; but see Berenbaum and Zangerl 1988). The explanation for the observed lack of trade-offs may lie in the fact that the above defensive mechanisms may be directed against different sets of herbivores (Mauricio 1998) and may interact synergistically (Berenbaum and Neal 1985; Hay et al. 1994). Correlations between chemical and mechanical defenses may also be obscured by the difference in the timescale at which they operate (Ward and Young 2002). The production of mechanical defenses such as thorns is irreversible and may integrate a response over several years, while the production of secondary metabolites is more variable on a shorter timescale. Finally, our failure to detect significant negative associations between different classes of defensive compounds and between chemical and mechanical defenses may be due to the limited number of studies available in these categories. Clearly, more studies assessing genetic correlations between the above defense types are needed.

Evidence of trade-off was found only between constitutive and induced defenses. Negative association between the above defense types was revealed by two different

methods: combining correlations between constitutive defenses and induction ratios and combining probabilities from tests of slopes of the regression of induced defenses on constitutive levels. The first method may produce negative spurious correlations, but the second method is free of this bias (Gianoli 2002; Traw 2002). The magnitude of correlations was similar for reported and calculated correlations and was not affected by the aim of the study. In addition, fail-safe numbers were reasonably high, suggesting that the results of the analysis are robust to publication bias. Our results thus support the prediction that constitutive and induced defenses will be negatively correlated (Mattson et al. 1988; Karban and Myers 1989; Herms and Mattson 1992). However, even though the correlation between constitutive and induced defenses was significant, variation in constitutive defense levels explained only 20.5% of variation in induced responses. This indicates that factors other than the constitutive defense levels (e.g., environmental variation) may be more important determinants of the magnitude of induced responses in plants. In addition, recent studies on conifers (Raffa and Smalley 1995; Litvak and Monson 1998) indicate that the initial assumption that plants with high levels of constitutive defenses will obtain little benefit from possessing inducible defenses (Mattson et al. 1988; Karban and Myers 1989; Herms and Mattson 1992) may not hold since the two types of defenses are not functionally redundant and provide different benefits to the plant. For instance, while constitutive levels of monoterpenes in conifers reduce the survival and performance of herbivores, the induced production of monoterpenes counteracts the depletion of the constitutive pool caused by a mass herbivore attack (Raffa and Smalley 1995) or by the volatilization of monoterpenes (Litvak and Monson 1998).

Overall, our survey provides little evidence that genetic trade-offs between defensive traits significantly constrain the evolution of multiple defenses. To a large extent, plants appear to be jacks-of-all-trades, masters of all: they may successfully produce several types of defense without paying considerable trade-offs. Therefore, the original view that multiple defenses are costly and functionally redundant should be replaced by the idea that environmental variability and positive interactions among defenses can make many combinations of defenses possible and evolutionarily advantageous. Our results also strengthen concerns about the problem of publication bias against nonsignificant results in ecological meta-analyses (Jennions and Møller 2002; Kotiaho and Tomkins 2002). To avoid this problem, meta-analyses should whenever possible include both studies that directly report the measures of outcome to be included in the analysis and studies that provide raw data suitable for calculation of the effect size of interest.

Table A1: Characteristics of studies included in the meta-analysis and among-defense correlations

Reference[a]	Plant	Type of trade-off[b]	Aim of study	Measure of association	Source	Trait 1	Trait 2	r	N	m^c	P^d
Adler et al. 1995	*Plantago lanceolata*	CWG	Trade-off assessment	Reported	Table 2	Aucubin	Catapol	.762	30		
Bowers and Stamp 1992	*Plantago lanceolata*	CWG	Other	Calculated	Table 2	Aucubin	Catalpol	.767	5		
Duncan et al. 2001	*Picea sitchensis*	CWG	Other	Reported	Table 1	α-pinene	β-pinene	.874	30		
Duncan et al. 2001	*Picea sitchensis*	CWG	Other	Reported	Table 1	α-pinene	Camphene	.921	30		
Duncan et al. 2001	*Picea sitchensis*	CWG	Other	Reported	Table 1	β-pinene	Camphene	.750	30		
Hakulinen et al. 1995	*Salix myrsinifolia*	CWG	Other	Calculated	Fig. 1	Salicortin	Salicin	.179	9		
Hiltunen 1976	*Pinus sylvestris*	CWG	Other	Calculated	Tables 3, 4	α-pinene	3-carene	−.970	15		
Julkunen-Tiitto et al. 1995	*Salix myrsinifolia*	CWG	Other	Calculated	Table 1	Salicin	Salicortin	.712	6		
Julkunen-Tiitto et al. 1995	*Salix myrsinifolia*	CWG	Other	Calculated	Table 1	Salicortin	2′-O-acetyl-salicortin	−.892	6		
Lindroth and Hwang 1996	*Populus tremuloides*	CWG	Other	Reported	Table 1	Salicortin	Tremulacin	.83	31		
Nichols-Orians et al. 1993	*Salix sericea*	CWG	Other	Reported	P. 540	Salicortin	2′-cinnamoyl salicortin	.478	16		
Orians et al. 1996	*Salix sericea*	CWG	Other	Reported	P. 721	Salicortin	2′-cinnamoyl salicortin	.14	13		
Osier et al. 2000	*Populus tremuloides*	CWG	Other	Calculated	Table 1	Salicin	Tremulacin	.211	10		
Osier et al. 2000	*Populus tremuloides*	CWG	Other	Calculated	Table 1	Salicin	Salicortin	.006	10		
Osier et al. 2000	*Populus tremuloides*	CWG	Other	Calculated	Table 1	Salicortin	Tremulacin	.949	10		
Shonle and Bergelson 2000	*Datura stramonium*	CWG	Other	Reported	Table 5	Hyoscyamine	Scopolamine	.4623	100		
Zangerl et al. 1989	*Pastinaca sativa*	CWG	Other	Reported	Table 4	Bergapten	Xanthotoxin	.603	20		
Zangerl et al. 1989	*Pastinaca sativa*	CWG	Other	Reported	Table 4	Bergapten	Imperatorin	.488	20		
Zangerl et al. 1989	*Pastinaca sativa*	CWG	Other	Reported	Table 4	Imperatorin	Xanthotoxin	.550	20		
Agrawal et al. 2002	*Raphanus raphanistrum*	CBG	Other	Reported	Table 3	Indolyl glucosinolates	Non-indolyl glucosinolates	.16	28		
Hakulinen et al. 1995	*Salix myrsinifolia*	CBG	Other	Calculated	Fig. 1	Salicortin	Chlorogenic acid	−.496	9		
Hwang and Lindroth 1997	*Populus tremuloides*	CBG	Other	Calculated	Fig. 3	Phenolic glycosides	Condensed tannins	.226	13		
Julkunen-Tiitto et al. 1995	*Salix myrsinifolia*	CBG	Other	Calculated	Table 1	Salicortin	Chlorogenic acid	−.584	6		
Julkunen-Tiitto et al. 1995	*Salix myrsinifolia*	CBG	Other	Calculated	Table 1	2′-O-acetyl-salicortin	Chlorogenic acid	.527	6		
Julkunen-Tiitto et al. 1995	*Salix myrsinifolia*	CBG	Other	Calculated	Table 1	Salicortin	Condensed tannins	.678	6		
Julkunen-Tiitto et al. 1995	*Salix myrsinifolia*	CBG	Other	Calculated	Table 1	2′-O-acetyl-salicortin	Condensed tannins	−.457	6		
Julkunen-Tiitto et al. 1995	*Salix myrsinifolia*	CBG	Other	Calculated	Table 1	Chlorogenic acid	Condensed tannins	−.667	6		
Kaundun et al. 2000	*Pseudotsuga menziesii*	CBG	Other	Calculated	Table 2	Proanthocyanidins	Flavonol aglycones	−.104	10		
Lindroth and Hwang 1996	*Populus tremuloides*	CBG	Other	Reported	Table 1	Phenolic glycosides	Condensed tannins	−.39	31		
Adler et al. 1995	*Plantago lanceolata*	CBC	Trade-off assessment	Reported	Table 2	Catalpol	Verbascoside	.588	30		
Adler et al. 1995	*Plantago lanceolata*	CBC	Trade-off assessment	Reported	Table 2	Aucubin	Verbascoside	.586	30		
Haskins and Gorz 1986	*Sorgum bicolor*	CBC	Trade-off assessment	Reported	P. 3	Leucoantho-cyanidins	Dhurrin	−.680	11		
Mutikainen et al. 2002	*Betula pendula*	CBC	Trade-off assessment	Reported	Table 2	Flavonol glycosides	Resin droplets	−.66	10		
Ross and Jones 1983	*Lotus corniculatus*	CBC	Other	Calculated	Table 4	Condensed tannins	Cyanogeneic glycosides	−.932	6		

Reference[a]	Species	[b]				Constitutive	Induced			[c]	[d]
Agrawal et al. 2002	*Raphanus raphanistrum*	CM	Other	Reported	Table 3	Indolyl glucosinolates	Trichome density	.15	28		
Agrawal et al. 2002	*Raphanus raphanistrum*	CM	Other	Reported	Table 3	Indolyl glucosinolates	Leaf toughness	−.30	28		
Agrawal et al. 2002	*Raphanus raphanistrum*	CM	Other	Reported	Table 3	Non-indolyl glucosinolates	Trichome density	−.01	28		
Agrawal et al. 2002	*Raphanus raphanistrum*	CM	Other	Reported	Table 3	Non-indolyl glucosinolates	Leaf toughness	−.19	28		
Mauricio and Rausher 1997	*Arabidopsis thaliana*	CM	Other	Reported	P. 1438	Trichome density	Glucosinolates	.381	144		
Bi et al. 1994	*Glycine max*	CI	Other	Calculated	Tables 1, 3	Constitutive lipoxygenases	Induction ratio of lipoxygenases	.514	5	1.33	.230
Brody and Karban 1992	*Gossypium hirsutum*	CI	Trade-off assessment	Reported	*F* on p. 303	Inverse of mite density on control plants	% reduction in mite density on induced plants	−.147	10	1.08	.412
Ding et al. 2000	*Triticum* sp.	CI	Other	Calculated	Fig. 7*B*	Ferulic acid in control plants	Induction ratio of ferulic acid	.122	5	1.28	.323
English-Loeb et al. 1998	*Vitis* spp.	CI	Trade-off assessment	Reported	P. 301	Inverse of mite density on control plants	% reduction in mite density on induced plants	−.310	7	.31	.132
Havill and Raffa 1999	*Populus* spp.	CI	Other	Calculated	Table 3	Inverse of consumption on control plants	% reduction in consumption on induced plants	−.601	12	.42	.011
Hopkins et al. 1998	*Brassica napus*	CI	Other	Calculated	Fig. 4	Constitutive glucosinolates	Induction ratio of glucosinolates	−.632	8	.75	.287
Keinänen et al. 1999	*Betula pendula*	CI	Trade-off assessment	Calculated	Fig. 2	Constitutive DHPPG in fertilized plants	Induction ratio of DHPPG	−.031	10	1.01	.493
Keinänen et al. 1999	*Betula pendula*	CI	Trade-off assessment	Calculated	Fig. 2	Constitutive flavone aglycones in fertilized plants	Induction ratio of flavone aglycones	−.416	10	.51	.131
Leszczynski and Dixon 1990	*Triticum aestivum*	CI	Other	Calculated	Table 2	Constitutive DIMBOA aglucones	Induction ratio of DIMBOA aglucones	−.954	4	.21	.027
Ruuhola et al. 2001	*Salix myrsinifolia*	CI	Other	Calculated	Fig. 4	Constitutive salicylates	Induction ratio of salicylates	−.658	6	.88	.244
Traw 2002	*Brassica nigra*	CI	Trade-off assessment	Reported	Fig. 2*A*	Constitutive trichome density	Induction ratio of trichome density	−.702	47	.51	.001
Traw 2002	*Brassica nigra*	CI	Trade-off assessment	Reported	Fig. 2*B*	Constitutive sinigrin	Induction ratio of sinigrin	−.386	47	.67	.029
Traw 2002	*Brassica nigra*	CI	Trade-off assessment	Reported	Fig. 2*C*	Constitutive glucobrassicin	Induction ratio of glucobrassicin	−.381	47	.79	.174
Underwood et al. 2000	*Glycine max*	CI	Trade-off assessment	Reported	P. 86, fig. 3	Beetle preference for other genotypes	Beetle preference for undamaged plants	−.37	6		
van Dam and Vrieling 1994	*Cynoglossum officinale*	CI	Other	Calculated	Figs. 1, 2	Constitutive pyrrolizidine alkaloids	Induction ratio of pyrrolizidine alkaloids	−.316	17	.79	.135

[a] References are listed in the reference list titled "Studies Included in the Meta-analysis (Appendix)."

[b] CBC = between classes of chemical compounds; CBG = between groups of chemical compounds within a class; CI = between constitutive and induced defenses; CM = between chemical and mechanical defenses; CWG = between individual compounds within a group.

[c] m = the slope of the regression of absolute levels of induced defenses on constitutive levels.

[d] P = one-tailed probability of t-test for $m < 1$.

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