

Damage-induced changes in woody plants and their effects on insect herbivore performance: a meta-analysis

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We conducted a meta-analysis of 68 studies published between 1982 and 2000 in which the responses of woody plants to natural or simulated herbivore damage and/or insect herbivore performance on control and damaged plants were measured. Cumulative meta-analyses revealed dramatic temporal changes in the magnitude and direction of the plant and herbivore responses reported during the last two decades. Studies conducted in the 1980s reported increase in phenolic concentrations, reduction in nutrient concentrations and negative effect on herbivore performance, consistently with the idea of induced resistance. In contrast, in the early 1990s when the idea that some types of plant damage may result in induced susceptibility was generally accepted, studies reported non-significant results or induced susceptibility, and smaller effects on herbivores. The above changes may reflect paradigm shifts in the theory of induced defenses and/or the differences between study systems used in the early and the more recent studies. Overall, plant growth and carbohydrate concentrations were reduced in damaged plants despite enhanced photosynthetic rates. Damage increased the concentrations of carbon and phenolics, while terpene concentrations tended to decrease after damage; changes in nutrient concentrations after damage varied according to nutrient mobility, inherent plant growth rate, ontogenetic stage and plant type (deciduous/evergreen). Early season damage caused more pronounced changes in plants than late season damage, which is in accordance with the assumption that vigorously growing foliage has a greater capacity to respond to damage. Insect growth rate and female pupal weight decreased on previously damaged plants, while herbivore survival, consumption and male pupal weight were not significantly affected. The magnitude and direction of herbivore responses depended on the type of plant, the type of damage, the time interval between the damage and insect feeding (rapid/delayed induced resistance), and the timing of the damage.

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Induced responses of plants to herbivore damage have been studied extensively since the 1970s. These responses include changes in plant chemical composition, phenology, morphology, photosynthesis and growth (reviewed by Karban and Baldwin 1997). The above changes have been considered either as active defensive reactions against further herbivory (Rhoades 1979) or as compensatory changes for coping with reduced photosynthetic area and biomass (Trumble et al. 1993, Gerhardt 1998) and the resulting nutrient stress (Tuomi

et al. 1984). This research has shown that both plant responses to herbivory and effects of the responses on herbivores vary widely. Nitrogen concentrations of plant tissue, for example, have been found to either increase following damage (Piene and Percy 1984, Ericsson et al. 1985, Wagner and Evans 1985, Wagner 1988) or decrease (McClure 1980, Tuomi et al. 1984, Myers and Williams 1987). Similarly, while some studies have reported an increase in the production of defensive secondary compounds following damage

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(Wagner and Evans 1985, Tuomi et al. 1988a), others have failed to detect any effect (Chapin et al. 1985, Julkunen-Tiitto et al. 1995). In early studies it was assumed that induced changes in plants always have a negative impact on herbivores, resulting in slower growth, longer development time, lower fecundity and/or asynchrony between plant and herbivore development, and leading ultimately to a reduction in subsequent herbivore damage to the plant (induced resistance, Haukioja and Hakala 1975). However, later studies have revealed that the consequences of induced changes in plants for herbivores may vary from induced resistance to induced susceptibility (reviewed by Haukioja 1990, Karban and Baldwin 1997).

The variation observed in plant responses to damage may depend on the plant type, ontogenetic stage and growth rate, and on the timing, amount and type of damage (reviewed by Karban and Baldwin 1997). The traditional view has been that evergreens express induced resistance to a lesser extent than deciduous plants (Wagner 1988). This is because evergreens store carbon and nutrients in their foliage, so that herbivory results in the loss of most of their reserves; deciduous plants, on the other hand, store carbon in the stems and roots, and are therefore able to produce carbon-based defenses in response to herbivory (Bryant et al. 1988, Tuomi et al. 1988b). It has been also assumed that induced resistance is stronger in inherently fast-growing plants than in slow-growing ones (Karbon and Baldwin 1997), for several reasons. First, fast-growing plants allocate most of their resources to growth and as a result may have a lower capacity to produce constitutive defenses (Bryant et al. 1983, Coley et al. 1985, Mattson et al. 1988, Herms and Mattson 1992). Induced defenses may therefore represent a less costly alternative for fast-growing plants. Second, the rate of metabolism in slowly-growing plants may be too slow to generate quick and effective responses to damage (Karbon and Baldwin 1997). Furthermore, many of the mechanisms of induced responses are associated with growth processes, and fast-growing plants may therefore have a better capacity to respond. For the same reasons induced responses are believed to be more pronounced in early season than in late season foliage (Karbon and Baldwin 1997). The timing of the damage may also cause variation in compensatory responses, since the latter rely mainly on translocation of nutrients and carbohydrates from shoot and root reserves (Webb 1981, van der Meijden et al. 1988), which experience seasonal changes (Kramer and Kozlowski 1979).

The two most commonly studied types of herbivory in plants are defoliation (usually caused by insects) and browsing (caused by mammalian herbivores). In experimental studies of woody plant induced responses, the above damage types are applied to the plants either by using herbivores or by mimicking herbivore damage mechanically (e.g. with scissors). Simulated herbivory

may cause different changes in the plant as compared to natural herbivore damage due to differences in the amount, timing and spacial pattern of damage or the absence of specific chemical elicitors of induced responses (Schultz 1988, Baldwin 1990). Furthermore, in contrast to defoliation, browsing has been shown to induce susceptibility in a host plant (Danell and Huss-Danell 1985, Danell et al. 1985, Haukioja et al. 1990). Haukioja et al. (1990) suggested that this difference may be due to the release of apical dominance when the apical buds are removed by mammalian browsing. In addition to the type of damage, the amount of damage may also affect plant responses (reviewed by Karban and Baldwin 1997). In some cases, moderate damage has been found to cause the greatest effect (Brown et al. 1991), while in other studies either the response increased linearly with an increase in damage level (Lewinsohn et al. 1991), or the damage level had no effect at all (Valentine et al. 1983).

The potential evolutionary benefit of induced resistance for a plant is to decrease further consumption of the plant's biomass (Bryant et al. 1991). Although consumption is the variable which directly affects plant fitness, retarded herbivore growth, lower fecundity and increased mortality are also indirectly important because they may modify the timing of peak consumption and reduce the population density of the next herbivore generation. It is unclear, however, whether changes in herbivore performance have any bearing at the population level (Fowler and Lawton 1985, Myers 1988). The variation observed in herbivore responses to induced changes in plants may be caused by variability in the induced responses of plants or by variability in the effects of plant responses on herbivores. The effects on insect herbivores may depend on the herbivore feeding guild and specialization, and on whether the effects are expressed as rapid or delayed. Rapid induced resistance (RIR) affects the performance of the same herbivore generation which caused the damage, while delayed induced resistance (DIR) affects the next herbivore generation (Haukioja and Hanhimäki 1985). Rhoades (1979) proposed that RIR involves "qualitative defenses" that are effective against generalists but not specialists, in contrast to DIR, which involves "quantitative defenses" and is effective against both specialists and generalists. In addition, specialist herbivores may be better adapted to cope with the defenses of their host plant than generalists. Reavey (1991), on the other hand, has argued that generalist herbivore species may not be able to detect minor changes in their host plants caused by damage; thus specialists may be more severely affected by induced resistance than generalists.

Previous reviews of plant induced responses to herbivory and effects of the responses on herbivores have been either narrative or based on vote-counting procedures (Wagner 1988, Haukioja 1990, Coleman and Jones 1991, Karban and Baldwin 1997). These reviews

have demonstrated great variability in plant and herbivore responses, and have suggested several possible sources of variation. The most recent review, Hawkes and Sullivan (2001), examined the impact of herbivory on plant growth and reproduction by means of meta-analysis. Meta-analysis has several advantages over narrative reviews and vote-counting: it allows assessment of the magnitude and significance of the effect across studies, and reveals the relative importance of the different study characteristics contributing to the magnitude of the effect (Gurevitch and Hedges 1993). In the present paper, we use the meta-analytic approach to examine general patterns and sources of variation in induced changes of plants and in the effects of these changes on insect herbivores. We review induced changes in plant chemical characteristics which may be of importance for subsequent herbivory (concentrations of water, nutrients, carbohydrates and secondary compounds) and the accompanying changes in plant growth and photosynthesis. Furthermore, we examine changes in insect herbivore performance measured in terms of pupal mass, herbivore growth rate, survival and consumption. We have restricted the scope of our review to woody plants; we have also excluded specific plant responses, such as volatiles, and have focused on more general, non-specific plant responses. As possible sources of variation in plant and herbivore responses we examine several characteristics of the study plant, the herbivore species whose performance was measured, and experimental design. We also consider temporal trends in the magnitude of the reported effects of induced changes from the earliest to the most recent studies, since changes in the magnitude of research findings with time appear to be common in ecology (reviewed by Jennions and Møller 2002).

Material and methods

The database

The database was compiled by conducting keyword searches in the Current Contents, Biological Abstracts and Biosis Preview databases, covering studies published between 1980 and 2001, and by surveying the reference sections of the papers obtained and of recent reviews on the topic (Karban and Baldwin 1997). To be included in the analysis, a study had to meet the following criteria: 1) plants and herbivores had been randomly assigned to the treatments by the experimenter; 2) the herbivory treatment had an appropriate control, which did not undergo herbivore damage during the experiment; 3) means, some measure of variance, and the sample sizes of the control and experimental groups were provided in the article in numerical or graphic form. On the basis of these criteria, we excluded studies in which plants were assigned

to herbivory and control treatments not randomly but according to the extent of natural herbivore damage they received (Faeth 1986, Leather et al. 1987, Glyphis and Puttick 1989, Trewella et al. 1997). The problem with these studies is that the differences observed between the experimental and control groups could be due either to induced responses or to differences in constitutive resistance, which affect herbivore diet selection. Experiments where the control group had been protected with insecticide during a natural herbivore outbreak (Piene and Percy 1984, Kaitaniemi et al. 1998), however, were included, as these were considered not to suffer excessively from the problems mentioned above. We excluded studies examining the effects of bark beetle attack, since induced responses in this case may be elicited by a bark-beetle vectored fungus.

Our final database consisted of 68 studies published between 1982 and 2000, conducted on 52 woody plant species and 19 insect herbivore species (see Appendix). Studies of the database contained 574 measurements of plant responses to natural or simulated herbivore damage, and 264 measurements of herbivore performance on control and damaged plants.

Response variables

We included in the database measurements of plant responses that are likely to be of importance for herbivores: concentrations of water, nutrients, carbohydrates and secondary compounds. We also included responses in terms of plant growth and photosynthesis, in order to test whether changes in plant chemical composition were always accompanied by changes in growth. Growth measurements were included only in the case of studies where other plant or herbivore variables were also measured; studies reporting plant growth measurements alone were excluded, since the impact of herbivory on plant growth and reproduction has been examined in a recent meta-analysis (Hawkes and Sullivan 2001). Some of the plant response variables were grouped for the analyses. The groups and their individual variables in the database were: area-based photosynthesis rate (measured as the net amount of carbon fixed per unit leaf area), mass-based photosynthesis rate (measured as the net amount of carbon fixed per unit leaf mass), plant growth (leaf area, shoot length, plant biomass, plant height), carbohydrate concentrations (starch, sugars, total non-structural carbohydrates), carbon concentration, nutrient concentrations (nitrogen, potassium, magnesium, calcium, sulphur, phosphorus), water concentration, phenolic concentrations (condensed tannins, hydrolyzable tannins, phenolic glycosides, catechin, total phenolics), protein-precipitation capacity of the tannins (PPC) and terpene concentrations (monoterpenes and sesquiterpenes).

Insect performance variables included were the ones most commonly measured in the studies examined: herbivore growth rate, pupal mass, survival and consumption. Experiments measuring growth, pupal mass and survival were conducted either as feeding trials on detached leaves and shoots in the laboratory or by rearing insects on experimental trees in the field. Growth rate was measured either as the relative growth rate (RGR) or as the duration of a development period, for example an instar. RGR is calculated as the growth of a herbivore during a feeding trial divided by the duration of the trial. If both RGR and development time were reported in the same paper, only RGR was included in the database. If the pupae were sexed, we recorded changes in pupal mass for each sex separately. Three different experimental designs were used to measure consumption: laboratory feeding trials where just one type of foliage, either damaged or intact, was offered to the herbivore (no-choice tests); laboratory choice tests, where both damaged and intact leaves were offered to the herbivore; and choice tests in which the consumption of damaged and control plants was compared in the field. The herbivores used in the experiments were mostly Lepidoptera or Hymenoptera (sawfly) larvae, except for one study where chrysomelid beetle, *Plagioderma versicolora*, was used.

The individual measurements from the papers were selected according to the following rules. When several damage levels or different damage types (e.g. simulated and insect) were used in a study, all of them were included. In both cases, different plant individuals were used for different damage levels and types; the dependence was therefore not considered to be excessive. When responses were measured at different time intervals after the damage using the same experimental plants or herbivores, the measurement resulting in the largest difference between treatment and control was selected. When the effects of herbivory on plants had been measured under different nutrient conditions, the non-fertilized treatment or natural nutrient level were chosen. If the same variable was measured in different tissues of the same study plants, we selected only foliage measurements. If the performance of several herbivore species was measured in the same study, all species were included.

Explanatory variables

To explain variation in plant responses we recorded the following variables: 1) Publication year. 2) Plant growth rate. Objective categorization of plant inherent growth rates is difficult because personal opinions may differ (Karban and Baldwin 1997) and the growth rate is not constant throughout the life of the plant. To keep the error as small as possible, we used only two growth rate classes, categorizing plant species as either fast- or

slow-growing, using information provided in original studies or in reviews by Karban and Baldwin (1997) and Loehle (1988). 3) Plant type: deciduous/evergreen plant. This division was essentially the same as gymno/angiosperms, with a few exceptions (e.g. *Larix* spp.); it was thus impossible to separate the effects of leaf longevity from those of plant phylogeny. 4) Plant ontogenetic stage. The study plants were classified as seedlings (less than two years old at the beginning of the experiment), saplings (from two years of age to the first reproductive event) or mature. The average time of first reproduction for different plant species was found in Loehle (1988). 5) Type of damage. Insect defoliation, simulated defoliation (clipping, tearing or hole-punching of leaves) and simulated mammal browsing were used in the papers. Simulated mammal browsing included simulation of hare or moose damage by pruning of the branches. There were too few cases of root damage ($N = 12$), so this damage type was excluded. 6) Extent of damage (%). The extent of the damage could be defined unequivocally for defoliation (insect and simulated) but not for browsing, and only when the damage was applied to the whole plant. Most damage treatments were conducted during just one growing season. If the damage was applied over several growing seasons, the damage percent could not be defined. 7) Timing of damage. The timing of the damage in relation to plant phenology was difficult to determine, as the timing of budbreak for the study plant in the study area was seldom reported. For this reason, and since many experiments had been carried out in Finland, this comparison was conducted for the Finnish experiments only. The timing of the damage in Finland was classified as early seasonal (May–June) or late seasonal (July–August). 8) Unit of experiment and localization of damage. There were two kinds of experimental designs with respect to the unit of the experiment: treatments were assigned either to different plants (damaged and control plants) or to different parts of the same plants (e.g. branches or ramets). In the first case the damage could be applied either to the whole plant or locally; in the second case the damage was always local. Three groups were thus considered with respect to experimental unit and damage localization: “local damage, within-plant control”, “whole plant damage, control in different plant”, and “local damage, control in different plant”.

To explain variation in herbivore responses to induced changes in plants, we used the variables 1–7 mentioned above as well as the following ones: 9) Herbivore feeding specialization. Insect herbivores were classified as monophagous (feeding on one or a few plant species belonging to the same genus), oligophagous (feeding on several plant genera belonging to the same family), or polyphagous (host plants belong to different families). We used for classification the information provided in the original studies and in

Benson (1958) and Kontuniemi (1960). 10) Rapid/delayed induced response. The time interval of induced responses can be classified on the basis of either plant life cycle (Bryant et al. 1988, Clausen et al. 1991) or herbivore life cycle (rapid and delayed, Haukioja 1990). The latter is used here, since it provides information on population level consequences.

Meta-analysis

We conducted all analyses using the MetaWin 2.0 statistical program (Rosenberg et al. 2000). To estimate the mean effect of the damage, we calculated for each individual measurement the difference between the means of the experimental and control group divided by their pooled standard deviation and multiplied the result by a correction term to remove small-sample-size bias. The calculation resulted in a measure of the effect size (Hedges' d , Gurevitch and Hedges 1993). For plant response variables, positive effect size (d) thus indicates an increase in the value of the variable measured in damaged plants as compared to control plants. For herbivore response variables, negative effect size indicates a reduction in herbivore performance on damaged plants as compared to control plants (induced resistance) whereas positive effect size indicates induced susceptibility. For some herbivore variables (e.g. developmental time and mortality) we changed the sign of the effect size so as to be able to compare them correctly; a positive effect size for herbivore growth rate and survival implies that herbivores grow faster and survive better on damaged plants. We conducted separate meta-analyses for each response variable and mixed models of meta-analysis were used for all analyses (Gurevitch and Hedges 1993). The magnitude of the treatment effect was considered to be statistically significant when the 95% confidence interval of the effect size did not include zero (Gurevitch and Hedges 1993). We report bootstrap confidence intervals (Adams et al. 1997), since the distribution of most variables did not meet the normality assumption (Shapiro–Wilk test: $P < 0.05$). The effects of explanatory variables were examined using categorical and continuous models; the significance of the effect was inferred from heterogeneity statistics (Q). Interpretation of the effects of explanatory variables may be problematic if they are not independent of one other (for example all deciduous plants in the database may be fast-growers and evergreens slow-growers). We therefore examined the associations between explanatory variables by conducting Chi-square tests of independence (Sokal and Rohlf 1995). If a significant association between explanatory variables was revealed, the effects of each variable were examined separately at each level of the other variable (Koricheva 2002). For plant variables, no significant associations between explanatory variables was found.

Our conclusions may be flawed if published studies represent a biased sample of all studies conducted on the subject. One of the most common forms of publication bias, also known as the “file-drawer problem” (Rosenthal 1979), occurs when non-significant results are less likely to be published than statistically significant results (Csada et al. 1996, Palmer 1999). We used funnel plots and fail-safe sample sizes to test for the occurrence of publication bias in our data; funnel plots represent scatter plots of effect size versus sample size (Light and Pillemer 1984, Palmer 1999) and fail-safe numbers indicate the number of measurements with zero effect size that would need to be added to the database to change a result from significant to non-significant (Rosenthal 1979). Another type of bias that may threaten the validity of ecological meta-analyses is the tendency to perform experiments on organisms which are more likely to yield statistically significant results (research bias *sensu* Gurevitch and Hedges 1999). To explore this bias, we analyzed whether the plant and herbivore species most often studied provided larger magnitudes of effect size than other species.

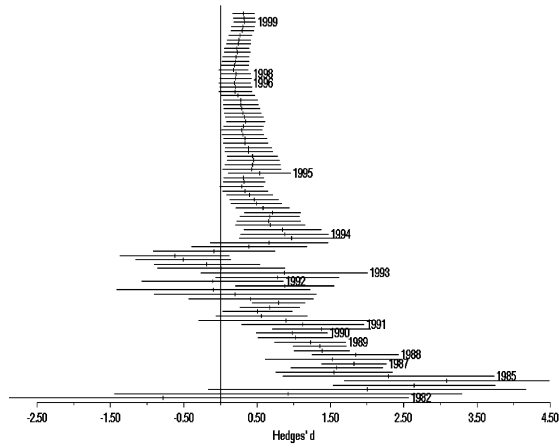
We also conducted cumulative meta-analyses (Rosenberg et al. 2000, Ioannidis and Lau 2001) to find out how the magnitude of effect size changed with publication year. Cumulative meta-analysis represents a series of meta-analyses in which studies are successively added to the analysis in a predetermined order (e.g. chronological). The summary meta-analytical statistics (mean effect size and its variance) are recalculated at each step. Typically, as studies are added to the analysis, the cumulative effect size first changes greatly from analysis to analysis; it later stabilizes around the mean value for the whole set of studies. However, when the magnitude of the effect size reported in individual studies changes continuously with time, as has been reported in several ecological studies (Jennions and Møller 2002), no stabilization of the cumulative effect size takes place.

Results

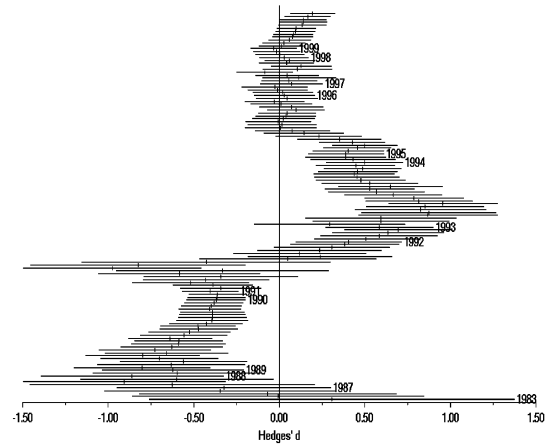
Temporal trends and possible biases

Cumulative meta-analysis revealed dramatic changes in the magnitude and the direction of reported changes in phenolic and nutrient concentrations with publication year (Fig. 1). Studies published in the 1980s reported significant increase in phenolic concentrations and decrease in nutrient concentrations after damage. In the late 1980s the magnitude of the changes reported in phenolic concentrations began to decrease, and by 1992 the cumulative effect size for phenolics was no longer statistically significant. For nutrients, a dramatic shift from significantly negative to significantly positive effect occurred in 1991. A second shift occurred in 1993,

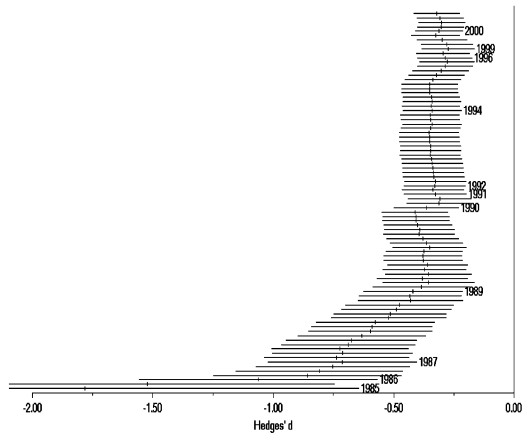
Phenolic concentration



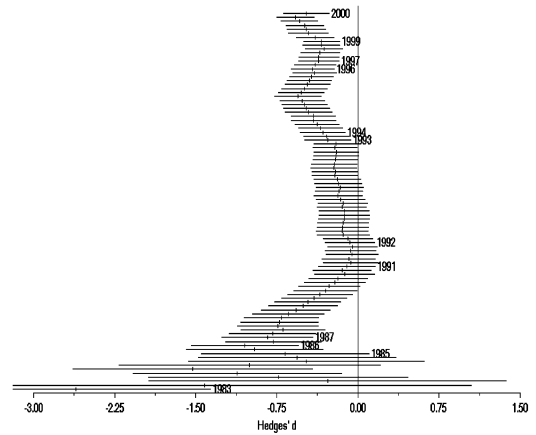
Nutrient concentration



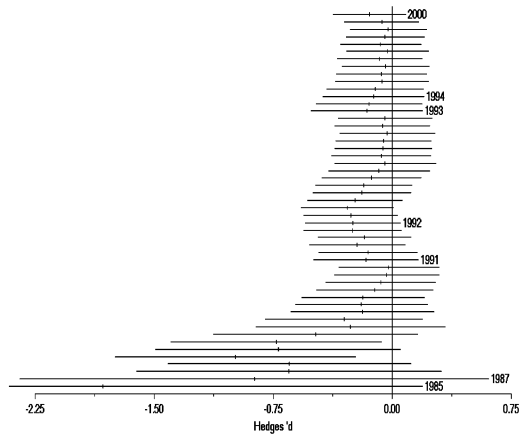
Herbivore growth



Pupal mass



Herbivore survival



Consumption

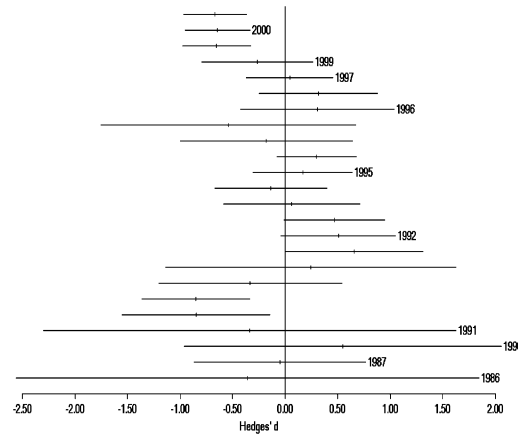


Fig. 1. Cumulative meta-analysis plots for plant phenolic and nutrient concentrations and herbivore performance measures illustrating temporal changes in effect size with year of publication. Cumulative effect sizes and 95% confidence intervals are displayed for each step of the analysis. The first analysis is conducted for the first two studies (in chronological order) and is illustrated at the bottom of the graph; the analysis including all studies is at the top of the graph. Measurements from the same publication year are added in random order and year of publication is marked next to the first observation from that year included in the analysis. Calculations are based on fixed effects.

when the magnitude of the cumulative effect size began to decrease again for nutrients and to increase for phenolics. Stabilization of the magnitude of effect size for phenolics and nutrients around the present mean values began only after 1995, as indicated by the reduction in variance. For the other plant response variables there were too few different publication years to conduct cumulative analyses.

The magnitude of reported changes in insect performance on damaged plants also clearly changed with publication year (Fig. 1). Early studies conducted in the 1980s tended to report stronger negative effects of plant damage on insect growth, pupal mass and survival than more recent studies conducted in the late 1990s. In the case of the insect growth rate, the magnitude of the effect decreased by a factor of almost four from 1985 till 2000, but remained statistically significant. In the case of pupal mass, a dramatic reduction in the magnitude of the effect size took place between 1983 and 1990; by 1991 the cumulative effect size was no longer significantly different from zero. After 1994, however, the magnitude of the effect size began to increase and became significant again. The current magnitude of the effect of induced plant responses on pupal mass is nevertheless only half of that reported in the mid-1980s. The tendency towards a reduction in the magnitude of effect size with time is also evident for survival data, although the cumulative effect size remained non-significant most of the time. Finally, consumption data showed no clear temporal trends and no tendency towards stabilization of the effect (Fig. 1).

Among experiments measuring induced changes in plants, the plant species most often studied were Scots pine (*Pinus sylvestris* L., 21% of measurements in the database) and mountain birch (*Betula pubescens* ssp. *czerepanovii* (Orlova) Hämet-Ahti [= *B. pubescens* ssp. *tortuosa* (Ledeb.) Nyman], 12% of measurements). We compared the results of experiments using these species with the results of studies conducted with other species. For phenolics and carbohydrates there were no differences between the results with the species most often studied and other species. There was, however, an increase in nutrient concentrations in Scots pine which was absent in other study plants ($Q_b = 6.33$, $P = 0.012$, $df = 1$, $d_{\text{pine}} = 0.478$, 95% CI [0.226;0.735], $N = 21$; $d_{\text{others}} = -0.071$, 95% CI [-0.296;0.144], $N = 103$). Mountain birch and Scots pine were also the most often used plant species in experiments where herbivore performance was measured (together accounting for 58% of all measurements). Pupal mass decreased significantly more after damage when herbivores were grown on mountain birch than on other host plants (Scots pine not included) ($Q_b = 6.51$, $P = 0.010$, $df = 1$, $d_{\text{birch}} = -0.791$, [-1.086; -0.479], $N = 18$; $d_{\text{others}} = -0.1291$, [-0.525;0.205], $N = 29$). Survival, however, decreased significantly less on Scots pine than on other plants ($Q_b = 3.97$, $P = 0.046$, $df = 1$, $d_{\text{pine}} = 0.039$,

[-0.236; 0.339], $N = 30$; $d_{\text{others}} = -0.377$, [-0.800; -0.004], $N = 18$). The herbivore species most often studied in studies of effects on insect herbivores was the autumnal moth *Epirrita autumnata* Bhk. (28% of all measurements). No differences were however found between autumnal moth larvae and other herbivore species in the magnitude of the effect of induced changes in host plant quality on herbivore performance.

Fail-safe numbers (Fig. 2A, B) for most of the response variables were high enough to consider the results robust with regard to publication bias. For carbon and phenolic concentrations and female pupal mass, however, were fail-safe numbers less than $5 \times N + 10$ (Rosenthal 1979). The “funnel effect” (Light and Pillemer 1984) was observed in most of the funnelplots of our data (not shown): as sample size increases variation due to sampling error decreases, and the values “funnel” down toward the true effect size, which implies the absence of a publication bias. For photosynthesis and plant growth measurements funnel plots were not symmetrical around their mean effect sizes; very large negative effects of photosynthesis and very large positive effect sizes of plant growth (over-

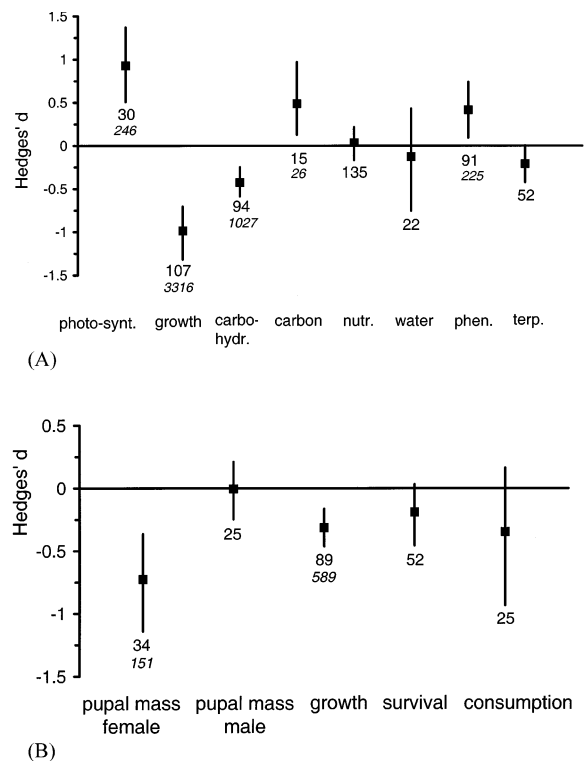


Fig. 2. Means of Hedges' d (effect size), 95% confidence intervals and sample sizes for (A) effects of herbivore damage on plant response variables (B) the effects of host plant damage on herbivore performance. Rosenthal's fail-safe numbers are reported under sample size in italics when the effect is significant. A significantly positive effect size implies an increase in the measured variable after damage.

compensation) were absent, and significant correlations between effect sizes and sample sizes were observed as a result ($r_{\text{growth}} = 0.227$, $P = 0.018$, $N = 107$; $r_{\text{phot}} = -0.393$, $P = 0.032$, $N = 30$). These patterns, however, are unlikely to represent the result of publication bias, since it is improbable that the negative effects of herbivory on photosynthesis or positive effects on growth (consistent with the overcompensation scenario) would be underreported. There were no significant correlations between effect size and sample size for any other variables.

General patterns and sources of variation in plant induced responses

The photosynthesis rate of the study plants increased significantly after damage (Fig. 2A); there was no difference between area-based and mass-based measurements ($d_{\text{area-based}} = 0.903$, 95% CI [0.513; 1.334]; $d_{\text{mass-based}} = 0.742$, 95% CI [0.389; 1.169], $Q_b = 0.28$, $df = 1$, $P = 0.600$). Further comparisons were conducted only for area-based photosynthesis, for which we had more measurements. The effects of plant dam-

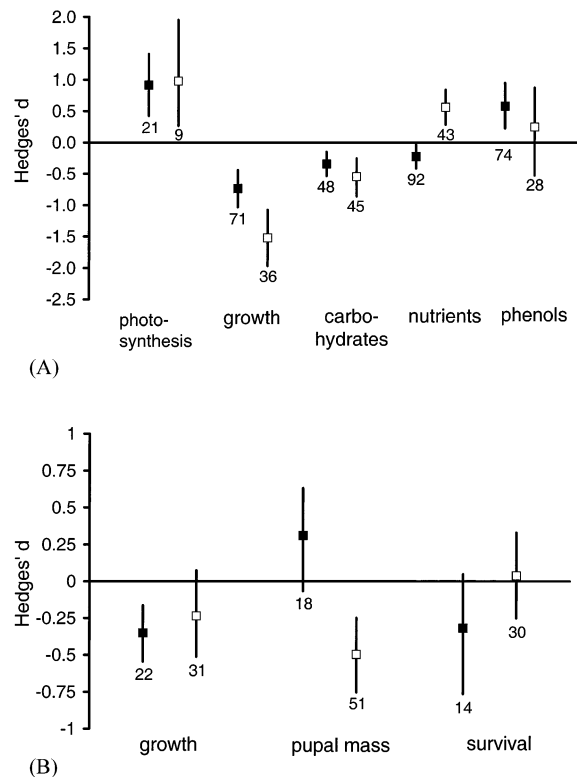


Fig. 3. Means of Hedges' d, 95% confidence intervals and sample sizes for (A) plant induced responses to herbivore damage (B) effects of plant induced responses on herbivore performance as affected by the type of the plant. Comparisons for herbivore performance measures were conducted only for fast-growing plants. ■ = deciduous, □ = evergreen.

age on photosynthesis were similar in evergreen and deciduous plants (Fig. 3A, $Q_b = 0.02$, $df = 1$, $P = 0.900$). There were too few photosynthesis measurements from slow-growing plants to compare changes in photosynthesis levels in fast- and slow-growing plants.

Plant growth after damage was significantly retarded (Fig. 2A). The growth rate of evergreen plants was reduced more than the growth of deciduous plants (Fig. 3A, $Q_b = 8.63$, $df = 1$, $P = 0.003$), but the plant inherent growth rate did not affect the extent to which plant growth was retarded after damage (Fig. 4A, $Q_b = 0.47$, $df = 1$, $P = 0.491$). Among different growth measures, leaf area and plant mass were reduced to a greater extent than height growth and shoot length ($Q_b = 19.67$, $df = 3$, $P < 0.001$, $d_{\text{area}} = -1.690$, 95% CI [-2.790; -0.864], $N = 16$; $d_{\text{mass}} = -1.123$, 95% CI [-1.775; -0.572], $N = 23$; $d_{\text{height}} = -0.272$, 95% CI [-0.457; -0.103], $N = 18$; $d_{\text{shoot}} = -0.545$, 95% CI [0.902; -0.202], $N = 36$).

Concentrations of carbohydrates decreased significantly after damage (Fig. 2A). The effects tended to be more pronounced for sugars ($d_{\text{sugar}} = -0.377$, 95% CI

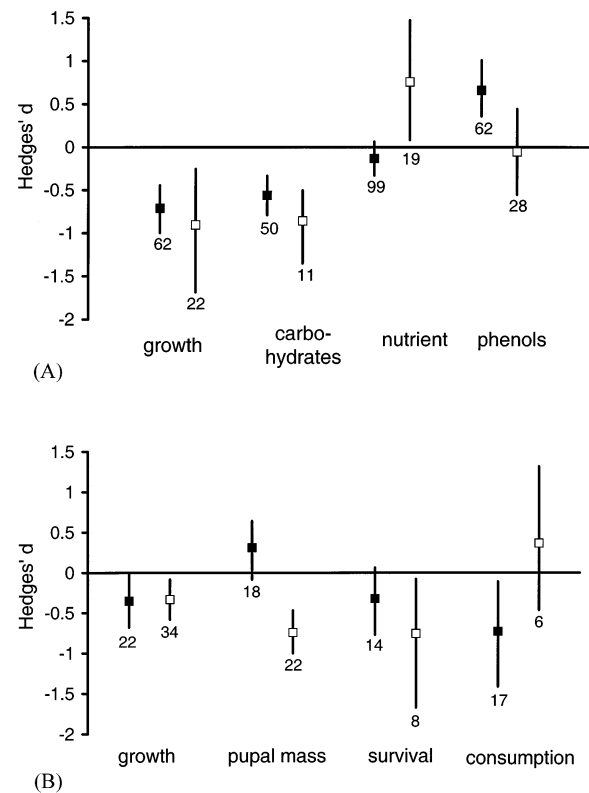


Fig. 4. Means of Hedges' d, 95% confidence intervals and sample sizes for (A) plant induced responses to herbivore damage as affected by plant inherent growth rate (B) effects of plant induced responses on herbivore performance on inherently fast-growing and slow-growing host plants. Comparisons for herbivore performance measures were conducted only for deciduous plants. ■ = fast-growing species, □ = slow-growing species.

[-0.653; -0.098], $N = 33$) than for starch concentrations ($Q_b = 3.32$, $df = 1$, $P = 0.068$, $d_{\text{starch}} = 0.077$, 95% CI [-0.340; 0.551], $N = 13$). The magnitude of reductions in carbohydrate concentrations was similar for deciduous and evergreen plants (Fig. 3A, $Q_b = 1.40$, $df = 1$, $P = 0.237$), and for slow- and fast-growing plants (Fig. 4A, $Q_b = 1.49$, $df = 1$, $P = 0.222$). In contrast to carbohydrates, carbon concentrations increased significantly after damage (Fig. 2A). Comparisons among different types of plants could not be conducted, since all carbon measurements were from studies using fast-growing evergreens.

When all types of mineral nutrients were considered together, there was no significant change in nutrient concentrations after damage (Fig. 2A). There was, however, a significant variation in responses among different types of nutrients (Fig. 5, $Q_b = 11.22$, $df = 4$, $P = 0.024$). Nitrogen concentrations increased significantly in foliage produced after damage (Fig. 5). Potassium concentrations tended to increase, while concentrations of magnesium and calcium decreased and phosphorus concentrations were unaffected (Fig. 5). Concentrations of nutrients increased after damage in evergreen plants but decreased in deciduous plants (Fig. 3A, $Q_b = 21.95$, $df = 1$, $P < 0.001$); nitrogen concentrations of deciduous plants did not change at all while concentrations in evergreen plants increased significantly ($Q_b = 11.95$, $df = 1$, $P < 0.001$; $d_{\text{decid}} = -0.093$, 95% CI [-0.440; 0.258], $N = 46$; $d_{\text{evergr}} = 0.637$, 95% CI [0.379; 0.912], $N = 32$). The plant inherent growth rate had a significant effect on nutrient change: nutrient concentrations increased in slow-growing plants, but tended to decrease in fast-growing ones (Fig. 4A, $Q_b = 12.85$, $df = 1$, $P < 0.001$). Water concentrations did not differ between damaged and control plants (Fig. 2A).

Damage significantly increased phenolic concentrations (Fig. 2A). The protein-precipitation capacity of tannins also increased significantly despite the small number of cases ($d_+ = 1.125$, 95% CI [0.695; 1.886], $df = 8$). There were no significant differences between

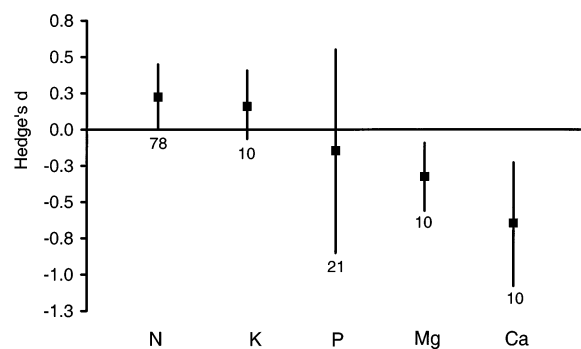


Fig. 5. Means of Hedges' d , 95% confidence intervals and sample sizes for effects of herbivore damage on concentrations of different nutrients.

different phenolic groups (Fig. 6, $Q_b = 6.13$, $df = 3$, $P = 0.106$). Accordingly, there was no difference between deciduous and evergreen plants in phenolic responses (Fig. 3A, $Q_b = 0.25$, $df = 1$, $P = 0.614$). However, the increase in phenolics was significant only in deciduous plants (Fig. 3A). There was a marginally significant difference between fast-growers and slow-growers: phenolic concentrations increased in fast-growing plants, but did not change in slow-growers (Fig. 4A, $Q_b = 2.82$, $df = 1$, $P = 0.091$). In contrast to phenolics, there was a marginally significant decrease in terpene concentrations after damage (Fig. 2A). Terpenes were measured only in evergreens and there were few slow-growers, so further comparisons could not be made.

There were significant differences in induced changes depending on the plant ontogenetic stage. The growth of seedlings was reduced more than the growth of saplings (Fig. 7A, $Q_b = 14.08$, $df = 2$, $P < 0.001$), and phenolic concentrations increased after damage more in saplings than in seedlings (Fig. 7A, $Q_b = 10.99$, $df = 2$, $P = 0.004$). Concentrations of carbohydrates decreased more in seedlings than in mature plants (Fig. 7A, $Q_b = 7.13$, $df = 2$, $P = 0.028$). Nutrient concentrations tended to increase in seedlings, but decreased in saplings (Fig. 7A, $Q_b = 7.54$, $df = 2$, $P = 0.023$).

There were no differences for any plant or herbivore variables between the effects of simulated and natural insect damage. These were therefore combined as "defoliation" treatment and were compared to simulated mammal browsing treatments. Damage type had a significant effect on carbohydrate concentrations ($Q_b = 7.28$, $df = 1$, $P = 0.006$): defoliation decreased concentrations more than simulated mammal browsing (Fig. 8). A comparison of different damage types on photosynthesis and terpene measurements could not be conducted because most of the experiments in which these variables were measured used simulated defoliation. The effects of damage type on other response variables were not significant. Early season damage caused a significant increase in phenolic concentrations

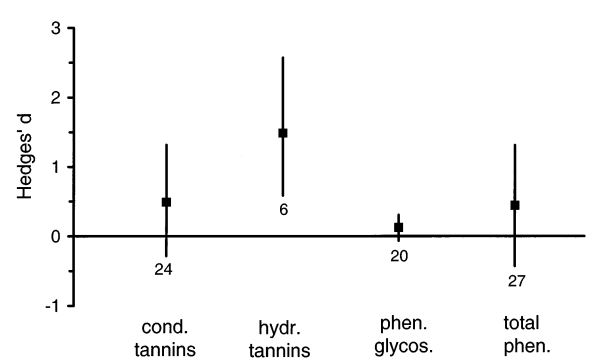
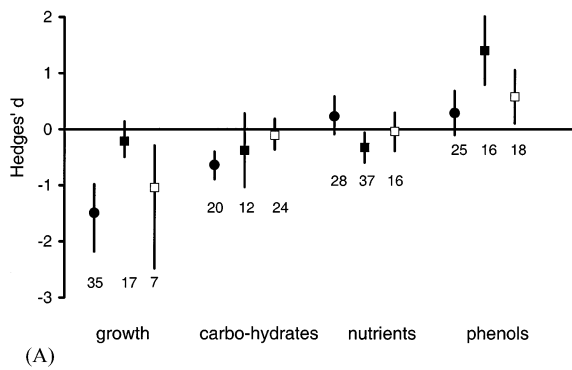
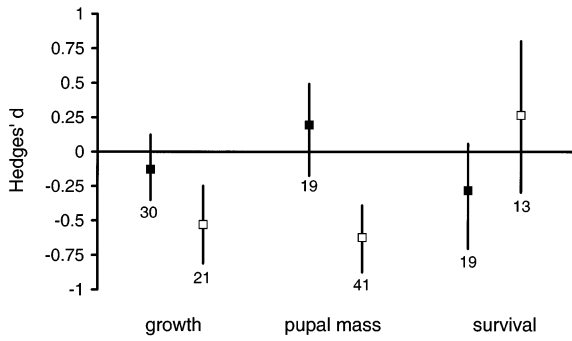


Fig. 6. Means of Hedges' d , 95% confidence intervals and sample sizes for effects of herbivore damage on concentrations of different phenolics.



(A)



(B)

Fig. 7. Means of Hedges' *d*, 95% confidence intervals and sample sizes for (A) plant induced responses to herbivore damage (B) effects of plant induced responses on herbivore performance as affected by plant ontogenetic stage. ● = seedling, ■ = sapling, □ = mature.

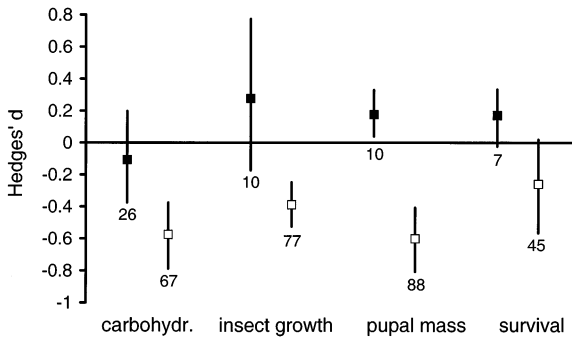
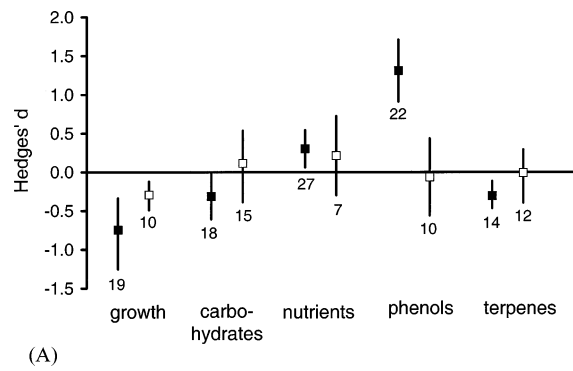
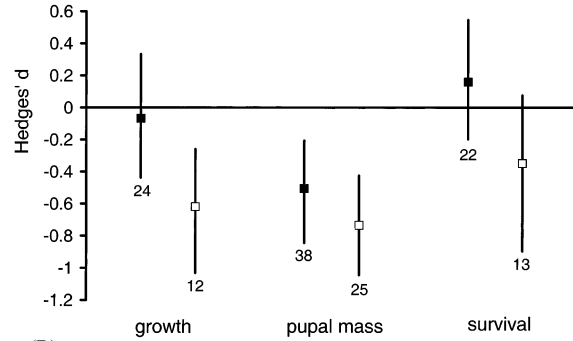


Fig. 8. Means of Hedges' *d*, 95% confidence intervals and sample sizes for induced changes in carbohydrate concentration and effects of plant induced responses on herbivore performance as affected by the type of damage. ■ = browsing, □ = defoliation (insect and simulated defoliation pooled).

for Finnish experiments, while late season damage had no effect (Fig. 9A, $Q_b = 7.77$, $df = 1$, $P = 0.005$). For other variables there were no significant differences, but there was a trend towards early damage causing more changes (Fig. 9A). Changes in carbohydrate concentrations were significantly dependent on the extent of damage: greater damage caused a greater decrease in



(A)



(B)

Fig. 9. Means, 95% confidence intervals and sample sizes for (A) plant induced responses to herbivore damage (B) effects of plant induced responses on herbivore performance as affected by the timing of damage. Data are from experiments conducted in Finland only. ■ = early seasonal, □ = late seasonal.

carbohydrates ($Q_{reg} = 13.94$, $df = 49$, $P < 0.001$). The extent of the damage did not explain variation in other response variables. The time interval between treatment and response measurement had no significant effect on any plant variable. Most experiments were conducted with whole plant damage and control in different plants (see explanatory variables). For phenolics, there was no difference between the effects of local damage with within-plant control, local damage with control in a different plant and whole-plant damage with control on a different plant ($Q_b = 3.84$, $df = 2$, $P = 0.147$). There was also no difference between the effects of local damage and whole-plant damage (control on different plant) for nutrients ($Q_b = 2.34$, $df = 1$, $P = 0.126$) or for terpenes ($Q_b = 1.38$, $df = 1$, $P = 0.241$).

General patterns and sources of variation in effects of plant induced responses on herbivore performance

There were only few studies of changes in herbivore performance on slow-growing evergreen species in our database; the evergreen species most commonly studied was *Pinus sylvestris*, which was classified as a fast

grower. The effect of the inherent growth rate of the host plant on herbivore performance was therefore examined for deciduous species only. Similarly, comparison of the effects between deciduous and evergreen host plants was conducted for fast-growing species only.

The growth rate of herbivores was significantly lower on damaged plants than on control plants (Fig. 2B). The magnitude of the effect was independent of whether growth was measured as RGR or as development time ($Q_b = 1.90$, $df = 1$, $P = 0.169$; $d_{\text{rgr}} = -0.256$, 95% CI $[-0.414; -0.074]$, $d_{\text{time}} = -0.482$, 95% CI $[-0.706; -0.254]$), and the above variables were therefore pooled for further analysis. The effects of induced changes on herbivore growth rates did not differ either between deciduous and evergreen fast-growing plants (Fig. 3B, $Q_b = 0.39$, $df = 1$, $P = 0.530$) or between fast- and slow-growing deciduous plants (Fig. 4B, $Q_b = 0.01$, $df = 1$, $P = 0.909$). Similarly, there was no difference between mature plants and saplings (Fig. 7B, $Q_b = 64.12$, $df = 1$, $P = 0.326$). The degree of feeding specialization had no significant effect on the magnitude of changes in growth rate ($Q_b = 3.40$, $df = 2$, $P = 0.180$). However, only the growth rate of oligophagous and polyphagous herbivores was significantly reduced on damaged plants ($d_{\text{poly}} = -0.261$, 95% CI $[-0.507; -0.015]$, $N = 33$; $d_{\text{oligo}} = -0.525$, 95% CI $[-0.824; -0.225]$, $N = 19$; $d_{\text{mono}} = -0.0726$, 95% CI $[-0.348; 0.259]$, $N = 20$). Browsing and defoliation had significantly different effects (Fig. 8, $Q_b = 9.86$, $df = 1$, $P = 0.002$): browsing had no effect, while defoliation reduced growth. The difference between the effects of early-season and late-season damage was marginally significant (Fig. 9B, $Q_b = 3.53$, $df = 1$, $P = 0.061$): only late-season damage caused a significant decrease in herbivore growth. The effect of damage extent was not significant ($Q_{\text{reg}} = 0.24$, $df = 36$, $P = 0.624$). There was no significant difference between the effects on growth rate of rapid and delayed induced resistance (Fig. 10, $Q_b = 1.96$, $df = 1$, $P = 0.162$), although only delayed responses had a significant negative effect on the herbivore growth rate.

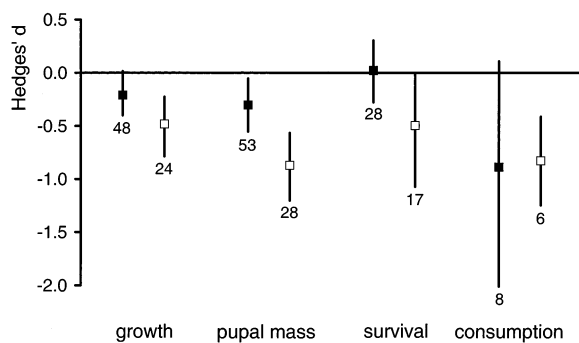


Fig. 10. Means of Hedges' d , 95% confidence intervals and sample sizes for effects of rapid and delayed induced responses on herbivore performance. ■ = RIR, □ = DIR.

Pupal mass was significantly lower on previously damaged trees as compared to controls ($d_+ = -0.480$, 95% CI $[-0.670; -0.301]$, $df = 96$). There was a significant difference between the responses of female and male insects: female pupal mass decreased, but male pupal mass did not change (Fig. 2B, $Q_b = 8.00$, $df = 1$, $P = 0.005$). The effect of host plant damage was different in deciduous and evergreen fast-growing plants (Fig. 3B, $Q_b = 12.22$, $df = 1$, $P < 0.001$): pupal mass decreased only on evergreen host plants and tended to increase on deciduous plants. The growth rate of the plant also had a significant effect (Fig. 4B, $Q_b = 18.85$, $df = 1$, $P < 0.001$): pupal mass decreased only on slow-growing deciduous host plants and tended to increase on fast-growing deciduous plants. Pupal mass decreased significantly on mature plants compared to saplings (Fig. 7B, $Q_b = 13.77$, $df = 1$, $P < 0.001$). The degree of feeding specialization had no significant effect on the magnitude of changes in pupal mass ($Q_b = 0.70$, $df = 2$, $P = 0.706$; $d_{\text{poly}} = -0.452$, 95% CI $[-0.732; -0.174]$, $N = 46$; $d_{\text{oligo}} = -0.639$, 95% CI $[-0.925; -0.351]$, $N = 26$; $d_{\text{mono}} = -0.412$, 95% CI $[-0.829; -0.069]$, $N = 25$). Browsing and defoliation had significantly different effects: browsing increased pupal mass whereas defoliation decreased it (Fig. 8, $Q_b = 6.38$, $df = 1$, $P = 0.012$). There was no difference between the effects on pupal mass of early and late damage (Fig. 9B, $Q_b = 0.84$, $df = 1$, $P = 0.361$). Effect of damage extent was not significant ($Q_{\text{reg}} = 0.39$, $df = 45$, $P = 0.532$). Delayed induced resistance caused a stronger reduction in pupal mass than rapid induced resistance (Fig. 10, $Q_b = 7.67$, $df = 1$, $P = 0.006$).

Survival was not significantly affected by induced changes in plants (Fig. 2B). There were no differences between deciduous and evergreen fast-growing host plants (Fig. 3B, $Q_b = 1.89$, $df = 1$, $P = 0.169$) or fast- and slow-growing deciduous plants (Fig. 4B, $Q_b = 1.05$, $df = 1$, $P = 0.307$). There was likewise no difference between mature study plants and saplings (Fig. 7B, $Q_b = 2.35$, $df = 1$, $P = 0.125$). The degree of feeding specialization had no significant effect on the magnitude of changes in herbivore survival ($Q_b = 2.27$, $df = 2$, $P = 0.321$). However, only the survival of polyphagous herbivores was significantly reduced on damaged plants ($d_{\text{poly}} = -0.414$, 95% CI $[-0.842; -0.062]$, $N = 20$; $d_{\text{oligo}} = -0.022$, 95% CI $[-0.364; 0.310]$, $N = 20$; $d_{\text{mono}} = -0.036$, 95% CI $[-0.554; 0.499]$, $N = 12$). The difference between defoliation and browsing damage was not significant (Fig. 8, $Q_b = 1.59$, $df = 1$, $P = 0.207$), although the trend was the same as for growth rate and pupal mass: defoliation tended to reduce survival while browsing tended to increase it. The timing of the damage did not have a significant effect on the change in survival (Fig. 9B, $Q_b = 2.62$, $df = 1$, $P = 0.106$). The effect of damage extent was not significant (one outlier was removed from the data, $Q_{\text{reg}} = 1.70$, $df = 28$, $P = 0.193$). Rapid induced resistance had no

effect on survival, delayed induced resistance caused a significant reduction in survival (Fig. 10); this difference was marginally significant ($Q_b = 3.27$, $df = 1$, $P = 0.07$).

There was no significant decrease in consumption on damaged plants compared to controls (Fig. 2B). Due to the low number of no-choice tests and choice tests in the laboratory, we were unable to conduct comparisons between different experiment designs and there were not enough studies on evergreen plants to compare the effects of deciduous and evergreen host plants. There was a marginally significant difference between fast- and slow-growing deciduous host plants ($Q_b = 3.84$, $df = 1$, $P = 0.055$); consumption decreased on fast-growing plants after damage while on slow-growing plants there were no change (Fig. 4B). There were no difference between rapid and delayed responses (Fig. 10, $Q_b = 0.01$, $df = 1$, $P = 0.923$). Analyses of the effects of type, extent and timing of the damage and of herbivore specialization could not be conducted due to the small number of studies in each category.

Discussion

Paradigm shifts and research biases in studies of herbivore responses to induced changes in plants

Cumulative meta-analyses revealed dramatic temporal changes in the magnitude and direction of reported induced responses in plants and a decrease in the strength of research findings with time in studies of herbivore responses to induced changes. Significant positive and negative relationships between magnitude of research findings and year of publication have recently been reported in several other fields of ecology; they have been attributed to Kuhnian paradigm shifts, changes in methodological approach, bias in the choice of study systems or time lag in the publication of non-significant results (Alatalo et al. 1997, Simmons et al. 1999, Jennions and Møller 2002). While all of the above factors may contribute to the temporal trends observed in plant induced responses, the non-linear character of the changes in plant responses and the hypothesis-driven nature of studies suggest that the most parsimonious explanation is that offered by a shift in accepted paradigms.

Early studies, conducted in the 1980s, reported an increase in phenolic concentrations and a reduction in nutrient concentrations in response to damage. Temporal trends in reported changes in phenolic concentrations in damaged plants were almost a mirror image of those in nutrient concentrations, even though these measurements often came from different studies (see Appendix). Also, studies published in the 1980s reported much stronger negative effects on herbivore performance of induced changes in plants than more recent studies. These results support the idea that plants

may defend themselves actively against herbivores, which began to receive considerable attention in the 1970s (Green and Ryan 1972, Haukioja and Hakala 1975), and generated much enthusiasm among researchers. According to Kuhn (1996), the early stages of scientific revolutions are characterized by a less critical approach to research. During this time it is relatively easy to publish evidence supporting the current paradigm even when this evidence is based on methodologically flawed studies. Indeed, while studies published in the late 1970s and early 1980s tended to support the idea of induced resistance against herbivores, many of these experiments suffered from methodological problems; they might for instance be pseudoreplicated (Hurlbert 1984, Fowler and Lawton 1985, Neuvonen and Haukioja 1985). The paradigm shift began in the mid-1980s, when several studies demonstrated that the effects of defoliation are not always deleterious to herbivores (Niemelä et al. 1984, Roland and Myers 1987) and that some types of damage (e.g. browsing and the removal of apical buds, Danell and Huss-Danell 1985) may even increase the quality of foliage for subsequent herbivory (induced susceptibility sensu Haukioja 1990). By the early 1990s, the cumulative effect size of changes in phenolic concentrations and in pupal weight no longer differed from zero whereas for nutrient concentrations it became strongly positive. A second paradigm shift occurred in the early 1990s, when several reviews (Karban and Myers 1989, Haukioja 1990) and a book by Tallamy and Raupp (1991) introduced a more balanced view of induced responses and demonstrated that induced resistance and induced susceptibility represent just two ends of a spectrum of herbivore responses to changes in plant quality. Accordingly, the magnitude of cumulative effect size increased again for phenolic concentrations and pupal mass and decreased for nutrient concentrations during 1990s. By the late 1990s, the magnitude of effect size stabilized for most of the examined response variables.

To the best of our knowledge, cumulative meta-analysis has not been used previously to examine changes in effect size over time in ecological studies, although it is frequently used in medicine (Lau et al. 1992, Ioannidis and Lau 2001). Previous studies of temporal changes in the magnitude of effects in ecology examined correlations between the magnitude of the effect and publication year (reviewed by Jennions and Møller 2002). The latter method may fail to detect any trend if several contrary shifts in the magnitude and direction of the effect take place during the period in question, as was the case in our analysis for plant variables. The advantage of cumulative meta-analysis is that it makes it possible to uncover such non-linear temporal trends. Another benefit of cumulative meta-analysis is that it indicates whether the direction and the magnitude of the effect have stabilized to allow meaningful assess-

ment of the mean effect size. If each new study added to the analysis causes a significant change in the magnitude of the effect, and the variance around the mean effect remains high, analysts should wait for a more complete picture to evolve before conducting a review of a field.

In addition to paradigm shifts, the interpretation of the results of meta-analysis can also be confounded by research bias (*sensu* Gurevitch and Hedges 1999). Although reviewed experiments were conducted with a wide variety of plants (52 species) and insect herbivores (19 species), certain species (Scots pine, mountain birch and autumnal moth) were overrepresented. A system in which significant induced responses have been found in previous studies is likely to be studied more in the future; this may lead to overestimation of the magnitude of induced responses. We found that insects associated with mountain birch exhibited greater reductions in pupal mass on damaged trees than herbivores feeding on other plant species whereas survival of herbivores on damaged Scots pine trees was affected less than on other plant species. Therefore, induced resistance appears to be manifested stronger in mountain birch and weaker in Scots pine than in other tree species. Moreover, studies conducted on these two plant species were not equally distributed along the examined time period. Mountain birch was used in 50% of all studies on induced resistance conducted in 1980s, but only in 19% of studies conducted in 1990s (see Appendix). In contrast, all studies using Scots pine were conducted in 1990s. Therefore, the gradual accumulation of studies conducted on systems other than mountain birch, particularly in Scots pine, probably also contributed to the observed reduction with time in the strength of herbivore responses to induced changes in plants.

The sample sizes of the studies included were very low. In most experiments (86% of plant measurements, 93% of herbivore performance measurements) the sample size was 20 or less; thus the statistical power of most of the studies was low and conclusions from a single study may have been flawed for instance by differences between plant and herbivore individuals. Meta-analysis is a good method for overcoming these problems because the magnitude of the effect size does not depend on sample size.

Damage-induced changes in woody plants

The meta-analysis results indicated several compensatory changes in plants. The photosynthesis rate was accelerated in damaged plants compared to undamaged ones. Photosynthesis is known to be regulated by sink demands (Taiz 1991), which were elevated in plants recovering from damage. Despite the increased photosynthesis rate, however, growth of damaged plants were

reduced. A significant reduction in the growth of woody plants after herbivore damage has also been reported in a recent meta-analysis by Hawkes and Sullivan (2001). This suggests that the loss of photosynthetic area and resources could not be fully compensated. It is also possible that the reduction in nutrient status caused by damage accelerated root growth at the expense of the growth of aboveground tissues, which were measured here (Chapin 1980). As slow-growing plants have a higher initial cost of foliage production, lower rate of return and slower compensation rate, it has been assumed that the growth rate of inherently slow-growing plants will be more retarded than that of fast-growers (Coley et al. 1985), but we found no effect of plant inherent growth rate on changes in growth rate after damage. Regrowth has been shown to be limited mostly by the levels of carbohydrate and nutrient reserves (Webb 1981, McNaughton 1983, Trumble et al. 1993, Kobe 1997, Canham et al. 1999), and carbohydrate concentrations decreased in damaged plants according to our results. In deciduous and fast-growing plants this decrease may be also due to the use of carbohydrates not only for regrowth but also for production of phenolics. Contrary to carbohydrates, carbon concentrations, which were all measured in evergreen plants, were higher in damaged plants than in controls. This result contradicts the prediction that carbon concentrations will decrease in evergreen woody plants after defoliation, as evergreen plants store most of their carbon in foliage (Bryant et al. 1983). As the concentrations of carbohydrates, phenolics and terpenes either decreased or did not change in evergreens, the increase in carbon concentrations may imply an increase in the concentrations of amino acids or in structural polysaccharides (e.g. cellulose) or may represent a concentration effect caused by reduced weight of leaves/needles (Koricheva 1999).

There is generally a strong positive correlation between photosynthesis rate and nitrogen concentration in plants (Field and Mooney 1986, Evans 1989), as a large fraction of leaf nitrogen is contained in the carbon-fixing enzyme (RuBP). We also found that elevated rates of photosynthesis in damaged plants were associated with increased nitrogen concentrations. The latter change probably reflects increased acquisition of nitrogen in foliage for regrowth and photosynthesis due to the increased transportation of nitrogen reserves from the roots to the above-ground parts (Ta et al. 1990) and to increased nitrogen uptake by roots (Ruess 1988). It has been suggested that, in contrast to deciduous woody plants, the defoliation of woody evergreens may result in an increase in foliar nitrogen, since evergreen foliage has a high carbon/nitrogen ratio compared to roots (Bryant et al. 1988). The results of the meta-analysis support this prediction, as the nitrogen concentrations of deciduous plants did not change at all, while concentrations in evergreen plants increased signifi-

cantly. Responses of other nutrients to plant damage varied depending on their mobility in the plant tissues. Foliage concentrations of potassium, which is a mobile nutrient like nitrogen, tended to increase, while concentrations of calcium and magnesium (immobile nutrients) decreased. Increase in concentrations of mobile nutrients is probably due to their transport from damaged leaves and storage places to new growth, while decrease in less mobile nutrients that cannot be relocated might be caused by their losses with damaged tissues (Chapin 1980). Changes in nutrients thus may not be specific responses against herbivores but may be connected with plant regrowth processes.

An increase in phenolics is considered to be a common reaction to herbivory in woody plants (Karban and Baldwin 1997), and this view was supported by the meta-analysis: both phenolic concentrations and protein-precipitation capacity of tannins were higher in damaged plants as compared to the control. Phenolic concentrations increased significantly in fast-growing plants but did not change in slow-growers; this supports the expectation that induced resistance is stronger in fast-growing plants (Karban and Baldwin 1997). Increase in phenolics was significant only in deciduous plants whereas the phenolic concentrations of evergreens did not change and concentrations of other major class of carbon-based secondary compounds, terpenoids, tended to decrease in the foliage of damaged evergreens. These results support the traditional view that foliage of evergreens is not as responsive to herbivore damage as that of deciduous plants. However, evergreen plants may display other types of induced defenses such as induced resin flow (Lewinsohn et al. 1991) and hypersensitive responses (Karban and Baldwin 1997), which were beyond the scope of the present review.

It has been suggested that browsing will enhance growth in contrast to defoliation (Strauss 1991), but we found no difference between the effects of defoliation and simulated mammal browsing on growth. Simulated and natural defoliation also induced similar changes in the concentrations of plant chemical compounds; there is, however, evidence that simulated and natural herbivory induce different responses at the genetic and molecular levels and in the composition of the chemicals induced (Korth and Dixon 1997, Reymond et al. 2000). Early-season damage tended to cause more pronounced changes in plants than late-season damage. This was in accordance with the assumption that vigorously growing foliage has a greater capacity to respond to damage (Karban and Baldwin 1997). However, saplings and mature plants seemed to cope with damage better than seedlings (< 2 years old); the growth of saplings was reduced less and phenolic concentration increased more than in seedlings. Carbohydrate concentrations also decreased more in saplings than in mature plants. Seedlings suffered more from damage, possibly

because they have not accumulated as many resources as older plants.

Effects of induced changes in plants on herbivore performance

Herbivore performance measured as the growth rate and female pupal mass was considerably reduced by the induced responses of host plants to damage, indicating induced resistance. A reduction in female pupal mass may affect population densities of the next herbivore generation, since the pupal mass of Lepidoptera and Hymenoptera larvae has been shown to correlate with potential and realized fecundity (Haukioja and Neuvonen 1985, Honěk 1993, Tamaru et al. 1997). Interestingly, the pupal mass of males was not significantly affected by plant damage; this may indicate that male pupal weight is more canalized against disturbances than female pupal weight. Females may also suffer from a low quality diet more than males due to their larger contribution to the offspring. It would thus be beneficial in future studies of herbivore responses not to combine the performance and consumption measures of males and females.

We found no significant changes in herbivore survival and consumption on previously damaged plants. The lack of changes in survival indicates that a prolonged growth period of herbivores on previously damaged plants does not necessarily lead to increased mortality. This result contradicts the predictions of the "slow growth/high mortality" hypothesis (Feeny 1976, Clancy and Price 1987), which assumes that a longer development period of insect herbivores on low-quality hosts increases their exposure to predators and parasitoids and results in greater mortality. Furthermore, natural enemies may be attracted by volatiles released from induced plants (Dicke 1999). However, most of the experiments included in our analysis were conducted in the lab or in mesh bags in the field; this prevented insect exposure to natural enemies. The absence of changes in survival on previously damaged plants therefore indicates merely that induced changes in plants have no direct effect on herbivore mortality. The possibility that induced changes in the plant may affect herbivore mortality indirectly, via increased exposure to natural enemies, has to be explored in field experiments with uncaged herbivores.

The lack of significant changes in herbivore consumption on previously damaged plants is surprising, as a reduction of further herbivory is assumed to be the main evolutionary gain from induced resistance for a plant. It has been suggested that an increased amount of defensive compounds in damaged foliage may decrease the consumption of plant biomass by generalist herbivores (Brooks 1976, Hollingworth 1976). Specialist herbivores, however, may be able to handle increased

amounts of defensive compounds in damaged foliage by various biochemical compensation means, such as enzymatic transformation of toxins (Spencer 1988), and may increase consumption on induced plants to compensate for the reduced amount of nutrients (Moran and Hamilton 1980, Slansky and Wheeler 1992). Thus the lack of changes in consumption may indicate that the reduced consumption of induced plants by generalist herbivores was counterbalanced by compensatory feeding by specialists. We could not test this hypothesis due to the small number of cases available for each herbivore specialization category, but it certainly warrants further investigation. Induced changes in plant quality may also provide other benefits for the plant than a reduction in damage (Agrawal and Karban 1999). Increased herbivore movement in search for better quality diet causes the distribution of damage over a wider area, which may be easier for the plant to cope with (Edwards et al. 1991, Marquis 1992). Increased herbivore movement may also lead to a greater predation risk for herbivores (Bergelson and Lawton 1988). Finally, the consumption of plant biomass may not always correlate with plant reproductive capacity, which ultimately determines plant's fitness after herbivory.

There was a clear tendency for induced changes in plants to have stronger effects on the performance of the next generation of herbivores (delayed induced responses) than on the same generation that caused the damage (rapid induced responses). This could be due to a delay in plant responses or, in the case of experiments conducted in nature, the fact that the herbivores causing the induction are better prepared to compensate for the decrease in food quality than the next generation. The prevalence of DIR over RIR may have important implications for herbivore population dynamics, since DIR is assumed to cause cyclic fluctuations in insect herbivore populations (Haukioja and Hanhimäki 1985), while RIR is assumed to stabilise population dynamics (Haukioja 1982).

The effects of induced changes in plants on herbivore performance clearly depended on the type of damage: defoliation (both natural and simulated) reduced herbivore performance (induced resistance), while simulated mammal browsing significantly increased pupal weight and tended to increase insect growth and survival. Unlike defoliation, mammalian browsing releases apical dominance; this leads to the activation of previously suppressed modules and the redistribution of resources within plants, which often improves the quality of emerging foliage for herbivores (induced susceptibility, Haukioja et al. 1990). This, however, does not mean that there are no effective induced defenses against mammals. The induced production of thorns or spines on browsed branches has for instance been observed, and has been shown to deter mammalian browsers (Milewski et al. 1991). These responses, however, were

beyond the scope of the present review. Although the degree of feeding specialization had no significant effect on the magnitude of changes in herbivore performance, only the growth rates of oligophagous and polyphagous insects and the survival of polyphagous insects were significantly reduced on damaged plants. This finding supports the prediction that induced plant defenses are more effective against generalist herbivores than against specialists (van Dam et al. 1993).

Secondary compounds such as phenolics and terpenes have been shown to decrease the performance of both insects (Bennett and Wallsgrave 1994) and mammals (Dearing 1997), and nutrients have been shown to increase herbivore performance (Scriber and Slansky 1981). However, we found that damage-induced changes in plant secondary compounds and nutrients were in general poor predictors of herbivore responses. For instance, phenolic concentrations increased in response to damage in deciduous and fast-growing plants but not in evergreens or slow-growing plants. On the basis of these results, it might be assumed that induced resistance would be stronger in deciduous plants than in evergreens and in fast-growing plants than in slow growers. However, we found no consistent effects of leaf longevity or plant inherent growth rates on herbivore responses to induced changes in plants. The same contradiction between herbivore performance and measured plant variables existed also when comparing responses to early/late season damage or browsing/defoliation. These results imply that our understanding of the true mechanisms of plant resistance for these systems is still inadequate; the way we measure secondary chemicals and nutrients may not be what is really available to the herbivores. One reason might be that plant quality for herbivores is determined by the complex interaction of plant characteristics (Berenbaum 1995). The observed discrepancy between herbivore responses and changes in phenolic concentrations in damaged plants also supports the idea that primary functions of phenolics in plants may be other than antiherbivore defenses (Cooper-Driver and Bhattacharya 1998, Close and McArthur 2002). In addition, our analysis was restricted to non-specific changes in plants whereas herbivore damage may induce a number of more specific responses (such as production of volatiles) which may affect herbivores directly or indirectly.

Conclusions

The results of meta-analysis indicated that herbivore damage induces a number of changes in plants which affect performance of the herbivores. The magnitude and direction of plant induced responses and their effects on herbivore performance depend on the plant

type (deciduous vs evergreen), inherent growth rate and ontogenetic stage. In addition, herbivore responses were affected by the type and timing of damage, and the time interval between the damage and insect feeding. In general, our results indicate that induced changes in defoliated plants decrease insect herbivore performance (in terms of growth rate and pupal mass) as predicted by the induced defense theory. However, benefits of induced defenses for the plants in terms of reduced consumption of foliage by herbivores were observed only for the fast growing plants and for the next generation of herbivores (delayed induced responses). In addition, contrary to predictions, changes in herbivore performance appear to be poorly associated with changes in concentrations of secondary compounds and nutrients in the damaged plants. Several findings of our analysis also suggest new directions for studies of induced defenses, e.g. possible differential effects of induced changes on female and male herbivores and on specialists and generalists, indirect effects of induced changes on insect survival and benefits of induced defenses other than reduced consumption of foliage. Finally, our finding that both the magnitude and the direction of the effects may change dramatically over the years indicates that caution should be exercised in reviewing new hypothesis-driven fields of ecology. We therefore suggest that each formally conducted meta-analysis should be preceded by a cumulative meta-analysis; this would serve as an indicator of the robustness of the conclusions drawn from the analysis, much as the fail-safe number indicates the robustness of the results against publication bias.

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Appendix

References, plant and herbivore species (for which performance was measured) and measured variables for the studies used in the meta-analysis. Plant variables: plant growth (Gr), photosynthesis (Pho), concentrations of carbohydrates (CH), carbon (C), nutrients (Nutr), water (Wa), phenolics (Phe) and terpenes (Ter), protein-precipitation capacity of tannins (PPC). Herbivore variables: herbivore growth (Gr), pupal mass (P), survival (S) and consumption (C).

Reference	Plant species	Plant variables	Herbivore species	Herbivore variables			
Litvak and Monson 1998	<i>Abies concolor</i>	Ter	several species, not identified	C			
Bryant et al. 1991	<i>Acacia tortilis</i>	N, P, Phe					
Canham et al. 1994	<i>Acer rubrum</i>	Ch Gr, Pho N	Gr	Gr, P, S			
Canham et al. 1999	<i>Acer rubrum</i>						
Canham et al. 1999	<i>Acer saccharum</i>						
Kruger et al. 1998	<i>Acer saccharum</i>						
Myers and Williams 1987	<i>Alnus rubra</i>						
Bergelson and Lawton 1988	<i>Betula pendula</i>	Phe	<i>Malacosoma californicum</i> pl.	Gr, P, S			
Danell and Bergström 1989	<i>Betula pendula</i>	Gr, N, P, K, Ca, Mg, Na, Wa					
Mutikainen et al. 1996	<i>Betula pendula</i>	Gr Pho Gr, N Pho, N Gr, N Ch, N Gr, N, P, K, Ca, Mg, Na, Wa Gr, Phe	<i>Epirrita autumnata</i>	Gr			
Mutikainen et al. 2000	<i>Betula pendula</i>		<i>Epirrita autumnata</i>	Gr, P			
Ovaska et al. 1992	<i>Betula pendula</i>		<i>Lymantria dispar</i>	P			
Ovaska et al. 1993a	<i>Betula pendula</i>						
Ovaska et al. 1993b	<i>Betula pendula</i>						
Walls et al. unpubl.	<i>Betula pendula</i>						
Valentine et al. 1983	<i>Betula populifolia</i>						
Danell and Bergström 1989	<i>Betula pubescens</i>						
Hjälten et al. 1994	<i>Betula pubescens</i>				<i>Epirrita autumnata</i>	Gr, P, S	
Neuvonen and Danell 1987	<i>Betula pubescens</i>						
Hanhimäki 1989	<i>Betula pubescens</i> ssp. <i>tort</i>	<i>Amauronematus</i> sp.					Gr
Hanhimäki 1989	<i>Betula pubescens</i> ssp. <i>tort</i>	<i>Arge</i> sp.					Gr
Hanhimäki 1989	<i>Betula pubescens</i> ssp. <i>tort</i>	<i>Dineura</i> sp.	Gr				
Hanhimäki 1989	<i>Betula pubescens</i> ssp. <i>tort</i>	<i>Hemichroa</i> sp.	Gr				
Hanhimäki 1989	<i>Betula pubescens</i> ssp. <i>tort</i>	<i>Nematus</i> sp.	Gr				
Hanhimäki 1989	<i>Betula pubescens</i> ssp. <i>tort</i>	<i>Priophorus</i> sp.	Gr				
Hanhimäki 1989	<i>Betula pubescens</i> ssp. <i>tort</i>	<i>Pteronidea</i> sp.	Gr				
Haukioja et al. 1985	<i>Betula pubescens</i> ssp. <i>tort</i>	Gr	<i>Epirrita autumnata</i>	Gr, P, S			
Haukioja et al. 1990	<i>Betula pubescens</i> ssp. <i>tort</i>		<i>Epirrita autumnata</i>	Gr			
Kaitaniemi et al. 1997a	<i>Betula pubescens</i> ssp. <i>tort</i>		<i>Epirrita autumnata</i>	Gr			
Kaitaniemi et al. 1997b	<i>Betula pubescens</i> ssp. <i>tort</i>		<i>Epirrita autumnata</i>	Gr			
Kaitaniemi et al. 1998	<i>Betula pubescens</i> ssp. <i>tort</i>		Ch, N, Phe, PPC	<i>Epirrita autumnata</i>	Gr, P		
Kaitaniemi et al. 1999	<i>Betula pubescens</i> ssp. <i>tort</i>						
Kaitaniemi et al. 1999	<i>Betula pubescens</i> ssp. <i>tort</i>		Gr	<i>Operophtera brumata</i>	P		
Neuvonen and Haukioja 1984	<i>Betula pubescens</i> ssp. <i>tort</i>		Gr, N, P, Phe	<i>Epirrita autumnata</i>	Gr, C		
Neuvonen et al. 1987	<i>Betula pubescens</i> ssp. <i>tort</i>			<i>Epirrita autumnata</i>	Gr, P, S		
Ruohomäki et al. 1996	<i>Betula pubescens</i> ssp. <i>tort</i>			N, Phe	<i>Rheumaptera hastata</i>	P, S	
Tuomi et al. 1988a	<i>Betula pubescens</i> ssp. <i>tort</i>	Pho, N, P					
Hoogesteger and Karlsson 1992	<i>Betula pubescens</i> ssp. <i>tort</i>		Gr, N, P, Phe				
Bryant et al. 1993	<i>Betula resinifera</i>	N, P, Phe	several species, not identified	C			
Bryant et al. 1991	<i>Burkea africana</i>						
Cornelissen 1993	<i>Castanopsis fargesii</i>	Gr, N	several species, not identified	C			
Bryant et al. 1991	<i>Dichrostachys cinerea</i>	N, P, Phe					
Landsberg 1990	<i>Eucalyptus blakelyi</i>	Ch, N, Wa, Phe	several species, not identified	C			
Bryant et al. 1991	<i>Euclea natalensis</i>	N, P, Phe	several species, not identified	C			
Canham et al. 1994	<i>Fraxinus americana</i>	Gr	several species, not identified	C			
Bryant et al. 1991	<i>Grewia flavescens</i>	N, P, Phe					
Miller et al. 1990	<i>Juniperus occidentalis</i>	Gr, N	<i>Pristiphora erichsonii</i>	Gr, C			
Krause and Raffa 1992	<i>Larix decidua</i>	Gr, Pho, Ch					
Vanderklein and Reich 1999	<i>Larix leptolepis</i>		N, P, Phe	<i>Orgyia vetusta</i>	Gr, P, C		
Harrison and Karban 1986	<i>Lupinus arboreus</i>						
Bryant et al. 1991	<i>Ochna pulchra</i>	Gr, Phe	several species, not identified	C			
Stock et al. 1993	<i>Osteospermum sinuatum</i>						
Van der Heyden and Stock 1995	<i>Osteospermum sinuatum</i>	Gr, Ch					

Reference	Plant species	Plant variables	Herbivore species	Herbivore variables
Christiansen and Fjone 1993	<i>Picea abies</i>	Ch, N, P, K, Ca, Mg, S		
Litvak and Monson 1998	<i>Picea engelmannii</i>	Ter		
Quiring and McKinnon 1999	<i>Picea glauca</i>	Gr		
Litvak and Monson 1998	<i>Pinus contorta</i>	Ter		
Litvak and Monson 1998	<i>Pinus ponderosa</i>	Ter		
Wagner and Evans 1985	<i>Pinus ponderosa</i>	Phe		
Reich et al. 1993	<i>Pinus resinosa</i>	Ch		
Vanderklein and Reich 1999	<i>Pinus resinosa</i>	Pho, Ch		
Honkanen and Haukioja 1994	<i>Pinus sylvestris</i>	Gr, C, N, Wa		
Honkanen et al. 1999	<i>Pinus sylvestris</i>	Gr, Ch, N, Phe, Ter		
Lyytikäinen 1992a	<i>Pinus sylvestris</i>	N		
Lyytikäinen 1992a	<i>Pinus sylvestris</i>		<i>Microdiprion pallipes</i>	Gr, P, S
Lyytikäinen 1992a	<i>Pinus sylvestris</i>		<i>Gilpinia pallida</i>	Gr, P, S
Lyytikäinen 1992a	<i>Pinus sylvestris</i>		<i>Neodiprion sertifer</i>	Gr, P, S
Lyytikäinen 1992b	<i>Pinus sylvestris</i>		<i>Microdiprion pallipes</i>	Gr, P, S
Lyytikäinen 1992b	<i>Pinus sylvestris</i>		<i>Gilpinia pallida</i>	Gr, P, S
Lyytikäinen 1994	<i>Pinus sylvestris</i>	Ch, Phe	<i>Neodiprion sertifer</i>	Gr, P, S
Lyytikäinen 1994	<i>Pinus sylvestris</i>		<i>Gilpinia pallida</i>	Gr, P, S
Lyytikäinen-Saarenmaa 1999	<i>Pinus sylvestris</i>	Gr, C, N, Wa		
Niemelä et al. 1991	<i>Pinus sylvestris</i>	N, Wa		
Niemelä et al. 1991	<i>Pinus sylvestris</i>		<i>Neodiprion sertifer</i>	P, S
Niemelä et al. 1991	<i>Pinus sylvestris</i>		<i>Diprion pini</i>	P, S
Havill and Raffa 2000	<i>Populus nigra</i>		<i>Lymantria dispar</i>	Gr, S
Clausen et al. 1989	<i>Populus tremuloides</i>	Phe		
Kruger et al. 1998	<i>Populus tremuloides</i>	Gr, Pho		
Reichenbacher et al. 1996	<i>Populus</i> spp.	Gr		
Havill and Raffa 1999	<i>Populus</i> sp.		<i>Lymantria dispar</i>	Gr, C
Neuvonen et al. 1987	<i>Prunus padus</i>		<i>Epirrita autumnata</i>	Gr, P, S
Leather 1995	<i>Prunus padus</i>	Gr, N, P, K, Ca, Mg	several species, not identified	C
Canham et al. 1994	<i>Prunus serotina</i>	Gr		
Canham et al. 1999	<i>Prunus serotina</i>	Ch		
Stock et al. 1993	<i>Pteronia pallens</i>	Gr, Phe		
Van der Heyden and Stock 1995	<i>Pteronia pallens</i>	Gr, Ch		
Wold and Marquis 1997	<i>Quercus alba</i>	PPC	several species, not identified	C
Faeth 1992	<i>Quercus emoryi</i>	Phe	several species, not identified	C
Kudo 1996	<i>Quercus mongolica</i>	N		
Hunter and Schultz 1995	<i>Quercus prinus</i>	Phe		
Canham et al. 1999	<i>Quercus rubra</i>	Ch		
Hunter and Schultz 1995	<i>Quercus rubra</i>	PPC		
Lovett and Tobiesen 1993	<i>Quercus rubra</i>	Pho, N		
Schultz and Baldwin 1982	<i>Quercus rubra</i>	Wa, Phe, PPC		
Valentine et al. 1983	<i>Quercus velutina</i>	Ch, N	<i>Lymantria dispar</i>	P
Stock et al. 1993	<i>Ruschia spinosa</i>	Gr, Phe, PPC		
Van der Heyden and Stock 1995	<i>Ruschia spinosa</i>	Gr, Ch		
McPherson and Williams 1998	<i>Sabal palmetto</i>	Ch		
Bryant 1987	<i>Salix alaxensis</i>	Gr, N, P, Phe	several species, not identified	C
Raupp and Sadof 1991	<i>Salix alba</i>	N, Wa, Phe	<i>Plagiodera versicolora</i>	Gr, S
Zvereva and Kozlov 2000	<i>Salix borealis</i>		<i>Epirrita autumnata</i>	Gr
Zvereva and Kozlov 2000	<i>Salix borealis</i>		several species, not identified	C
Hjälten and Price 1996	<i>Salix lasiolepis</i>	Gr	several species, not identified	C
Julkunen-Tiitto et al. 1995	<i>Salix myrsinifolia</i>	Phe		
Julkunen-Tiitto et al. 1995	<i>Salix pentandra</i>	Phe		
Neuvonen et al. 1987	<i>Salix phylicifolia</i>		<i>Epirrita autumnata</i>	Gr, P, S
Neuvonen et al. 1987	<i>Sorbus aucuparia</i>		<i>Epirrita autumnata</i>	Gr, P, S
Tolvanen and Laine 1997	<i>Vaccinium myrtillus</i>	Ch, N		