

Insect performance and host-plant stress: a review from a biological control perspective

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Summary

Three hypotheses predict how insect herbivores perform on stressed host plants. The plant stress hypothesis (PSH) predicts improved insect performance on stressed hosts. The plant vigour hypothesis (PVH) predicts that insects closely associated with their host, such as gall-formers, will perform better on vigorously growing non-stressed hosts. The third hypothesis, the Insect Performance Hypothesis (IPH) predicts that wood-feeders, sap-feeders and miners will perform better on stressed hosts, while leaf-feeders and gall-formers will perform better on non-stressed hosts. These hypotheses were developed, however, without separating different types of plant stress. In this review we tested these hypotheses across five insect feeding-guilds and twelve host-plant stress types, from more than 200 published studies on insect performance. When all host-plant stress types were pooled, the results suggested wood, sap and leaf-feeders performed better on stressed host plants, while miners and gall-formers performed better on non-stressed host plants, thus supporting the PVH. However, when all insect feeding-guilds were pooled, it was found that host-plant-stress type also influenced insect performance, which was generally higher when host plants were growing under reduced moisture, light or CO₂, increased soil nitrogen or on younger plants. When host-plant-stress type and insect feeding-guild were separated, it was found that insect performance across feeding guilds varied with the type of host-plant stress encountered suggesting that insects in different feeding guilds may respond to different physiological and morphological changes in the plant. This review highlights the fact that insect performance is often significantly affected by host-plant stress, but that the direction of the response is variable. Although this review did not fully support any of the three theoretical hypotheses tested, there were consistent relationships between some insect-feeding guilds and host-plant-stress types that would allow the prediction on whether a specific biological control agent might perform better under a specific host-plant stress.

Keywords: environmental stress, insect performance hypothesis, insect plant interactions, plant stress hypothesis, plant vigour hypothesis.

Introduction

Environmental stress is a factor that reduces plant performance below that achieved under optimal conditions (Price 1991). All plants encounter stress, because optimal conditions are rarely encountered in the field

due to variations or fluctuations in environmental conditions. Several morphological and physiological changes may occur in plants under stress (Mattson & Haack 1987), depending on the plant species, and the severity, duration and type of stress encountered (Grime & Campbell 1991). Under moisture stress, for example, many plants show reduced leaf water, starch and carbohydrates,; and increased leaf nitrogen and soluble sugars (Miles *et al.* 1982, Mattson & Haack 1987, English-loeb *et al.* 1997). In contrast, low light levels can lead to reduced soluble sugars and increased leaf nitrogen and leaf water (Collinge & Louda 1988, Attridge 1990, Potter 1992).

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The morphological and physiological changes that occur in plants under stress may affect the performance of insect herbivores feeding on those plants (Mattson & Haack 1987). Several authors have suggested that changes in insect performance under host-plant stress may be predictable, although different authors have suggested different responses by insects to host-plant stress. White (1969, 1993) suggested that plants under stress become more susceptible to insect herbivores, with the increase in insect performance driven by increases in leaf soluble nitrogen (the plant stress hypothesis; PSH). In contrast, Price (1991) suggested that certain insects would perform better on more vigorously growing (non-stressed) host-plants, particularly herbivores closely associated with their host-plant (the plant vigour hypothesis; PVH). Price (1991) suggested that “herbivores closely associated” would include insects where the female selects the oviposition site within a few centimetres of where larvae will feed and that hatching occurs soon after oviposition. This hypothesis was based on observations of insect herbivores preferentially attacking young and vigorously growing plants and plant parts, over older plants or plant parts. Combining elements of both the PSH and the PVH, Larsson (1989) suggested that certain insect feeding-guilds (wood-feeding, sap-feeding and mining insects) perform better on stressed host-plants, whereas other insect feeding-guilds (leaf-feeding and gall-forming insects) perform better on vigorously growing host plants. This was termed the insect performance hypothesis (IPH). The rationale for this hypothesis was based on: a) woody plants under stress have reduced oleoresin flow, making them less resistant to attack by wood-feeders; b) sap-feeding insects generally encounter low nitrogen levels so that when a plant is stressed, with resulting higher nitrogen levels, insect performance improves; c) miners are able to avoid consuming harmful defensive compounds produced by the plant while taking advantage of the higher nitrogen content of stressed plants; d) leaf-feeders do not separate out the chemical fractions in their food as efficiently as other feeding-guilds that discriminate against defensive compounds in stressed plants, so do better on vigorously growing plants; and e) galling insects prefer large-sized buds, which are found on vigorously growing plants.

If insect herbivores perform differently when host plants are under stress, then this has important implications for the effectiveness of insect herbivores released as biological control agents. Herbivores may be more effective in reducing plant performance over certain parts of a plant species' range, depending on whether they perform better on stressed or vigorously growing plants. For example, knowing that an insect herbivore performs better on vigorously growing non-stressed host plants and that the same insect performs poorly on stressed host plants may indicate that an additional biological control agent that performs well on stressed plants, or other forms of control, are required in those parts of a plant's range where it is subject to stress.

Two studies have reviewed the evidence for relationships between insect performance and host-plant stress. Waring & Cobb (1992) assessed insect performance in relation to host-plant moisture and nutrient stress, reporting that the type of stress was a stronger predictor of insect performance than insect feeding-guild. In contrast, Koricheva *et al.* (1998) argued that the insect feeding-guild (using the same guilds as Larsson (1989)) could predict insect performance for host plants under moisture, light and pollution stresses. They used a meta-analysis to detect a weak but overall significant relationship consistent with the IPH.

The aim of this paper is to assess both the strength and variability of the relationship between insect performance and host-plant stress by collating the results of published studies that have examined insect performance across insect feeding-guilds and host-plant-stress types. If this relationship is to be of predictive use in biological control then it requires strong, consistent relationships between the performance of insect feeding-guilds and host-plant stress.

Materials and methods

Selection of insect feeding-guilds and stress types

This review assesses insect performance across five insect feeding-guilds on plants subject to 12 stress types. The insect feeding-guilds selected were wood-feeders, sap-feeders, miners, leaf-feeders and gall-formers. These are the same guilds considered in the IPH by Larsson (1989) and reviewed by Koricheva *et al.* (1998). These feeding-guilds can directly affect plant growth, unlike flower and seed-feeding guilds.

Stresses from five of the seven abiotic categories listed by Heinrichs (1988) as affecting plant growth were included: moisture (water deficit and excess), electromagnetic energy (light and ultraviolet-B radiation), physical and chemical properties of the soil (soil-nitrogen, salinity and acidity), air pollution (ozone, carbon dioxide, sulfur dioxide and acid rain) and mechanical damage (fire). Stresses caused by temperature or pesticides/growth regulators were not included, because these have strong, direct effects on insect performance as well as on host-plant growth. Plant age was also included as a “stress” because several authors have shown that insect performance is affected by age (Price *et al.* 1987, Caouette & Price 1989, Craig *et al.* 1989, Roininen *et al.* 1993), and age was a factor considered by Price (1991) in developing the PVH.

Selection of studies

Key word searches in CAB Abstracts were used to source studies. Studies were found by entering a stress type and herbivory (e.g. moisture and herbiv*) and by entering the name of each of the three hypotheses. Additional studies were found by searching the reference lists

of the papers collected. Studies were selected if they assessed the performance of individual insect species, where those species belonged to one of the five listed feeding-guilds, and where the host plant was under one of the 12 listed stresses. Studies measuring insect performance as changes in fecundity, abundance, growth rate or generation time in relation to host-plant stress were selected. Studies using only feeding rates or preferences were not included. Only papers written in English that could be obtained in New Zealand, and only studies that used herbivorous arthropods in the orders Insecta and Acari, were included.

Definition of a 'stressed host-plant'

A stressed host plant is defined as one with reduced growth relative to that experienced under optimal conditions (Price 1991). Stressed host plants were therefore found in environments with reduced moisture, light, UV-B, soil nitrogen, and CO₂; increased salinity, acidity, ozone, SO₂ and acid rain. Plants were also stressed after burning and as they aged.

Analytical approach

Meta-analysis is frequently advocated as the best approach for combining the results from several studies to provide an overall test of a hypothesis, because it assesses the magnitude of the effect across studies (Gurevitch & Hedges 1993). In this study, however, the primary interest was not in testing for an overall effect, but in examining variability in the outcome of studies assessing the relationship between insect performance and host-plant stress. A weak, but significant overall relationship between insect performance and host-plant stress, such as that found by Koricheva *et al.* (1998), may be of little practical significance if the aim is to reliably predict the performance of insect biological control agents on host plants in different parts of their range.

Vote counting has been criticised because it relies on the statistical significance reported in individual studies, which varies as a function of the sample sizes employed in those studies (Gurevitch & Hedges 1993). Studies could show a non-significant result but nevertheless show a consistent tendency towards a particular outcome, which would not be detected using a vote-counting approach, but is more likely to be detected using meta-analysis, which considers the reported effect sizes (Gurevitch & Hedges 1993). Nevertheless, the use of vote-counting in this study is justified on two grounds. First, most of the studies examined did not report the outcome of experiments in sufficient detail to be included in a meta-analysis. A vote counting approach allowed a greater number of studies to be included so that the variability of outcomes across different insect feeding-guilds and host-plant-stress types could be better assessed. Second, over three quarters of the studies examined reported a statistically

significant result one way or the other, allowing insect performance with regards to host-plant stress to be clearly categorised.

The number of studies that showed a significant positive relationship, a significant negative relationship, or no significant relationship (including studies that showed a non-linear response: that is, insect performance initially increased as stress intensity increased, but subsequently decreased) between insect performance and host-plant stress were tallied. The following additional information from each study was also collated: stress type, insect feeding-guild, arthropod family and species, and plant species.

Results

Data were collated from 201 studies on insect performance in relation to host-plant stress, from 105 papers published between 1955 and 2000. These 201 studies investigated the performance of 132 arthropod species (from 47 families and 7 orders) on 86 plant species.

When all stress types were pooled, the variability in the response of insect herbivores to host-plant stress was highlighted (Fig. 1). Of the 153 studies showing significant results, 77 showed that insect performance increased significantly on stressed host plants, whereas 76 showed that insect performance decreased significantly on stressed host plants, giving little support to the PSH. This data set supported the PVH ($\chi^2_1 = 6.8$, $p = 0.009$), as it was found that miners and gall-formers (this review considered those two guilds to be closely associated with the host plant) were represented in a greater proportion of studies showing a negative relationship between insect performance and host-plant stress, compared with other guilds that tended to show the opposite. The data set did not support the IPH, with only 38% of wood-feeders, sap-feeders and miners performing better on stressed hosts ($\chi^2_1 = 0.001$, $p = 0.971$).

When all feeding guilds were pooled, insect performance was higher on host plants growing under reduced moisture, light or CO₂, increased soil nitrogen or on younger plants (Fig. 2).

The data set also suggested that insect performance differs between insect feeding-guilds, depending on the host-plant-stress type encountered (Table 1). For example, the performance of leaf-feeders improved when host plants were growing under reduced moisture, light or CO₂, or increased soil nitrogen. The performance of miners improved when plants were growing under reduced CO₂, or increased moisture or soil nitrogen.

Several studies assessing the performance of leaf-feeders and miners also measured plant physiological responses to the stress being imposed. From these data, the performance of leaf-feeders tended to improve with increased plant nitrogen, while no clear and consistent physiological response was found for miners.

Insect performance and host-plant stress

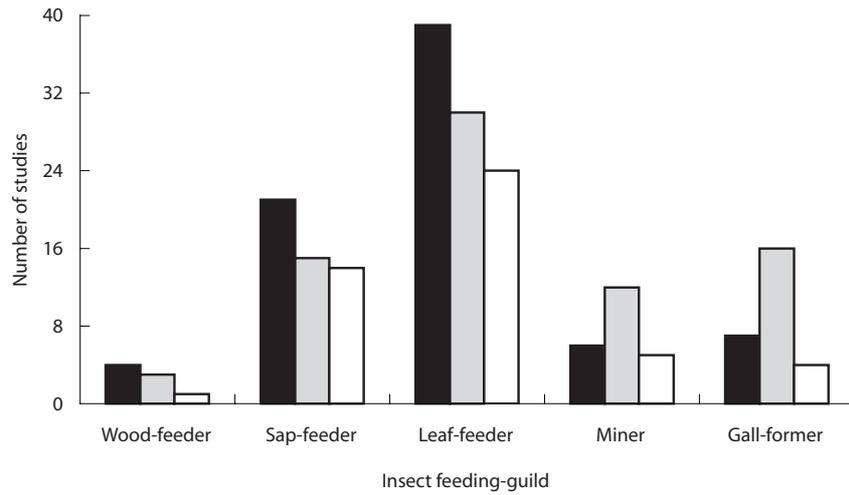


Figure 1. The number of studies where insect performance improved on stressed hosts (dark-shaded bars), improved on non-stressed hosts (light-shaded bars), or showed no relationship with host-plant stress (open bars), for five insect feeding-guilds.

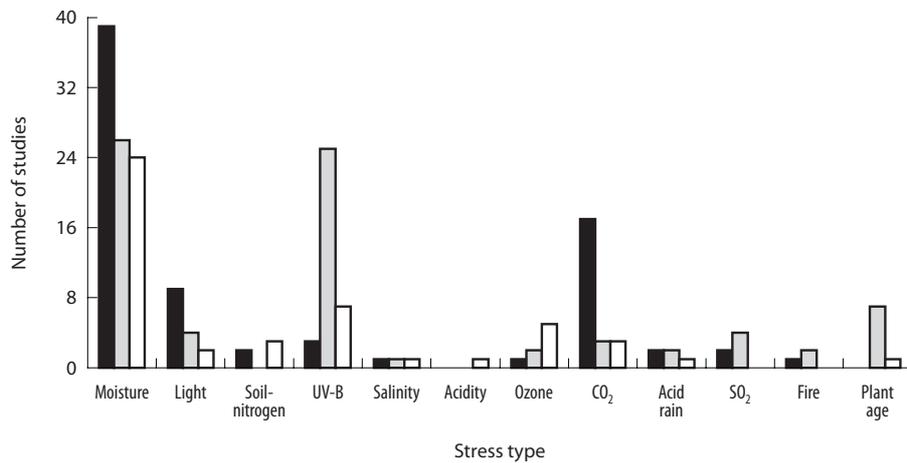


Figure 2. The number of studies where insect performance improved on stressed hosts (dark-shaded bars), improved on non-stressed hosts (light-shaded bars), or showed no relationship with host-plant stress (open bars), for 12 stress types.

Table 1. Predictions for improved insect performance on stressed host plants, on non-stressed host plants or when host-plant stress is not important across a range of stress types and insect feeding-guilds.

Insect feeding-guild	Improved insect performance		
	Stressed host plants	Non-stressed host plants	No relationship with stress
Wood-feeder			Moisture
Sap-feeder		CO ₂	Moisture
Leaf-feeder	Reduced moisture Reduced light Reduced CO ₂	Increased soil nitrogen	
Miner	Reduced CO ₂	Increased moisture Increased soil nitrogen	Light
Gall-former		Increased soil nitrogen Reduced plant age	Moisture

Discussion

Hypotheses predicting relationships between insect performance and host-plant stress may allow the identification of parts of a host-plant's range where insect herbivores released for biological control are likely to be effective and where other control strategies will be required. For this to be of practical use requires consistent relationships between insect performance and host-plant stress. However, the results of this study suggest that insect response to host-plant stress can vary greatly according to the feeding-guild that the insect belongs to and on the form of stress encountered by the host plant.

Figure 1 highlights the variability in the response of insect herbivores to host-plant stress, where insects in the same feeding-guilds showed both positive and negative performance responses to host-plant stress. Though this data set supported the PVH, it does not provide a reliable basis for predicting the performance of insect feeding-guilds under host-plant stress, as only 56% of mining and gall-forming insects showed a positive response to non-stressed host plants.

Waring & Cobb (1992) reported that stress type, not insect feeding-guild, was the more important determinant of insect performance on stressed and non-stressed hosts, while Koricheva *et al.* (1998) found the opposite. These contrasting results may have arisen because each study reviewed a different range of stress types. Waring & Cobb (1992) focused on moisture and nutrient stress, while Koricheva *et al.* (1998) reviewed moisture, light and pollution stresses. Results presented here showed that insect performance generally improved when hosts were under moisture deficit, and decreased when experiencing nutrient deficit, as indicated by soil nitrogen and as predicted by Waring & Cobb (1992). Consistent with Koricheva *et al.* (1998), these results also showed improved insect performance when host plants were under moisture, light and pollution stresses. If Koricheva *et al.* (1998) had considered a wider range of stress types, and included nitrogen stress under which insect performance appears to decline, their results may well have showed that stress type is an important determinant of insect performance.

Plant nitrogen levels probably explain the general association found between stress type and insect performance. In this review, improved insect performance occurred under reduced host-plant moisture, light and CO₂, increased host-plant soil nitrogen, and on younger host plants (Fig. 2); all of which have been generally associated with increased plant nitrogen.

These results indicate that, to predict insect performance in relation to host-plant stress, both insect feeding-guild and stress type must be considered. Small sample sizes prevented detailed statistical analysis of insect performance by feeding-guilds with plant stress, though some patterns emerged (Table 1). For instance, under moisture stress, leaf-feeders performed better on

stressed hosts. Waring & Cobb (1992) found that "chewers" (wood-borers, stem-borers, root-feeders, leaf-miners and leaf-chewers) all responded positively to moisture stress. As several feeding-guilds were included in this grouping, the results should be used cautiously, especially as our results indicated that miners performed better on non-stressed hosts. The results from this review support those of Waring & Cobb (1992) that leaf-feeders, miners and gall-formers performed better on fertilized (non-stressed) hosts and those of Koricheva *et al.* (1998) in that leaf-feeders performed better on light-stressed hosts. Bezemer & Jones (1998) found that, as CO₂ increased, sap-feeders' performance increased, and that the performance of leaf-feeders and miners decreased. This review supported those findings for leaf-feeders and miners, but insufficient data were collated on sap-feeders to compare findings. Wood-feeders showed little variation in performance in relation to stress type. This might be expected, given that the feeding site is somewhat removed from the actively growing host-plant tissue.

Larsson (1989) emphasized the need to first understand how plants respond to a stress, and then relate this to how it might affect insect performance. Different insect feeding-guilds may respond in different ways to different mechanisms. In this review, leaf-feeders appeared to respond positively to stresses (reduced moisture, light and CO₂ and elevated soil-nitrogen) associated with increased nitrogen, as did gall-formers. However, no clear plant-physiological mechanism was evident for miners, suggesting that they may be responding to another factor, such as changes in leaf morphology. Potter (1992) observed that changes in performance of a leaf-miner were related to changes in leaf structure rather than the nutritional quality of leaves. Details of plant physiological and morphological changes that occur under all the different stresses reviewed are beyond the scope of this study.

The results from this review indicate that the current plant stress – insect herbivory hypotheses do not adequately predict insect performance on stressed and non-stressed plants. However, based on the analyses, it is clear that the type of stress imposed on the plant, as well as the insect feeding-guild, is important in determining insect performance. There may be underlying associations between plant morphology and physiology and insect performance (e.g. available plant nitrogen) that are affected by the nature of the stress. The categories of feeding-guilds used in this analysis may also mask some trends in relationships. For instance, the category "miners" includes both stem and leaf miners, which may respond differently to applied stresses. Although current insect herbivory–plant stress hypotheses are too generalized at this stage to be helpful for improving weed biological control, our analysis does suggest possible benefits from the application of some of the results, particularly for leaf-feeders and miners.

For example, it is predicted that a leaf-feeding insect might perform better on host plants growing under drought-stressed conditions, in shade and with high soil nitrogen levels, while a miner might perform better in environments where host plants are receiving high moisture and soil nitrogen.

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