

## CRITICAL APPRAISAL

Critical appraisals allow the analytical review of existing knowledge on current topics of significance in ecological entomology. They should assess the worth or quality of the work in the field and suggest areas for investigation.

# Towards an empirically-based theory of herbivore demography

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**Summary.** Previous studies have synthesized life-table data from herbivore species to identify general trends in the demography of herbivorous insects. Frequency-based analyses were used to ascertain which of five mortality sources (enemies, plant factors, competition, weather, intrinsic developmental failure) and which of five ecological characteristics of herbivores (feeding biology, invasion status of the herbivore, latitude, cultivation, and successional status of the habitat) had important influences on mortality patterns.

Here these results are reinforced with a quantitative analysis that relies on actual numbers of herbivores killed at different developmental stages by each of the five mortality sources in different ecological settings. We also examine the relationship between taxonomic category (Coleoptera, Diptera, Lepidoptera, and Hymenoptera) and mortality.

The analysis identified developmental changes of herbivores as having an important influence on sources of mortality; feeding biology, latitude, and cultivation status also influenced the distribution of mortality sources. Other aspects of the herbivores' ecology and taxonomy had limited effects.

Natural enemies were identified as the most important mortality source overall, and their importance increased from the early larval stages to the pupal stages. They also kill more exophytic insects than endophytic insects, and kill a higher proportion of insects in cultivated habitats than in natural habitats.

Weather kills more temperate-zone immatures than tropical/subtropical immatures.

The results of the quantitative analysis generally confirm the earlier frequency-based tests.

Several predictions that can serve as the foundation of an empirically-based theory of herbivore demography are offered: (1) natural enemies are the dominant cause of mortality in exophytic herbivore populations and may compete more intensely than on endophytics; (2) plant factors and enemies play a more balanced role in endophytic populations; (3) exophytic species should be particularly susceptible to top-down effects, especially in agroecosystems; (4) plant defences will often have sublethal effects, but when they are lethal they will be most important as the hatchling larva is just getting established on the plant.

These predictions should be viewed as a challenge to engage in a broader way of thinking about herbivore demography.

**Key words.** Demography, herbivores, life tables, mortality factors, survival.

## Introduction

Recently, the study of herbivore demography has received considerable attention from both pest control specialists and researchers asking basic questions about population phenomena (Andow, 1990; Price, 1991a; Cappuccino, 1992; Rosenheim *et al.*, 1993; Swetnam & Lynch, 1993; Letourneau, 1994; Stiling, 1994; Cappuccino & Price, 1995; Preszler & Boecklen, 1996). The former have mainly been concerned with the suppression of pest populations, and the successful introduction and establishment of biological control agents against weeds. The latter have focused on fundamental issues of population regulation, interspecific interactions, and trophic dynamics. Although pest control specialists and population biologists have different reasons for studying herbivore populations, the ecological information they seek is fundamentally the same. One important question of interest to both groups is how the survivorship patterns and mortality sources of a herbivore population are influenced by their ecological setting. The answer will differ for each species, but perhaps there are generalizations that apply to broad ecological categories. Such generalizations are critical to the derivation of an effective empirically-based theory of herbivore demography (see Price, 1991a). By averaging across many individual studies of herbivore populations, consistent patterns may emerge from the idiosyncratic details of individual species and individual experiments, and the foundations of such a theory can be laid. The existence of numerous well-designed and executed life-table analyses in the basic and applied literature should make it possible to derive such patterns, and thus to predict which of the many ecological factors that potentially influence herbivore populations will have their greatest impact on demography.

The life-table literature has been the most productive source of information on herbivore demography. Life tables report stage-specific survival and sources of mortality for herbivore populations in a variety of ecological settings. Because the data are collected in a standard way, they can be compiled and synthesized to reveal central tendencies in different ecological categories without particular regard to the individual species making up each category. Even so, only a few authors have compiled life tables in an effort to discern general patterns in demography. Until recently, the focus of these studies was on either rates of density dependence and/or key factors in insect populations (Dempster, 1983; Strong *et al.*, 1984), or on the relationship between insect lifestyle and survivorship (Price, 1975; Cornell, 1990; Cornell & Hawkins, 1995). Cornell and Hawkins (1995), using a compilation of 530 life tables for 124 holometabolous herbivore species, took a different approach to life-table analysis by examining all mortality sources and attempting to associate these with five ecological variables of the insects: the successional stage of the habitat they occupy (early or late), habitat type (cultivated or natural), latitude

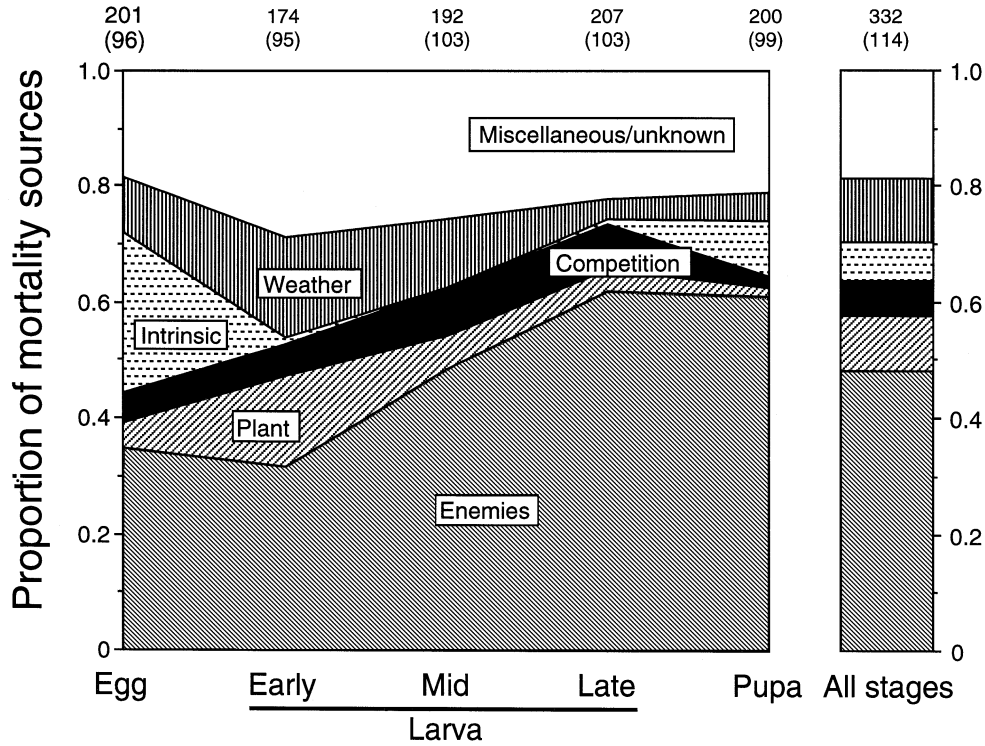
(temperate or tropical-subtropical), invasion status (native or introduced), and herbivore concealment (exophytic, endophytic, and mixed lifestyles). The methodology was qualitative, using the frequency with which mortality sources appeared as one of the three most important causes of death in the tables. Figure 1 summarizes the mortality spectrum for all holometabolous herbivores in the study. Similar figures were generated for subsets of the data broken down according to the ecological variables (Cornell & Hawkins, 1995).

A quantitative approach to life-table analysis was taken by Hawkins *et al.* (1997), who focused on mortality due to the three major types of natural enemies (predators, parasitoids and pathogens). In this study, life tables for seventy-eight insect species in which workers provided estimates of apparent mortality levels due to enemies, were analysed with respect to five of the variables included in the qualitative analysis, as well as the taxonomic category (Order) of the insects. Although statistically more rigorous than the frequency-based study, this analysis did not consider non-enemy mortality factors, and, hence, did not provide a full mortality spectrum.

In this paper the life-table literature is *reviewed*, but not in the traditional sense of summarizing the conclusions of the large numbers of studies that have been conducted over the past 50 years. Instead, the approach taken in the earlier analyses is developed. The goal is to synthesize quantitatively the data from a large number of life tables in order to provide a broadly-based answer to the questions raised above; namely, what are the major sources of mortality to which herbivorous insects are subject, and how are these sources influenced by an insect's ecological setting? It must be emphasized at the outset that it is not the goal of this paper to elucidate the relative roles of mortality factors in the population dynamics of herbivores. Although some of these factors may influence dynamics strongly, such influence cannot be inferred from life tables unless they are repeated and analysed over several generations. Unfortunately, multigenerational analyses are too rare to shed light on the broad relationships among ecology, mortality, and population dynamics.

## Methods

The analysis included all life tables in the previous compilation (listed in Cornell & Hawkins, 1995) that reported the actual numbers or percentages of immatures at five developmental stages killed by each of five mortality sources [natural enemies, competition (both intra- and inter-specific), weather, intrinsic mortality (unattributed developmental failure), and plant factors] in at least one immature stage. The data set comprises eighty-three life tables for seventy-nine species (four tables were for species in both exotic and native locations). Within these tables, all stages that exhibited any unknown mortality

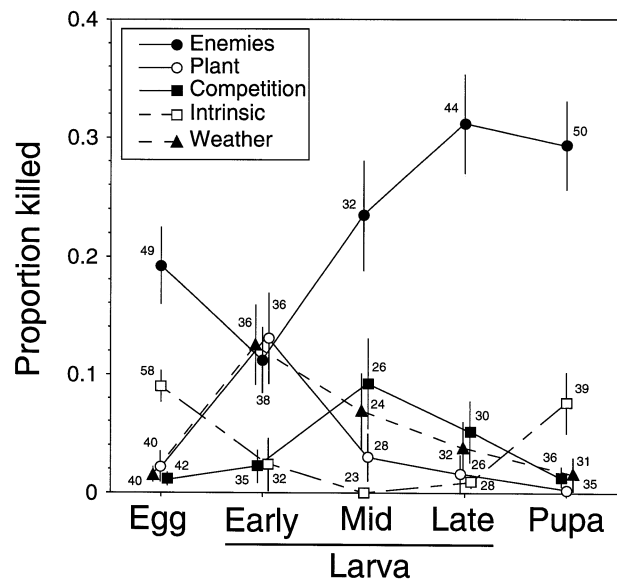


**Fig. 1.** Frequency-based analysis of herbivore mortality attributable to each of six causes of death at each of five developmental stages in 124 life tables. Numbers in parentheses are the total number of life tables used to generate the proportions on the y-axis for each developmental stage. Numbers above those in parentheses are sample sizes (instances of documented mortality) from which proportions are generated. The bar on the right represents mortality proportions for the entire pre-reproductive period, and the graph on the left breaks down the proportions by developmental stage (from Cornell & Hawkins, 1995). Reprinted with permission by University of Chicago Press.

were excluded. In those stages remaining, factors not responsible for any mortality were scored as a zero. When multiple life tables for a herbivore species were generated in a single study, death rates were calculated from numbers summed over all tables. Optimally, all life tables would have complete information on all mortality sources at all developmental stages, and the data set would comprise 2075 values (83 cases  $\times$  5 stages  $\times$  5 mortality sources). As many tables were incomplete or listed unknown mortality sources, only 894 values (43% of the optimal number) were available for the analysis.

Data on survivorship were reported as, or converted into, stage-specific mortality, which is simply the proportion of a cohort entering the population as eggs that dies from one developmental stage to the next. The proportions of individuals killed were compared in relation to five variables: herbivore feeding biology (exophytic vs. endophytic), latitudinal zone (tropics/subtropics vs. temperate), habitat type (cultivated vs. natural), Order (Coleoptera, Diptera, Lepidoptera, or Hymenoptera), invasion status (native vs. exotic), and succession (early vs. late).

Statistical analysis was heavily constrained, because the inclusion of zeros and the large number of empty cells (stages) violated the assumptions of both standard parametric tests and general maximum-likelihood methods. Consequently, analysis was restricted to testing main effects with ANOVA of ranked



**Fig. 2.** Mean proportion ( $\pm 1$  SE) of herbivores killed by five mortality sources at each of five developmental stages. Numbers near points are sample sizes.

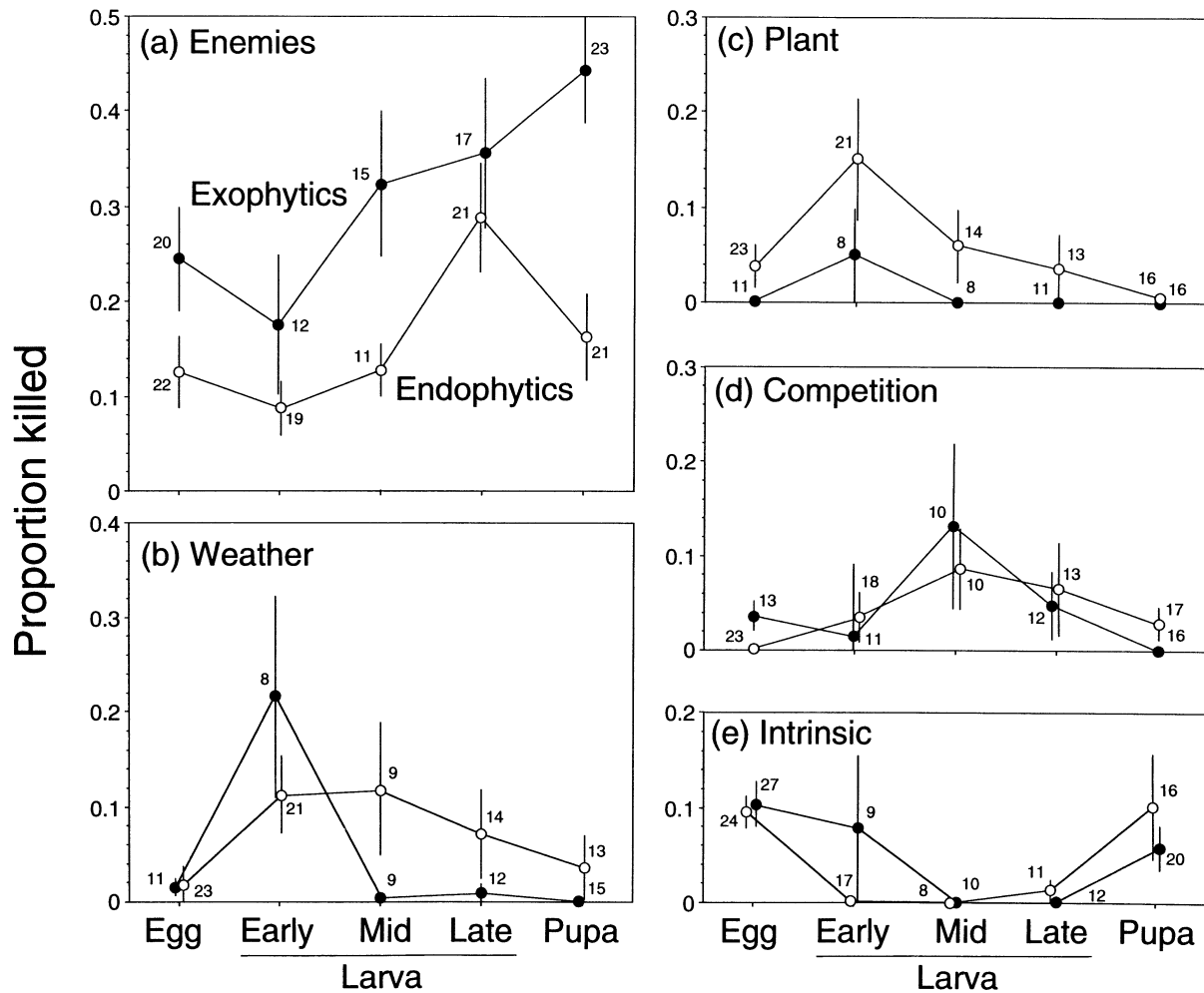


Fig. 3. Mean proportion ( $\pm 1$  SE) of exophytic and endophytic herbivores killed at each of five developmental stages.

data, employing the protocols for handling many ties and significance tests described by Zar (1984). Changes in mortality rates as herbivores mature were initially examined with a two-way ANOVA (developmental stage  $\times$  mortality source). The ecological and taxonomic factors were tested with six, three-way ANOVAs (factor  $\times$  developmental stage  $\times$  mortality source). In all cases, only main treatment effects could be tested, because interaction terms in multifactorial analyses are uninterpretable when using ranked data (Seaman *et al.*, 1994). Although the interactions among each factor, stage, and mortality source cannot be evaluated statistically, arithmetic means for each analysis are presented to identify general trends in insect survivorship and to show potential interactions among mortality factors and the independent variables.

## Results

Total mortality did not differ across developmental stages (two-way ANOVA:  $H = 4.19$ ,  $P > 0.5$ ), indicating that the risk of dying does not change as herbivores mature. However,

differences in the cause of death were highly significant ( $H = 292.46$ ,  $P < 0.0001$ ). Enemies kill the highest proportion of herbivores across all stages by a substantial margin ( $0.230 \pm 0.017$ ,  $n = 212$ ), followed by weather ( $0.052 \pm 0.011$ ,  $n = 162$ ), intrinsic mortality ( $0.051 \pm 0.008$ ,  $n = 179$ ), plant factors ( $0.041 \pm 0.011$ ,  $n = 167$ ), and competition ( $0.034 \pm 0.008$ ,  $n = 168$ ). There were also clear changes in the spectrum of mortality sources as herbivores aged (Fig. 2). Enemies are the most important cause of death at all stages except the early larval instars, but they become particularly lethal after the mid-larval stages when herbivores become more conspicuous and rewarding. In addition, some enemies (e.g. many koinobiont parasitoids and pathogens) attack herbivores early in development but do not kill them until they reach the later larval or pupal stages, accentuating enemy-induced death rates in late development. Death from plant factors and weather peaks in the early larval stages when herbivores have just hatched and must begin feeding. Vulnerability to plant defences, desiccation, and drowning are extreme as larvae seek and establish feeding sites on the host. Intrinsic mortality is most apparent in the egg and pupal stages during embryonic and

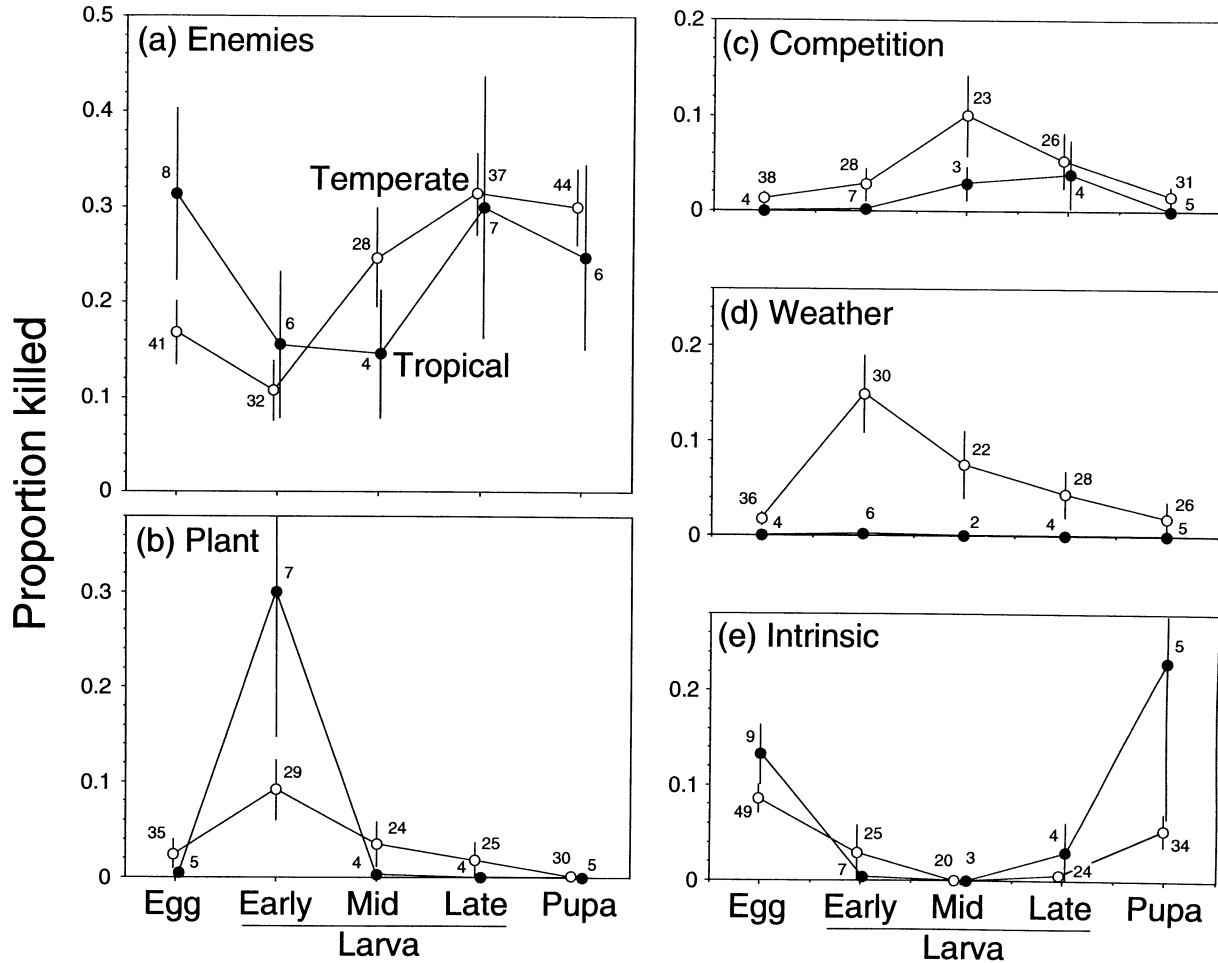


Fig. 4. Mean proportion ( $\pm 1$  SE) of herbivores killed in temperate and tropical habitats.

metamorphic development. In contrast, competition, although never particularly high, is most important in the mid-larval instars when the larvae are feeding actively, and tapers off in the egg and pupal stages. Competition in inactive developmental stages involves cannibalism by feeding larvae.

None of the five ecological factors or the taxonomic factor showed significant main effects on mortality in the three-way ANOVAs (all  $P > 0.05$ ), indicating that the ecological settings in which insects occur have little influence on survivorship (although mortality source was highly significant in all analyses;  $P < 0.001$ ). However, in three cases, specific causes of death did show relationships with ecological attributes of herbivores or their habitats. A comparison of herbivore lifestyles revealed that exophytic species suffer higher rates of enemy-induced mortality than endophytics in all developmental stages (Fig. 3). In contrast, endophytics suffer more from plant-caused death, presumably because endophytics form a more intimate association with the host and are less able to move about and seek out more benign feeding sites once they become sequestered. No other mortality source showed a clear pattern with lifestyle.

Latitude of the study site also interacted with mortality source to some extent (Fig. 4). As would be expected in the harsher, more variable climates at higher latitudes, weather kills more temperate-zone insects than tropical-subtropical insects. Unexpectedly, competition may also be more lethal in the temperate zone, a result that belies the conventional wisdom that species interactions are more intense in tropical regions (although the difference, albeit consistent across stages, was small). Plant factors are substantially more lethal for early-instar larvae in the tropics, consistent with the hypothesis that plant defences may generally be stronger there (Coley & Aide, 1994, but see below).

Cultivation status of the habitat was the third ecological factor to interact with mortality source (Fig. 5). Interestingly, enemy-induced mortality is higher in cultivated than in natural habitats. An expected consequence of high enemy-mortality is a reduction in competition, and that is also the case; competition in natural systems exceeds that in cultivated habitats for all actively feeding developmental stages. It is not coincidental that the mortality pattern for plant factors in cultivated habitats is very similar to that found for tropical insects (cf. Figs 4b

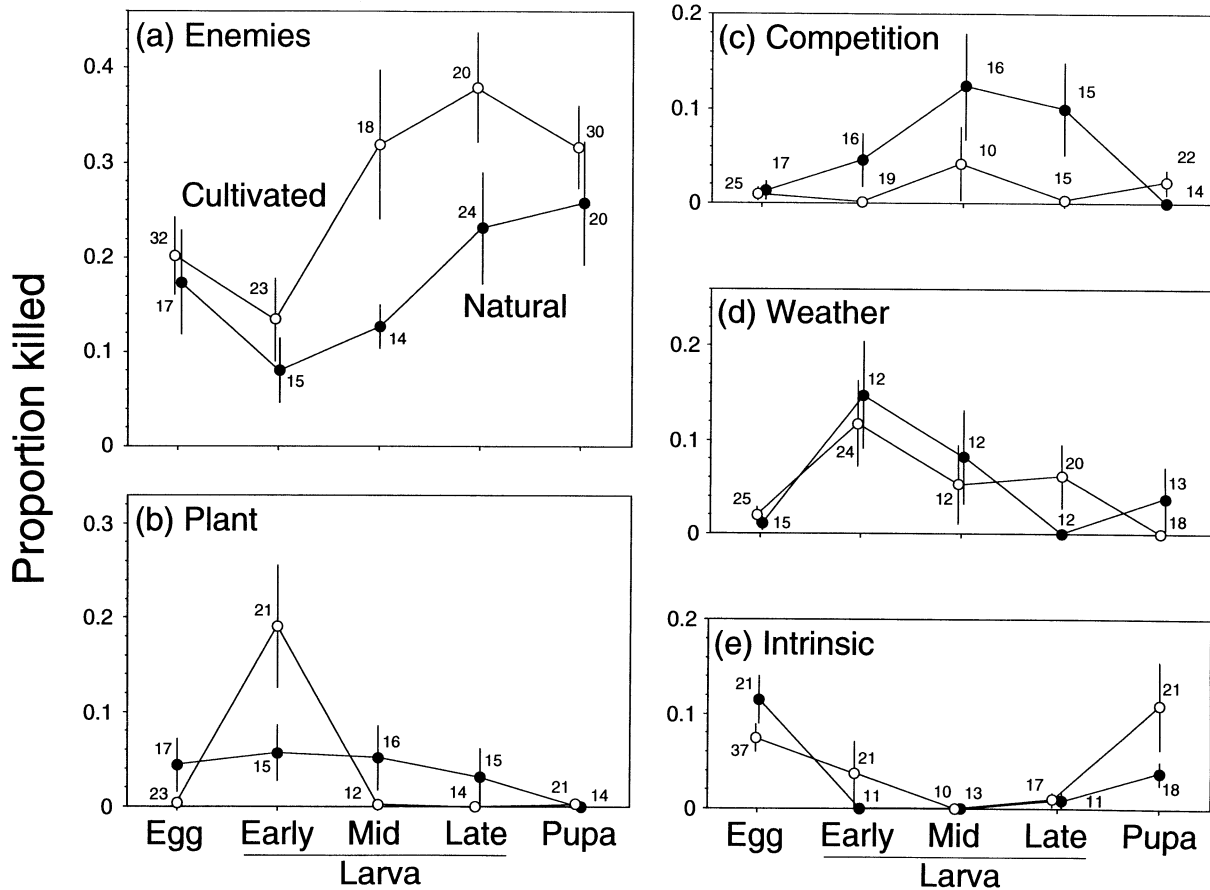


Fig. 5. Mean proportion ( $\pm 1$  SE) of herbivores killed in natural and cultivated habitats.

and 5b); very few life tables have been constructed for tropical insects in natural habitats, and, hence, the tropical insects are a subset of the cases in the cultivated category. There were insufficient data to tease apart a potential interaction between these two variables.

The Order to which herbivores belong (Fig. 6), their invasion status (Fig. 7), and the successional stage of the habitat they occupy (Fig. 8) show few independent relationships with sources of mortality that are consistent across most or all developmental stages. Thus, although they may play a role in herbivore population dynamics in specific systems, they appear to contribute little to general demography.

## Discussion

The proportion of herbivore populations killed by the various mortality factors identify the insects' developmental stage as the primary source of variation in mortality factors for immatures. Moreover, the quantitative distribution of mortality sources across stages mirrors closely the pattern found in the more comprehensive frequency-based analysis (cf. Figs 1 and 2), suggesting that patterns are robust to the method used to estimate mortality. The primary lesson gleaned from life tables is that enemies dominate the herbivore mortality spectrum and

competition is relatively weak, consistent with the predictions of trophic dynamic theory (Hairston *et al.*, 1960; Slobodkin *et al.*, 1967). According to these predictions, enemy attacks on the second trophic level can alleviate the effects of competition by depressing populations below their resource-based limit. High rates of enemy attack thus provide a plausible explanation for the generally weak competition among herbivores observed here and elsewhere (Schoener, 1983; Strong *et al.*, 1984; but see Damman, 1993; Denno *et al.*, 1995).

A recent survey of experimental studies on herbivore populations comes to a more ambiguous conclusion about the relative effects of enemies and competition on herbivore demography (Denno *et al.*, 1995). Neither mortality factor dominated in the systems examined. Several reasons could explain the divergent conclusions: (1) experiments are better at detecting competition relative to enemy effects than life-table studies because competitive effects are often sublethal, (2) Denno *et al.*'s (1995) surveys included hemimetabolous species, which might be more likely to compete with one another than holometabolous species, or (3) the conclusions were based on only thirteen natural systems and thus might be more subject to sampling error than the larger life-table study. Any or all of these reasons might explain the discrepancy, at least in part, and more experiments and better life tables will be necessary to resolve it.

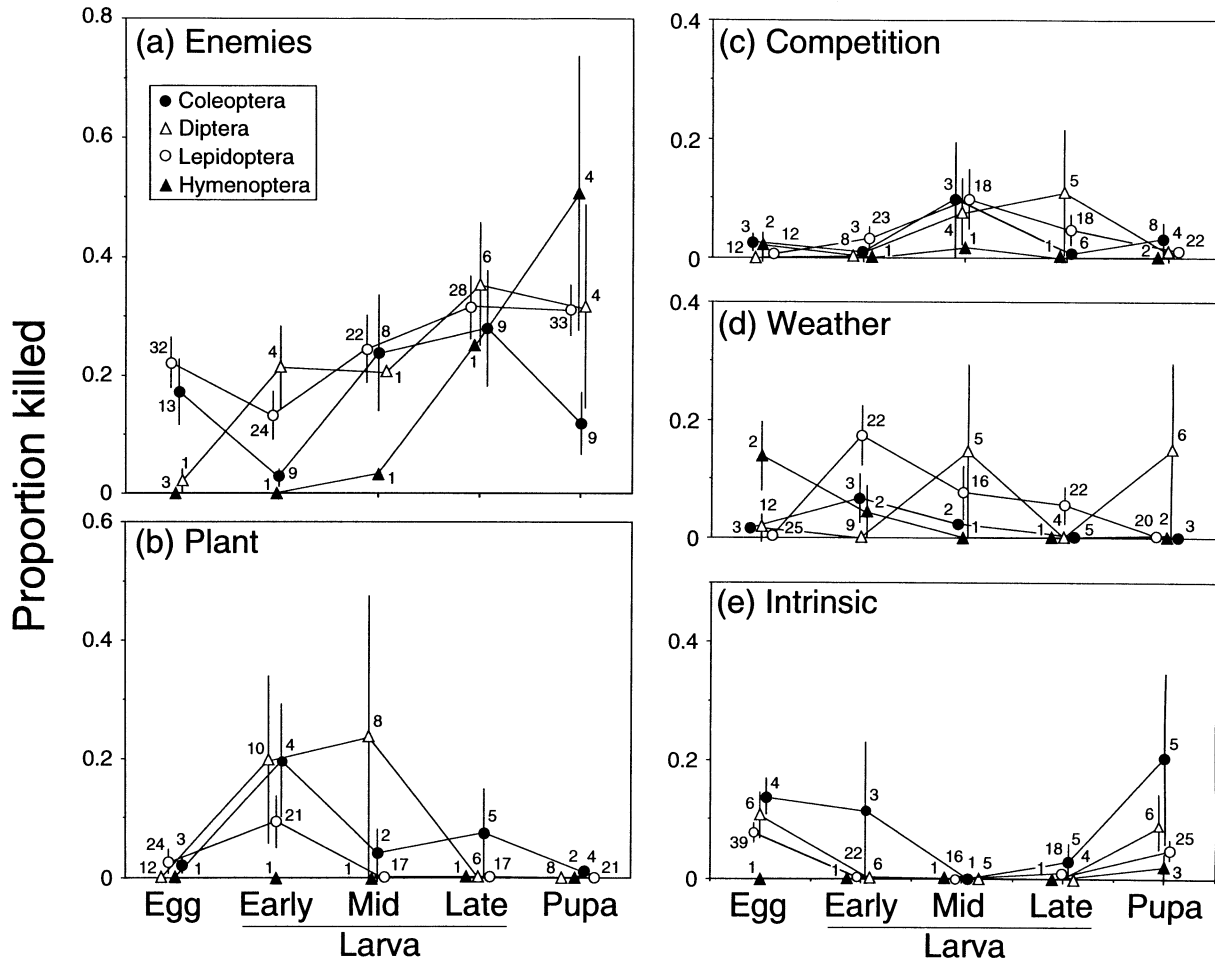


Fig. 6. Mean proportion ( $\pm 1$  SE) of herbivores killed in each of four Orders.

Another discrepancy between life-table data and other sources of data on insect populations is the dominance of enemies over plant factors. In the light of the recent work done on the importance of plant defence against herbivore attack (Duffy & Felton, 1991; Seldal *et al.*, 1994; Anon, 1995; Augner, 1995; Dussourd, 1995; Hunter & Schultz, 1995; Raffa & Smalley, 1995; Bodnaryk, 1996; Stamp & Yang, 1996), the relatively low importance of plant effects in this analysis is surprising. It is possible that life tables are biased against plant effects because plant defences were not well understood at the time many life-table analyses were carried out, and thus may have been misclassified or ignored. This possibility was tested crudely by classifying all life tables into two categories, those generated before, and those after, 1970. This date was chosen because Feeney's (1970) seminal paper on plant defences might have stimulated more attention to plant effects in subsequent life-table analyses. If so, plant effects should be more apparent in the post-1970 analyses. Although some post-1970 life tables captured substantial plant effects (e.g. Berryman, 1973), no overall differences in the frequency of enemy- vs. plant-induced mortality were detected ( $2 \times 2$  contingency table,  $P > 0.20$ ), suggesting that plant factors really do have smaller

effects than was suspected. The test does not rule out the possibility that life-table researchers were simply slow in responding to this shift in perspective, as the first explicit challenge of life-table methodology apropos of its distortion of plant effects did not appear until 1988 (Preszler & Price, 1988). Nor does it address the likelihood that Feeney's paper influenced experimental studies but had minimal impact on life-table research, or that plant effects are mostly sublethal and will only be detected with careful experiments. Given the interest in the relative roles of top-down vs. bottom-up forces on population dynamics and community structure (e.g. Lawton & McNeill, 1979; Pimm, 1982; Hawkins, 1992; Price, 1992; Strong, 1992; Harrison & Cappuccino, 1995; Chase, 1996; Hochberg, 1996; Polis & Strong, 1996), these discrepancies need to be resolved. It is also important to remember that life tables not only miss sublethal effects within immature stages, but they rarely follow the adult stage, where sublethal effects are likely to be manifested as reduced body size and fecundity, and where plant defences can substantially reduce natality by discouraging female oviposition (Preszler & Price, 1988).

The three-way ANOVAs of the ecological factors also generally confirm the earlier frequency-based tests for the effects of

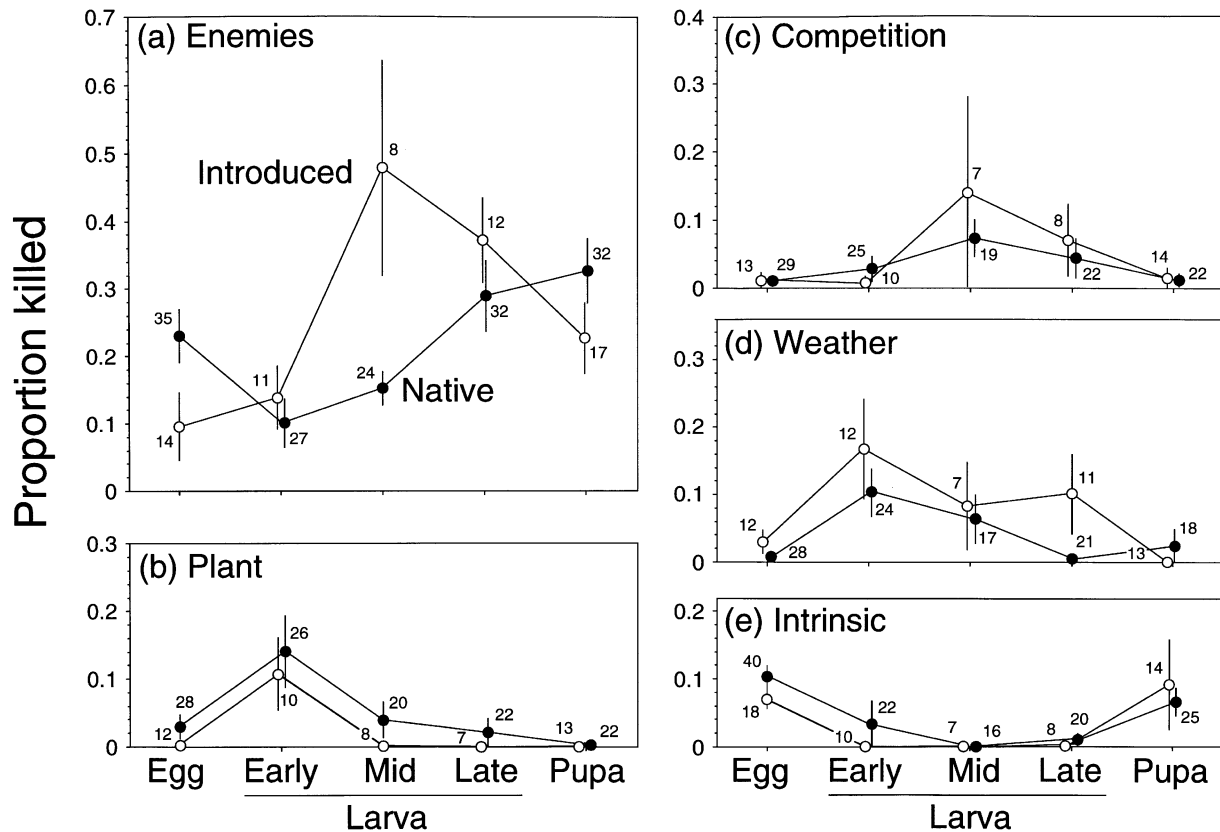


Fig. 7. Mean proportion ( $\pm 1$  SE) of herbivores killed in native and non-native locations.

ecology on mortality (cf. Figs 5–7, Cornell & Hawkins, 1995), with a few notable exceptions. The higher competition in temperate vs. tropical and cultivated vs. natural habitats, and the reciprocal changes between competition and enemy mortality in cultivated habitats, were not apparent in the earlier test. Thus, assuming that these patterns are not the result of bias in the subset of data chosen, the quantitative analysis was better at detecting subtler differences in mortality. The biological significance of the higher intensity of competition in temperate regions is questionable, because this slight difference is overshadowed by its general weakness in both regions. However, the greater effects of enemies in cultivated habitats are unambiguous and surprising in light of the assumption that natural systems have richer, more complex assemblages of enemies that keep herbivore populations below the level where competition is important. It certainly demands more study.

Finally, it is notable that, although at least some of the ecological factors that were examined influence how immature insects die, overall death rates were similar however the insects were categorized. This suggests that all *strategies* that insects employ are equally successful (see also Cornell, 1990). On the other hand, the larger sample of life tables analysed by Cornell & Hawkins (1995) found that herbivore lifestyle did influence survivorship, with endophytics suffering 5–10% less pre-adult mortality than exophytics. Presumably, the difference between

the studies is due to a reduced sample size in the quantitative data. The benefits of a concealed lifestyle may thus be subtle and distinguishable from high background variability in survivorship only when large numbers of cases are included. This can be confirmed only when more life tables are available.

Based upon the results of the previous frequency-based analysis and the quantitative analysis, several predictions are offered that can serve as a foundation for an empirically-based theory of herbivore demography. (1) Natural enemies are the dominant cause of mortality in exophytic herbivore populations, and as such will play a defining role in population limitation and in reducing interspecific competition among species that feed externally on plants. (2) As a result of their dominance on exophytic hosts, enemies should compete more intensely on exophytics than on endophytics. (3) Plant factors and enemies will play a more balanced role in the trophic dynamics of endophytic species. Strong plant  $\times$  enemy interactions are expected to be more prevalent in this group, and tri-trophic level effects will be more important. (4) Top-down limitation in terrestrial herbivore systems may be more prevalent in agroecosystems than in natural systems. (5) The lethal effects of plant defences will most likely be manifest as unsuccessful establishment of the hatchling larva on the host, whereas sublethal effects will be more apparent in the later developmental and adult stages. (6) Weather and climate will contribute more to the differences in population dynamics



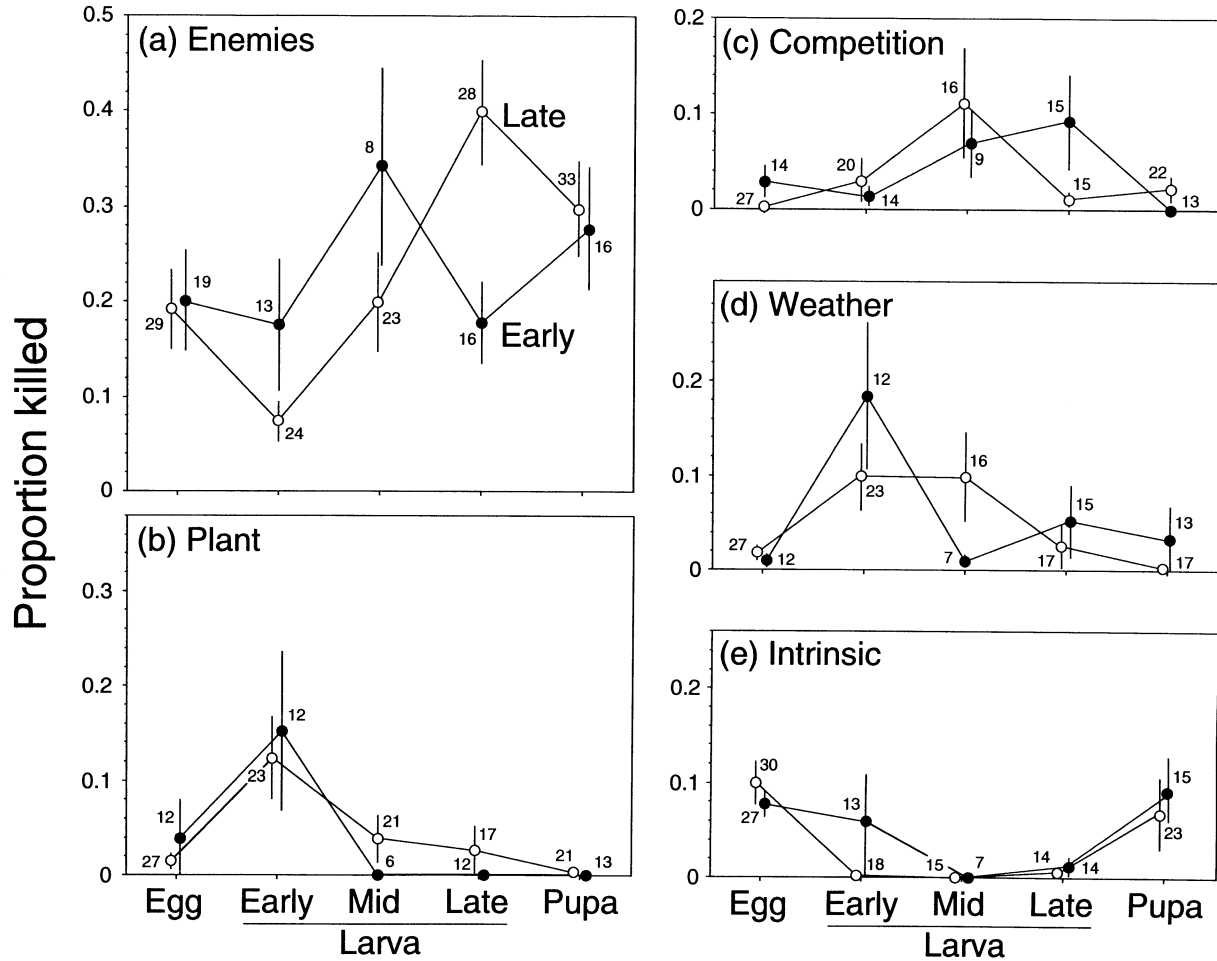


Fig. 8. Mean proportion ( $\pm 1$  SE) of herbivores killed in early and late successional plots.

between temperate and tropical species than enemies or competition. (7) A habitat's successional stage (structural complexity of vegetation) and a herbivore's taxonomic position will have little influence on herbivore survivorship and/or the mortality spectrum (in contrast to the predictions of Price, 1991b, 1994). (8) Invasion status will also have little influence on survivorship and mortality source. This prediction is especially counter-intuitive in light of the observed differences in the dynamics of pest species in native and non-native locations, but these differences are not reflected in survivorship and mortality source in life-table data.

These predictions should be viewed as challenges to engage in a broader way of thinking about herbivore ecology in future studies of herbivore populations, and it is hoped that they will provide a stimulus for more balanced approaches to hypothesis generation and testing in insect ecology.

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**References**

Andow, D.A. (1990) Population dynamics of an insect herbivore in simple and diverse habitats. *Ecology*, **71**, 1006-1017.  
 Anon (1995) Top plant defenses – the 10 most cited papers in plant herbivory, one of the 'hottest' areas of ecological research, were revealed and discussed. *The Scientist*, **9**, 12.  
 Augner, M. (1995) Low nutritive quality as a plant defense – effects of herbivore-mediated interactions. *Evolutionary Ecology*, **9**, 605-616.  
 Berryman, A.A. (1973) Population dynamics of the fir engraver, *Scolytus ventralis* (Coleoptera: Scolytidae). I. Analysis of population behavior and survival from 1964 to 1971. *Canadian Entomologist*, **105**, 1465-1488.

- Bodnaryk, R. (1996) Physical and chemical defenses of pods and seeds of white mustard (*Sinapsis alba* L.) against tarnished plant bugs, *Lygus-lineolaris* (Palisot-de-Beauvois) (Heteroptera, Miridae). *Canadian Journal of Plant Science*, **76**, 33–36.
- Cappuccino, N. (1992) The nature of population stability in *Eurosta solidaginis*, a non-outbreeding herbivore of goldenrod. *Ecology*, **73**, 1792–1801.
- Cappuccino, N. & Price, P.W. (eds) (1995) *Population Dynamics: New Approaches and Synthesis*. Academic Press, San Diego, California.
- Chase, J.M. (1996) Abiotic controls of trophic cascades in a simple grassland food chain. *Oikos*, **77**, 495–506.
- Coley, P. & Aide, T.M. (1994) Comparison of herbivory and plant defenses in temperate and tropical broad-leaved forests. *Plant–Animal Interactions: Evolutionary Ecology in Tropical and Temperate Regions* (ed. by N. E. Price, T. M. Lewinsohn, G. W. Fernandes and W. W. Benson), pp. 25–49. John Wiley & Sons, New York.
- Cornell, H.V. (1990) Survivorship, life history, and concealment: a comparison of leaf miners and gall formers. *American Naturalist*, **136**, 581–597.
- Cornell, H.V. & Hawkins, B.A. (1995) Survival patterns and mortality sources of herbivorous insects: some demographic trends. *American Naturalist*, **145**, 563–593.
- Damman, H. (1993) Patterns of herbivore interaction among herbivore species. *Caterpillars: Ecological and Evolutionary Constraints on Foraging* (ed. by N. E. Stamp and T. M. Casey), pp. 132–169. Chapman & Hall, New York.
- Dempster, J.P. (1983) The natural control of populations of butterflies and moths. *Biological Reviews*, **58**, 461–481.
- Denno, R.F., McClure, M.S. & Ott, J.R. (1995) Interspecific interactions in phytophagous insects: competition reexamined and resurrected. *Annual Review of Entomology*, **40**, 297–331.
- Duffy, S.S. & Felton, G.W. (1991) Enzymatic antinutritive defenses of the tomato plant against insects. *ACS Symposium Series*, **449**, 166.
- Dussourd, D.E. (1995) Entrapment of aphids and whiteflies in lettuce latex. *Annals of the Entomological Society of America*, **88**, 163–172.
- Feeny, P.P. (1970) Seasonal changes in oak leaf tannins and nutrients as a cause of spring feeding by winter moth caterpillars. *Ecology*, **51**, 565–581.
- Hairton, N.G., Smith, F.E. & Slobodkin, L.B. (1960) Community structure, population control, and competition. *American Naturalist*, **94**, 421–425.
- Harrison, S. & Cappuccino, N. (1995) Using density-manipulation experiments to study population regulation. *Population Dynamics: New Approaches and Synthesis* (ed. by N. Cappuccino and P. W. Price), pp. 131–147. Academic Press, London.
- Hawkins, B.A. (1992) Parasitoid–host food webs and donor control. *Oikos*, **65**, 159–162.
- Hawkins, B.A., Cornell, H.V. & Hochberg, M.E. (1997) Predators, parasitoids, and pathogens as mortality agents in phytophagous insect populations. *Ecology*, **78**, 2145–2152.
- Hochberg, M.E. (1996) An integrative paradigm of monophagous parasitoid–host interactions. *Oikos*, **77**, 556–560.
- Hunter, M.D. & Schultz, J.C. (1995) Fertilization mitigates chemical induction and herbivore responses within damaged oak trees. *Ecology*, **76**, 1226–1232.
- Lawton, J.H. & McNeill, S. (1979) Between the devil and the deep blue sea: on the problem of being an herbivore. *Population Dynamics* (ed. by R. M. Anderson, B. D. Turner and L. R. Taylor), pp. 223–244. Blackwell, Oxford.
- Letourneau, D.K. (1994) Bean fly, management-practices, and biological control in Malawian subsistence agriculture. *Agriculture, Ecosystems and Environment*, **50**, 103–111.
- Pimm, S.L. (1982) *Food Webs*. Chapman & Hall, London.
- Polis, G.A. & Strong, D.R. (1996) Food web complexity and community dynamics. *American Naturalist*, **147**, 813–846.
- Preszler, R.W. & Boecklen, W.J. (1996) The influence of elevation on tri-trophic interactions – opposing gradients of top-down and bottom-up effects on a leaf-mining moth. *Ecoscience*, **3**, 75–80.
- Preszler, R.W. & Price, P.W. (1988) Host quality and sawfly populations: a new approach to life table analysis. *Ecology*, **69**, 2012–2020.
- Price, P.W. (1975) *Insect Ecology*. John Wiley & Sons, New York.
- Price, P.W. (1991a) Darwinian methodology and the theory of insect herbivore population dynamics. *Annals of the Entomological Society of America*, **84**, 465–473.
- Price, P.W. (1991b) Evolutionary theory of host and parasitoid interactions. *Biological Control*, **1**, 83–93.
- Price, P.W. (1992) Plant resources as the mechanistic basis for insect herbivore population dynamics. *Effects of Resource Distribution on Animal–Plant Interactions* (ed. by M. D. Hunter and P. W. Price), pp. 139–173. Academic Press, London.
- Price, P.W. (1994) Evolution of parasitoid communities. *Parasitoid Community Ecology* (ed. by B. A. Hawkins and W. Sheehan), pp. 472–491. Oxford University Press, Oxford.
- Raffa, K.F. & Smalley, E.B. (1995) Interaction of pre-attack and induced monoterpane concentrations in host conifer defense against bark beetle fungal complexes. *Oecologia*, **102**, 285–295.
- Rosenheim, J.A., Wilhoit, L.R. & Armer, C.A. (1993) Influence of intraguild predation among generalist insect predators on the suppression of an herbivore population. *Oecologia*, **96**, 439–449.
- Schoener, T.W. (1983) Field experiments on interspecific competition. *American Naturalist*, **122**, 240–285.
- Seaman, J.W., Jr, Walls, S.C., Wise, S.E. & Jaeger, R.G. (1994) Caveat emptor: rank transformation methods and interaction. *Trends in Ecology and Evolution*, **9**, 261–263.
- Seldal, T., Dybwad, E., Andersen, K.J. & Hogstedt, G. (1994) Wound-induced proteinase-inhibitors in grey alder (*Alnus incana*) – a defense mechanism against attacking insects. *Oikos*, **71**, 239–245.
- Slobodkin, L.B., Smith, F.E. & Hairton, N.G. (1967) Regulation in terrestrial systems, and the implied balance of nature. *American Naturalist*, **101**, 109–124.
- Stamp, N.E. & Yang, Y.L. (1996) Response of insect herbivores to multiple allelochemicals under different thermal regimes. *Ecology*, **77**, 1088–1102.
- Stiling, P. (1994) Coastal insect herbivore populations are strongly influenced by environmental variation. *Ecological Entomology*, **19**, 39–44.
- Strong, D.R. (1992) Are trophic cascades all wet? Differentiation and donor-control in speciose ecosystems. *Ecology*, **73**, 747–754.
- Strong, D.R., Lawton, J.H. & Southwood, R. (1984) *Insects on Plants: Community Patterns and Mechanisms*. Harvard University Press, Cambridge, Massachusetts.
- Swetnam, T.W. & Lynch, A.M. (1993) Multicentury regional scale patterns of western spruce budworm outbreaks. *Ecological Monographs*, **63**, 399–424.
- Zar, J.H. (1984) *Biostatistical Analysis*, 2nd edn. Prentice-Hall, Englewood Cliffs, New Jersey.

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