

CRITICAL APPRAISAL

Effects of insects on primary production in temperate herbaceous communities: a meta-analysis

MALCOLM D. COUPE and JAMES F. CAHILL, JR Department of Biological Sciences, University of Alberta, Canada

Abstract. 1. The effects of insects on primary production in temperate herbaceous communities were investigated in a meta-analysis. The following hypotheses were tested: (1) the effect of insects on primary production depends on community type, (2) the effect of insects on primary production varies as a function of productivity, (3) insects have a greater effect on primary production in communities with low species diversity, and (4) insects have a larger effect on primary production during outbreaks.

2. Data were collected from 24 studies in which insecticides were used to suppress insects in self-sown or pastoral communities. Effect sizes were calculated from sprayed and control plot standing crop or yield, expressed as the log response ratio, $\ln(\text{sprayed plot phytomass/control plot phytomass})$.

3. There was a significant increase in primary production as a result of insect suppression. Forb-dominated communities showed a more variable response than graminoid communities. During outbreaks, insects had a greater negative impact on primary production. Effect size was unaffected by productivity or plant species richness.

4. Although insects lower primary production in a diversity of temperate herbaceous communities, the basic measures by which such communities are often described have little effect on the proportional impact that insects have on primary production. While outbreaks are significant predictors of higher negative impact on primary production, causes of outbreaks are not always related to traits of the plant community.

Key words. Insecticide, meta-analysis, outbreak, plant community, primary production, productivity, species richness.

Introduction

Though insects are ubiquitous in herbaceous communities, their effect on primary production is much debated (Crawley, 1989; Carson & Root, 2000). Insects outweigh vertebrates as much as 10-fold in temperate terrestrial ecosystems (Pimentel & Andow, 1984), but may have little effect on primary production if their populations are limited by natural enemies (Hairston *et al.*, 1960; Schmitz *et al.*, 2000) or food quality, rather than food quantity (Hartley & Jones, 1997). Though most investigators measuring the

effects of insects on primary production assert that they are measuring the effects of insect herbivory (Fraser & Grime, 1997; Carson & Root, 2000), insects fill additional ecological roles relevant to production, including accelerating nutrient cycling (Seastedt & Crossley, 1984; Blumer & Diemer, 1996; Belovsky & Slade, 2000) mediating plant competition (Clay *et al.*, 1993; Ramsell *et al.*, 1993), and predation (Moran & Hurd, 1998). Thus, it is not self-evident that their net effect on plant growth should be negative. While agronomists have often drawn attention to the fact that insect suppression increases yield in sown pasture (White & French, 1968; Henderson & Clements, 1977), results in self-sown communities are more varied, with insects in some cases decreasing primary production (Fraser & Grime, 1997; Carson & Root, 2000) but in others having no effect (Gibson *et al.*, 1990; M. D. Coupe and J. F. Cahill, unpubl. data).

Correspondence: Malcolm Coupe, Department of Biological Sciences, University of Alberta, Edmonton, Alberta, Canada, T6G 2E9. E-mail: mcoupe@ualberta.ca

This variability in response could depend on several attributes of the community. These include bottom-up influences such as the food quality of its constituent plant species and top-down influences such as the traits of the dominant insects, and abundance and effectiveness of natural enemies. Primary productivity has been proposed as one factor modulating the relative strengths of bottom-up and top-down influences on herbivore numbers (Oksanen *et al.*, 1981). For example, systems with low productivity contain lower food supply, and plants of lower food quality and palatability (bottom-up control; Coley *et al.*, 1985; Ritchie, 2000), retarding growth of insect herbivore populations, and lessening their potential to influence primary production directly (Olf & Ritchie, 1998). Alternatively, insect herbivores in more productive plant communities may experience greater population control from natural enemies, which could reduce their impact on plant growth (Fraser & Grime, 1997). If both top-down and bottom-up factors operate simultaneously, insects should affect primary production most at intermediate productivity. These hypotheses lead to three mutually exclusive predictions of the relationship between primary production with and without insect herbivory (Fig. 1a).

The effects of insects on primary production may also be influenced by plant species diversity. This topic has been of interest to agro-ecologists who seek to understand why pest outbreaks are more frequent in monocultures than in polycultures (Andow, 1991). Root (1973) hypothesised that in more diverse agricultural communities, population density of specialist insect herbivores is limited by decreased foraging efficiency (the resource concentration hypothesis), or greater abundance and effectiveness of natural enemies (the natural enemies hypothesis). These hypotheses have been supported by studies showing lower specialist insect herbivore abundance and greater natural enemy abundance in polyculture (Altieri *et al.*, 1985; Schellhorn & Sork, 1997); however outbreaks are relatively rare in any particular site, and as they involve single species of insects, they are in contrast to the diverse suite of insects (and plants) that typify natural herbaceous communities (Faeth, 1987). The prediction that insects will have a lower proportionate effect on primary production of more speciose plant communities has yet to be tested across a wide diversity of insect herbivore pressure and plant community types.

Community type could also affect the response of plants to insect removal. Strong *et al.* (1984) described the conceptual gradient between communities as random assortments of populations with little density dependence and fluctuating species composition, and predictable systems maintained by tight inter-specific competition, with little top-down control of insect herbivores. They maintained that insect community composition correlates with plant community composition in some cases (*Spartina* saltmarshes) but not in others (bracken fern patches). Root and Cappuccino (1992) found large temporal variability and little intra-guild competition in the insect communities of botanically similar old fields. Even if insect communities show limited concordance with plant communities, the effects of insects on primary production

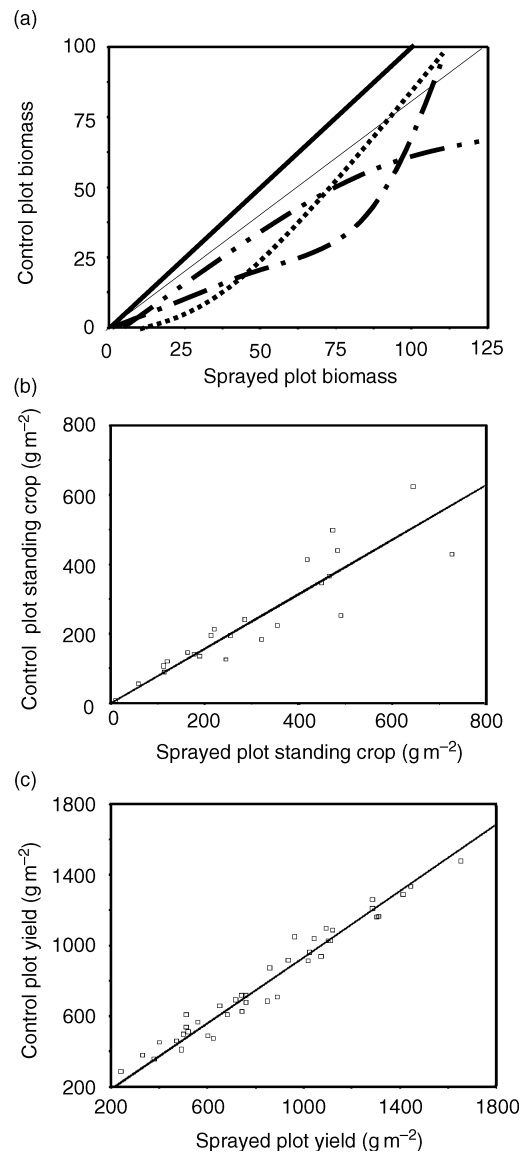


Fig. 1. Models and data depicting the relationship between primary production with and without insecticide application. (a) Alternative models of how the relative strength of herbivory should vary with productivity result in distinct predictions on the form of the relationship between plant biomass in sprayed plots and unsprayed plots. (1) If insect suppression has no effect on plant growth, there should be a linear relationship between control plot biomass and sprayed plot biomass with a slope = 1 (—). (2) If there is a constant proportional increase in primary production due to insect suppression, then there will be a linear relationship between sprayed plot biomass and control plot biomass, with a slope < 1 (—; 25% shown here). A quadratic relationship indicates either (3) an increasing effect of insect suppression at higher productivity (---; bottom-up control), or (4) a decreasing effect of insect suppression at higher productivity (-.-.-; top-down control). (5) If both top-down and bottom-up processes influence herbivory strongly, there should be a cubic relationship between sprayed and unsprayed biomass (· · ·). (b) The observed relationship between primary production of sprayed and unsprayed plots for standing crop data. (c) The observed relationship for yield data. In both b and c, neither the quadratic nor the cubic terms improved the fit of the model significantly.

could depend on community type, if dominant plant species vary in palatability or susceptibility to herbivore attack.

A common technique used by investigators to address the community-level impact of insect herbivory is chemical exclusion with insecticides (Henderson & Clements, 1977; Brown & Gange, 1992). Community response measures such as plant cover and biomass are compared between sprayed and unsprayed plots. This method examines the effects of all insects, without excluding elements of community regulation such as disturbance, grazing, and natural abiotic conditions. Despite a growing body of research using this approach, a quantitative synthesis of the effects of chemical exclusion of insects on the primary production of herbaceous communities is lacking. A meta-analysis was used to test the following questions: (1) What is the average effect size of insect suppression on total above-ground phytomass? (2) Does effect size vary as a function of plant species composition? (3) Is the effect size modulated by primary productivity? (4) Is there a correlation between effect size and plant species richness?

Methods

Literature search and paper selection

A search was conducted for experiments in which insecticides were used to examine the effect of insects on above-ground net primary production of a temperate herbaceous plant community using two primary sources: (1) The Web of Science (1975–2002), a citation database of scientific papers from multiple disciplines, including ecological and agronomic journals. A list of the keyword combinations and author searches used is included in Appendix 1. (2) Biological Abstracts (on paper) from 1950 to 1983. The section *Economic Entomology: Field, Flower, and Truck Crops* was searched, followed by a search of the electronic Biological Abstracts (1984–2001) using the same keywords as above. The literature cited by these studies was also searched for additional potential papers for inclusion. As the same publications were found repeatedly using these different search methods, the search probably captured most of the peer-reviewed published papers on this topic in English. Unpublished data from an ongoing research programme (M. D. Coupe and J. F. Cahill, unpubl. data) and two other studies (Bowers, 1976; Gibson *et al.*, 1990) were also included.

Each paper was reviewed to check whether it met the following selection criteria: (1) The study included measures of community phytomass at the plot level. If data were separated by constitutive parts (life form, species, etc.), they were summed to obtain a plot-level measure. Studies that examined the response of only a single species to insect suppression were rejected. (2) The study was conducted outdoors, in a natural or semi-natural system. Microcosms, mesocosms, and greenhouse studies were excluded. Planted monocultures were excluded, because they differ from natural communities in many respects, including selection of

the plant species for palatability and uniform spacing of plants (Altieri, 1994), in addition to their differences in species richness. Studies were not excluded *a priori* due to species composition, so communities could consist of native or introduced species. Twenty-three acceptable studies were identified, providing 66 data points (Appendix 2). As there was a preponderance of studies in pasture, the data-set is a non-random selection of herbaceous communities and the conclusions may not be applicable to all temperate systems.

Data acquisition and classification

Because some studies reported data from more than one site, study sites were considered to be independent data points if they showed strong differences in botanical composition and/or they were separated by ≥ 5 km. Several studies had more than one treatment, but only the treatment using the broadest spectrum insecticide (most insects affected) was compared with the control (no insecticide). When more than one broad-spectrum insecticide was used, the one with the least-known impact on non-target organisms (such as nematodes, earthworms, and molluscs) was chosen. Non-target effect information was obtained from within that paper and others in the meta-analysis whose authors used the same insecticide. Results are presented from the peak control phytomass ($\text{g dry weight m}^{-2}$), measured during the first year for which data were available. Phytomass was reported as annual yield in some cases (sown pasture) and as standing crop in others (some pasture, grassland, all forb-dominated communities). Annual yield is a compounded measurement of production from several harvests of standing crop in the same location, so measurements of yield and standing crop could not be combined for all analyses. As the interval between the initiation of spraying and biomass measurement varied between 21 and 2190 days in the studies, there is concern that effect sizes will be biased as a function of the duration of the study; however, for the full set of data there was no relationship between effect size and study duration ($F_{1,65} = 2.929$, $r^2 = 0.043$, NS), and thus no time-weighting was conducted, as has been necessary in other studies (Downing *et al.*, 1999). This concern was addressed further by trial analyses of time-weighted data, but they did not change the conclusions of the study. This does not mean that effects are not cumulative; when the last measurement taken in each study was subtracted from the measurement included in the study data, the change in effect size was positive in 35 out of 50 cases ($\chi^2 = 8$, $P < 0.01$) but small relative to the mean effect size in the results.

Each study site was assigned to one of five community types: young pasture, mature pasture, native grassland, mature forb, and young forb. Young pastures ($n = 27$), were defined as graminoid communities sown with grazing-adapted grasses such as *Lolium*, and with clover, < 10 years old. Mature pastures ($n = 27$) were defined as graminoid communities also sown with grazing-adapted grasses, but allowed to grow untilled for ≥ 10 years prior to the study,

during which forbs and grasses not part of the original seed mix were able to establish. Native grassland ($n=3$) was defined as a perennial-dominated, self-sown graminoid community. Mature forb communities ($n=6$) in the data-set were either an old field in the eastern U.S.A. (Carson & Root, 2000) or one of five communities in an upland dale (Fraser & Grime, 1997). Young forb communities ($n=3$) were defined as self-sown communities, dominated by forbs, early in succession, established by removing mature plant communities. Annual plants form a large proportion of their phytomass. Sites were also classified according to whether or not a documented insect outbreak occurred there during the study. Outbreaks were reported in five of the 66 sites.

Species-richness measures were derived from tables and graphs, and were only available for 32 sites. Most anecdotal accounts of plant species richness were not used, unless they supplemented data from tables or graphs, or resulted from personal communication with the author (Wilson *et al.*, 1995). When biomass or cover measures were given, they sometimes included categories such as grass weeds or dicots recorded as minor components of the community (Henderson & Clements, 1977). Unless there was more detailed information in the text, each was scored conservatively as one species. Thus, in all cases, a minimum estimate of species richness is used in the analyses.

Statistical analyses

In order to contrast methods for making generalisations about the effects of insects on primary production, a vote count was the first method of analysis. Studies were scored according to whether or not individual experiments rejected the null hypothesis at $P < 0.05$. Following the vote count, more sophisticated meta-analytical methods were used. The metric of effect size is the log response ratio (L), the natural log of the ratio (R) between the mean phytomass of the sprayed (X_S) and control (X_C) groups [$\ln(R) = \ln(X_S/X_C)$; Hedges *et al.*, 1999]. Thus, L expresses the proportional effect of insect suppression on phytomass, with positive values indicating greater phytomass in sprayed plots. The best approach to meta-analysis of numeric data incorporates measures of both mean, and variability around the mean, of each data point (Gurevitch & Hedges, 1999), however the majority of studies did not provide measures of variability. Therefore, two separate analyses were conducted; one using just the studies providing measures of variability and sample size ($n=15$), and one with all 66 data points, treating individual experiments as single data points throughout (Gurevitch & Hedges, 1999).

MetaWin 2.0 (Rosenberg *et al.*, 2000) was used for analyses of the data for which measures of variability were available. A structured random-effects model was run, which assumes a random component of between-study variation in means in addition to variation in means due to sampling error (Rosenberg *et al.*, 2000). Habitat type (e.g. mature field, young forb) served as a categorical

variable in the model. For the confidence interval, a bootstrapped effect size estimate was calculated (Adams *et al.*, 1997), presented in the text as a back-transformed (unlogged) value. The α value was set at 0.01 to account for the inefficiency of log response ratio equations in avoiding Type I errors at sample sizes lower than 20 (true probability content as low as 91% with $\alpha=0.05$; Hedges *et al.*, 1999). Although this result is presented as a 95% confidence interval, the true probability content is unknown, and probably slightly different. For the full data-set (including those measures that lacked estimates of variability), an ANOVA was performed using SPSS 10.0 (SPSS Inc., 2000). Community type and outbreak status were treated as fixed factors with L as the response variable. A planned *post hoc* comparison of means was made between young pasture and mature pasture, the two habitat types for which the most data were available.

The most direct way to determine whether the net effects of insects on plant growth varied as a function of productivity would be to perform a simple regression between effect size (L) and productivity; however, as L is calculated as the ratio between unsprayed and sprayed plot biomass, and the sprayed plot biomass is the surrogate measure of productivity in these herbaceous communities (Knapp *et al.*, 1998), this would result in a regression that includes the same data in both axes, and could force a significant negative relationship between L and sprayed biomass even with simulated data (Jackson, 1997). An alternative method of analysis was therefore needed that could avoid the use of ratios and determine the form of the relationship between sprayed plot biomass and unsprayed plot biomass in each site directly. If insects have no net effect on plant growth at any level of productivity, there should be a linear relationship with a slope = 1 between sprayed and unsprayed plot biomass. If insects have a constant proportional effect on primary production, independent of productivity, the relationship will be linear with a slope < 1. Increasingly negative effects with productivity are indicated by a significant and negative quadratic term, while decreasingly negative effects would be indicated by a significant and positive quadratic term. A unimodal relationship between productivity and the proportional effects of insects on plant growth would result in a sigmoid relationship between sprayed and unsprayed biomass, and would be indicated by a significant cubic term in the regression (Fig. 1a).

Describing the relationship between two variables is notoriously difficult so two methods were chosen: a stepwise regression and a generalised additive model. In both analyses, above-ground biomass in the control plots served as the response variable, and biomass in the sprayed plots served as the independent variable. In the stepwise regression, the squared and cubed terms of sprayed biomass as independent variables were also included, added in the order linear, quadratic, cubic. Following the methods of Cahill and Casper (2000), this method tested whether adding the quadratic or cubic terms increased the F ratio of the model significantly. The generalised additive model was run using a spline with three degrees of freedom, testing whether

the inclusion of this non-linear term improved the fit of the model significantly compared with a simple linear relationship. The generalised additive model allows a more powerful method of detecting non-linearity than the stepwise regression, which is important here as biological meaning will be inferred from the observed relationship. The stepwise regression was run in SPSS 10.0 (SPSS Inc., 2000), and the generalised additive model was run using PROC GAM in SAS 8.2 (SAS Institute, 2002). Both analyses were run separately for standing crop and annual yield.

The effects of plant species richness on L were also investigated using stepwise regression and a generalised additive model. In these analyses, the ln-transformed species richness (and a quadratic term) served as the independent variable(s), and L served as the response variable.

A common critique of using chemical suppression on insects is that effects on non-target organisms can lead to incorrect interpretations (Wall & Reichman, 2000). Organisms other than insects were affected by some insecticides in this analysis (Shure, 1971; Clements *et al.*, 1982). All papers were recorded whose authors reported effects on earthworms or nematodes, or used an insecticide for which such non-target effects were found in another study, as this was the most common non-target effect. Studies using such insecticides found lower effect sizes than studies using other insecticides ($t = 3.69$, d.f. = 36, $P = 0.001$), and thus the estimates of insect effects are probably underestimates of the *true* effect.

Results

Average effect sizes in different habitats

Twenty of the 66 study sites reported a significant negative effect of insects on plant biomass, with only a single site reporting a significant positive effect of insects on plant biomass, a finding attributed to non-target effects of the insecticide (Clements *et al.*, 1982). Analysis of the effect sizes indicated that, on average, insect suppression increased above-ground primary production significantly. The back-transformed 95% confidence interval for the full data-set (unweighted) was: $R = 1.151 \pm 0.057$ (Fig. 2). The back-transformed 95% confidence interval for the partial data-set (weighted by variance) was: $R = 1.23 \pm 0.18$. These results indicate an increase in primary production of 15 and 23% respectively, in response to insect suppression.

Effect size varied among community types ($F_{4,61} = 3.230$, $P < 0.05$), but there was significant non-homogeneity of variances ($F_{4,62} = 4.813$, $P < 0.01$) (Fig. 2). This variability appears to be driven by the mature forb communities as when they were removed, the remaining variances were homogeneous ($F_{3,56} = 1.051$, NS) and there was no community effect ($F_{3,56} = 2.162$, NS). Random removals of six studies from the data-set indicated that this change was not due simply to a loss of statistical power, suggesting that the effects of insects on production in mature forb communities may be different from their effects in other

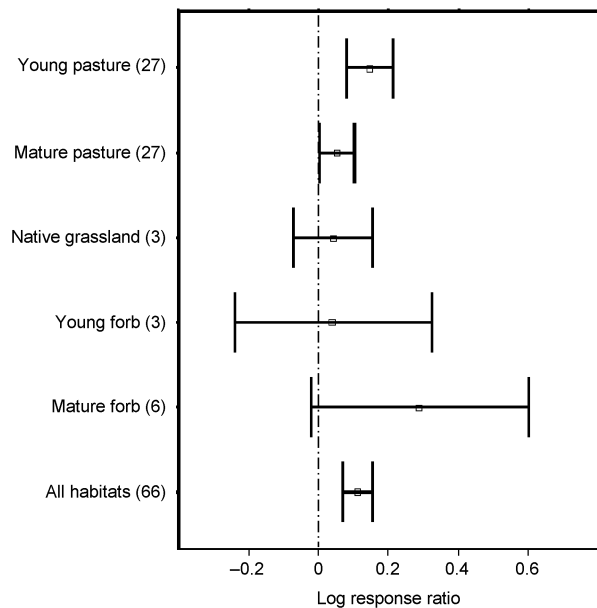


Fig. 2. Estimated effect sizes due to insect suppression for each community type in the full (unweighted) data-set (95% CI). The dashed line corresponds to no effect. Mean effect sizes do not vary between community types.

community types. Effect sizes did not differ between mature pasture and young pasture (Tamhane's T2, difference in averages $L = 0.094$, $P = 0.226$). In the data-set with variation, habitat had no effect on effect size [between-group heterogeneity (Q) = 1.22, NS]. Insect suppression during outbreaks resulted in a greater proportional increase in production than did suppression in non-outbreak communities ($F_{1,64} = 32.173$, $P < 0.001$). Of the five outbreaks that occurred, four occurred in young pasture.

Productivity and species richness

In the analyses to determine whether the effects of insect suppression vary with productivity, a linear relationship best described the relationship between sprayed and unsprayed biomass and yield in both the stepwise regression (Table 1, Fig. 1b,c) and the generalised additive model (Table 1). Because a higher-order term was not necessary to describe this relationship, it is concluded that the effects of insects on primary production are independent of productivity.

The analysis of all data to determine the effects of plant species richness produced similar results. Neither a linear nor a quadratic term could explain significantly variation within the data for both the stepwise regression and the generalised additive model (Table 1, Fig. 3). This indicates that the proportional effect of insects on productivity are independent of plant species richness.

Table 1. Results from stepwise regression (SWR) and generalised additive models (GAM) describing the relationship between the effects of insect suppression on production, and productivity, and plant species richness respectively. Both stepwise regression and the generalised additive model were used to determine whether the relationships between the effect and response variables are linear or non-linear. All linear models for the productivity regressions were significant ($P < 0.001$), and the goal of that analysis was to determine whether the addition of the higher-order terms improved the fit of the model significantly. The significance of the change in model fit was determined using the change in the F statistic in the stepwise regression, and by using a chi-square, thus *change* refers to actual value of the change in F due to the addition of higher-order terms in the stepwise regression, or the chi-square value comparing the generalised additive model with 3 d.f. spline to the generalised additive model without the spline. P_{change} refers specifically to the significance of the change in model fit due to the addition of the higher-order term.

		Productivity				Plant species richness			
	Term	Parameter estimate	$F_{\text{d.f.}}$	Change	P_{change}	Parameter estimate	$F_{\text{d.f.}}$	Change	P_{change}
Biomass	SWR	Linear	412.5 _{1,22}						
		Quadratic	413.1 _{1,21}	0.527	0.476				
		Cubic	414.3 _{1,20}	1.232	0.280				
Yield	SWR	Linear	0.757	7099.7 _{1,38}	2.96	0.398			
		Quadratic		7101.8 _{1,37}	2.130	0.153			
		Cubic		7101.9 _{1,36}	0.017	0.897			
All data	SWR	Linear	0.882		3.42	0.331			
		Quadratic					1.237		0.275
		Linear					0.0317	3.079	0.380

Discussion

Average effect sizes and habitat

On average, insects reduced plant biomass by 13% in these temperate herbaceous communities. The fact that biomass tends to be higher in treated plots suggests that herbivory is the dominant direct mechanism by which

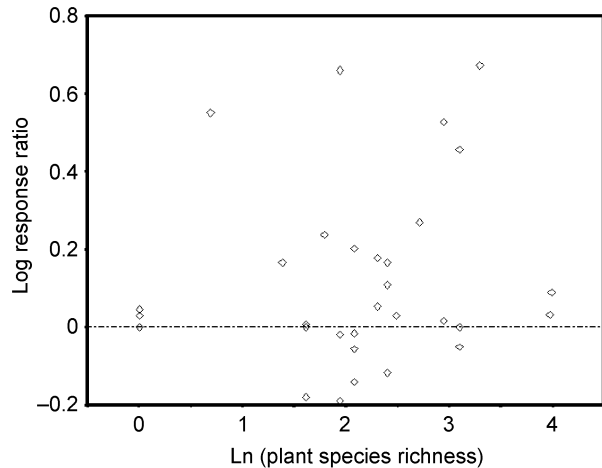


Fig. 3. The relationship between plant species richness and the effect size associated with insect suppression. The dashed line corresponds to no effect. Neither the linear nor the quadratic terms were significant in the stepwise regression or generalised additive model (Table 1), indicating that the net effects of insects on above-ground primary production are independent of plant species diversity.

insects affect primary production in these systems, and the discussion will be framed in that context. These values should be taken as a minimum effect of insect herbivory, as chemical suppression does not result in complete insect exclusion and insects also perform functions that can increase plant growth (e.g. increased nutrient cycling; Belovsky & Slade, 2000), reducing their net effect. Additionally, exclusion of foliar insects (as in most studies considered here) can improve performance of root-feeding insects, which could reduce the apparent effect of insect suppression on primary production (Seastedt & Reddy, 1991; Masters, 1995). Regardless, this magnitude of tissue loss due to insects is similar to that found in temperate forests (5–15% leaf area removed; Landsberg & Ohmart, 1989); however the hypothesis that insects decrease primary production to some degree has been in less doubt than the various hypotheses proposing that these effects vary as a function of community traits.

Overall, community type had no effect on mean effect size. This conclusion agrees with Landsberg and Ohmart's (1989) study showing uniformity in insect defoliation across many forest community types, however the significantly greater variance in mature forb communities suggests that community type does modulate insect impact on primary production, but not in a fashion predictable from the existing data. As a group, graminoids have lower investment in chemical defences than do dicotyledons, higher investment in structural defences, lower nitrogen concentrations, and greater tolerance to herbivory (Tscharntke & Greiler, 1995). Bigger and Marvier (1998) showed that invertebrates have a strong negative effect on forb growth, especially in comparison with vertebrates, while Moran and Hurd (1998) found that biomass of grasses, but not of forbs,

was increased by addition of a top arthropod predator in an old field. Although the larger average effect size in young pasture than in mature pasture was not significant, the relative frequency of outbreaks in young pasture suggests that these two community types are affected differently by insects. It is noteworthy that with its greater dominance of grazing-adapted plants and higher productivity (Clements *et al.*, 1987), young pasture can be thought of as the most agricultural of all habitat types considered here.

The greater effect size in outbreak conditions suggests that insect population fluctuation and species identity may explain variation in the impact of insects on primary production better than traits of the plant community. Fluctuation in natural enemy numbers, changes in host plant quality, and climate are all possible explanations for insect outbreaks (Berryman, 1987). Not all are related directly to the traits of the plant community considered here.

Effects of productivity

Neither top-down nor bottom-up control of insect herbivores appears to be dependent on productivity in these systems. The original advocates of the idea that top-down control varies as a function of productivity (Oksanen *et al.*, 1981) proposed that this phenomenon was most likely for relationships between plants and endotherms, arguing that invertebrates were more likely to be regulated by temperature than productivity *per se*. In a later review of the model and its evidence, Oksanen and Oksanen (2000) stated that not enough is known about the effects of folivorous insects on primary production to judge whether the model is applicable to them. Indeed, individual studies suggest that the effects of top-down and bottom-up forces on insect herbivores and primary production do vary as a function of productivity. Fraser and Grime (1997) examined the Oksanen and Fretwell model (top-down control; Oksanen *et al.*, 1981) for insects and found that insect impact on primary production was greatest at intermediate levels of productivity, while Ritchie (2000) showed that insect herbivore populations were limited by food quality in nitrogen-poor environments but not limited by top-down forces in more productive environments; however this meta-analysis reveals that, overall, the effects of insects on plant growth are independent of productivity. A similar conclusion was made by a recent meta-analysis of invertebrate effects on cover and biomass (Schadler *et al.*, 2003), although their analysis included biomass in effect size calculations and on the *x*-axis, the potential source of confounding discussed in the methods section (Jackson, 1997). Any conclusion on this topic is, however, clouded by the lack of knowledge of insect herbivore effects on root productivity, which in grasslands constitute an average of 53% of annual productivity (Gill & Jackson, 2000). Although above-ground insect herbivory is known to reduce root growth (Burlinson & Hewitt, 1982; Cain *et al.*, 1991), no studies have evaluated differences between habitats or along a productivity gradient, in the effects of insect herbivory on roots.

Effects of species richness

The lack of a relationship between species richness and response to insect suppression suggests that even if plant diversity affects specialist herbivore load or natural enemy attack rate, these differences do not translate into effects on primary production. Comparison of this result with the effects observed in agricultural systems is difficult because yield response to diversity manipulation is rarely measured (Risch, 1987) and, when it is, non-crop plants are not considered as contributors to yield (Altieri *et al.*, 1985; Schellhorn & Sork, 1997). In natural systems, Root's (1973) resource concentration hypothesis has been supported by studies finding greater defoliation (Kamata, 2000) and mortality (Cappuccino *et al.*, 1998) of the tree hosts of monophagous insects, when those hosts were growing in habitats with lower tree diversity or isolation. When Mulder *et al.* (1999) manipulated plant diversity in a grassland, however, they found that insect impact on production was actually greater at higher diversity. A companion study found no support for the prediction that natural enemies would become more abundant at higher diversity (Koricheva *et al.*, 2000). Significantly, the species composition of the plant mixtures was far more important to invertebrate abundance and trophic level composition, with the presence of nitrogen-rich legumes having the strongest effect.

Summary of results

The results demonstrate that insects depress primary production consistently in a variety of temperate herbaceous communities. More studies are necessary to determine how community types differ, but there is evidence that herbaceous community type is important to the magnitude of insect impact. The mechanisms for these community type effects are unclear, and may include differences in the plant community (palatability, susceptibility to herbivory) or the insect community (feeding mode, rates of population growth), or both. The evidence presented here suggests that these patterns are not affected by productivity or species diversity, two fundamental traits often used to describe plant communities.

Acknowledgements

We gratefully acknowledge the early assistance of Dean Adams and Rich Palmer for their advice on the execution and interpretation of meta-analysis, and Jens Roland for advice regarding data analysis. We also thank David Gibson and Kenneth Wilson for providing unpublished data, and Laughlan Fraser for assistance with interpretation of his data. The manuscript benefited from comments by Michael Cohen, Nat Cleavitt, Alan Gange, and an anonymous reviewer. The preparation of this manuscript was supported in part by an NSERC research grant to J.F.C. and a McAfee Rose Grant to M.D.C.

References

- Adams, D.C., Gurevitch, J. & Rosenberg, M.S. (1997) Resampling tests for meta-analysis of ecological data. *Ecology*, **78**, 1277–1283.
- Altieri, M.A. (1994) *Biodiversity and Pest Management in Agroecosystems*. Food Products Press, New York.
- Altieri, M.A., Wilson, R.C. & Schmidt, L.L. (1985) The effects of living mulches and weed cover on the dynamics of foliage- and soil-arthropod communities in three crop systems. *Crop Protection*, **4**, 201–213.
- Andow, D.A. (1991) Vegetational diversity and arthropod population response. *Annual Review of Entomology*, **36**, 561–586.
- Barker, G.M. (1984) Effects of Argentine stem weevil on productivity of grasses in the Waikato. *New Zealand Journal of Agricultural Research*, **27**, 93–102.
- Belovsky, G.E. & Slade, J.B. (2000) Insect herbivory accelerates nutrient cycling and increases plant production. *Proceedings of the National Academy of Sciences, U.S.A.*, **97**, 14412–14417.
- Berryman, A.A. (1987) The theory and classification of outbreaks. *Insect Outbreaks* (ed. by P. Barbosa and J. C. Schultz), pp. 3–30. San Diego Academic Press, San Diego, California.
- Bigger, D.S. & Marvier, M.A. (1998) How different would a world without herbivory be? A search for generality in ecology. *Integrative Biology*, **1**, 60–67.
- Blackshaw, R.P. (1984) The impact of low numbers of leatherjackets on grass yield. *Grass and Forage Science*, **39**, 339–343.
- Blumer, P. & Diemer, M. (1996) The occurrence and consequences of grasshopper herbivory in an alpine grassland, Swiss Central Alps. *Arctic and Alpine Research*, **28**, 435–440.
- Bowers, D.M. (1976) *Insect consumption of seeded rangeland herbage in a selected area of Diamond Fork Canyon, Utah County, Utah*. Unpublished MS thesis, Utah State University, U.S.A.
- Brown, V.K. & Gange, A.C. (1992) Secondary plant succession: how is it modified by insect herbivory? *Vegetatio*, **101**, 3–13.
- Brown, V.K., Leijn, M. & Stinson, C.S.A. (1987) The experimental manipulation of insect herbivore load by the use of an insecticide (malathion): the effect of application on plant growth. *Oecologia*, **72**, 377–381.
- Burlinson, W.H. & Hewitt, G.B. (1982) Response of needle-and-thread and Western wheatgrass to defoliation by grasshoppers. *Journal of Range Management*, **35**, 223–226.
- Cahill, J.F. & Casper, B.B. (2000) Investigating the relationship between neighbour root biomass and belowground competition: field evidence for symmetric competition belowground. *Oikos*, **90**, 311–320.
- Cain, M.L., Carson, W.P. & Root, R.B. (1991) Long-term suppression of insect herbivores increases the production and growth of *Solidago altissima* rhizomes. *Oecologia*, **88**, 251–257.
- Cappuccino, N., Lavertu, D., Bergeron, Y. & Regniere, J. (1998) Spruce budworm impact, abundance, and parasitism rate in a patchy landscape. *Oecologia*, **114**, 236–242.
- Carson, W.P. & Root, R.B. (1999) Top-down effects of insect herbivores during early succession: influence on biomass and plant dominance. *Oecologia*, **121**, 260–272.
- Carson, W.P. & Root, R.B. (2000) Herbivory and plant species coexistence: community regulation by an outbreaking phytophagous insect. *Ecological Monographs*, **70**, 73–99.
- Clay, K., Marks, S. & Cheplick, G.P. (1993) Effects of insect herbivory and fungal endophyte infection on competitive interactions among grasses. *Ecology*, **74**, 1767–1777.
- Clements, R.O., Bentley, B.R. & Nuttall, R.M. (1987) The invertebrate population and response to pesticide treatment of two permanent and two temporary pastures. *Annals of Applied Biology*, **111**, 399–407.
- Clements, R.O., Henderson, I.F. & Bentley, B.R. (1982) The effects of pesticide application on upland permanent pasture. *Grass and Forage Science*, **37**, 124–128.
- Clements, R.O., Murray, P.J., Bentley, B.R., Lewis, G.C. & French, N. (1990) The impact of pests and diseases on the herbage yield of permanent grassland at eight sites in England and Wales. *Annals of Applied Biology*, **117**, 349–357.
- Coley, P.D., Bryant, J.P. & Chapin, F.S. III (1985) Resource availability and plant antiherbivore defence. *Science*, **230**, 895–899.
- Crawley, M.J. (1989) The relative importance of vertebrate and invertebrate herbivores in plant population dynamics. *Insect-Plant Interactions I* (ed. by E. Bernays), pp. 45–71. CRC Press, Boca Raton, Florida.
- Dondale, C.D. (1972) Effects of carbofuran on arthropod populations and crop yield in hayfields. *Canadian Entomologist*, **104**, 1433–1437.
- Downing, J.A., Osenberg, C.W. & Sarnelle, O. (1999) Meta-analysis of marine nutrient-enrichment experiments: variation in the magnitude of nutrient limitation. *Ecology*, **80**, 1157–1167.
- Ellis, S.A., Clements, R.O. & Bale, J.S. (1990) A comparison of the effects of sward improvement on invertebrates, sward establishment and herbage yield. *Annals of Applied Biology*, **116**, 343–356.
- Faeth, S.H. (1987) Community structure and folivorous insect outbreaks: the roles of vertical and horizontal interactions. *Insect Outbreaks* (ed. by P. Barbosa and J. C. Schultz), pp. 135–171. San Diego Academic Press, San Diego, California.
- Fraser, L.H. & Grime, J.P. (1997) Primary productivity and trophic dynamics investigated in a North Derbyshire, UK, Dale. *Oikos*, **80**, 499–508.
- Gibson, D.J., Freeman, C.C. & Hulbert, L.C. (1990) Effects of small mammal and invertebrate herbivory on plant species richness and abundance in tallgrass prairie. *Oecologia*, **84**, 69–175.
- Gill, R.A. & Jackson, R.B. (2000) Global patterns of root turnover for terrestrial ecosystems. *New Phytologist*, **147**, 13–31.
- Goldson, S.L. & Trought, T.E.T. (1977) The effect of Argentine stem weevil on pasture composition in Canterbury. *Proceedings of the 33rd New Zealand Weed and Pest Control Conference*, **33**, 46–48.
- Gurevitch, J. & Hedges, L.V. (1999) Statistical issues in ecological meta-analysis. *Ecology*, **80**, 1142–1149.
- Hairston, N.G., Smith, F.E. & Slobodkin, L.B. (1960) Community structure, population control, and competition. *American Naturalist*, **94**, 421–425.
- Hartley, S.E. & Jones, C.G. (1997) Plant chemistry and herbivory, or why is the world green? *Plant Ecology* (ed. by M. Crawley), pp. 284–324. Blackwell Science, Oxford.
- Hedges, L.V., Gurevitch, J. & Curtis, P.S. (1999) The meta-analysis of response ratios in experimental ecology. *Ecology*, **80**, 1150–1156.
- Henderson, I.F. & Clements, R.O. (1974) The effect of pesticides on the yield and botanical composition of a newly-sown ryegrass ley and of an old mixed pasture. *Journal of the British Grassland Society*, **29**, 185–190.
- Henderson, I.F. & Clements, R.O. (1977) Grass growth in different parts of England in relation to invertebrate numbers and pesticide treatment. *Journal of the British Grassland Society*, **32**, 89–98.
- Jackson, D.A. (1997) Compositional data in community ecology: the paradigm or peril of proportions? *Ecology*, **78**, 929–940.
- Kamata, N. (2000) Population dynamics of the beech caterpillar, *Syntypistis punctatella*, and biotic and abiotic factors. *Population Ecology*, **42**, 267–278.

- Knapp, A.K., Briggs, J.M., Blair, J.M. & Turner, C.L. (1998) Patterns and controls of aboveground net primary production in tallgrass prairie. *Grassland Dynamics: Long-term Ecological Research in Tallgrass Prairie* (ed. by A. K. Knapp, J. M. Briggs, D. C. Hartnett and S. L. Collins), pp. 193–221. LTER Publications, New York.
- Koricheva, J., Mulder, C.P.H., Schmid, B., Joshi, J. & Huss-Danell, K. (2000) Numerical responses of different trophic groups of invertebrates to manipulations of plant diversity in grassland. *Oecologia*, **125**, 271–282.
- Landsberg, J. & Ohmart, C. (1989) Level of insect defoliation in forests: patterns and concepts. *Trends in Ecology and Evolution*, **4**, 96–100.
- Martin, N.A. (1974) Effect of four insecticides on the pasture ecosystem. *New Zealand Journal of Agricultural Research*, **17**, 485–494.
- Masters, G.J. (1995) The effect of herbivore density on host-plant mediated interactions between two insects. *Ecological Research*, **10**, 125–133.
- Moran, M.D. & Hurd, L.E. (1998) A trophic cascade in a diverse arthropod community caused by a generalist arthropod predator. *Oecologia*, **113**, 126–132.
- Mulder, C.P.H., Koricheva, J., Huss-Danell, K., Hogberg, P. & Joshi, J. (1999) Insects affect relationships between plant species richness and ecosystem processes. *Ecology Letters*, **2**, 237–246.
- Newbold, J.W. (1981) The control of leatherjackets in grassland by winter pesticide application. *Proceedings of Crop Protection in Northern Britain – 1981*, 207–211.
- Oksanen, L., Fretwell, S.D., Arruda, J. & Niemela, P. (1981) Exploitation ecosystems in gradients of primary productivity. *American Naturalist*, **118**, 240–261.
- Oksanen, L. & Oksanen, T. (2000) The logic and realism of the hypothesis of exploitation ecosystems. *American Naturalist*, **155**, 703–723.
- Olf, H. & Ritchie, M.E. (1998) Effects of herbivores on grassland plant diversity. *Trends in Ecology and Evolution*, **13**, 261–265.
- Pimentel, D. & Andow, D.A. (1984) Pest management and pesticide impacts. *Insect Science and its Application*, **5**, 141–149.
- Ramsell, J., Malloch, A.J.C. & Whittaker, J.B. (1993) When grazed by *Tipula paludosa*, *Lolium perenne* is a stronger competitor of *Rumex obtusifolius*. *Journal of Ecology*, **81**, 777–786.
- Risch, S.J. (1987) Agricultural ecology and insect outbreaks. *Insect Outbreaks* (ed. by P. Barbosa and J. C. Schultz), pp. 217–238. San Diego Academic Press, San Diego, California.
- Ritchie, M.E. (2000) Nitrogen limitation and trophic vs. abiotic influences on insect herbivores in a temperate grassland. *Ecology*, **81**, 1601–1612.
- Root, R.B. (1973) Organization of a plant–arthropod association in simple and diverse habitats: the fauna of collards, *Brassica oleracea*. *Ecological Monographs*, **43**, 95–124.
- Root, R.B. & Cappuccino, N. (1992) Patterns of population change and the organization of the insect community associated with goldenrod. *Ecological Monographs*, **62**, 393–420.
- Rosenberg, M.S., Adams, D.C. & Gurevitch, J. (2000) *Metawin. Statistical Software for Meta-analysis Version 2.0*. Sinauer Associates Inc., Sunderland, Massachusetts.
- SAS Institute (2002) *SAS 8.2*. SAS Institute, Nashville, Tennessee.
- Schadler, M., Jung, G., Auge, H. & Brandl, R. (2003) Does the Fretwell–Oksanen model apply to invertebrates? *Oikos*, **100**, 203–207.
- Schellhorn, N.A. & Sork, V.L. (1997) The impact of weed diversity on insect population dynamics and crop yield in collards, *Brassica oleracea* (Brassicaceae). *Oecologia*, **111**, 233–240.
- Schmitz, O.J., Hamback, P.A. & Beckerman, A.P. (2000) Trophic cascades in terrestrial systems: a review of the effects of carnivore removal on plants. *American Naturalist*, **155**, 141–153.
- Seastedt, T.R. & Crossley, D.A. Jr (1984) The influence of arthropods on ecosystems. *Bioscience*, **34**, 157–161.
- Seastedt, T.R. & Reddy, M.V. (1991) Fire, mowing, and insecticide effects on soil sternorrhyncha (Homoptera) densities in tallgrass prairie. *Journal of the Kansas Entomological Society*, **64**, 238–242.
- Shure, D.J. (1971) Insecticide effects on early succession in an old field ecosystem. *Ecology*, **52**, 271–279.
- SPSS Inc. (2000) *SPSS 10.0.7 for Windows*. SPSS Inc., Chicago, Illinois.
- Standell, C. & Clements, R.O. (1994) Influence of grass seed rate, herbicide (Bentazone), molluscicide (Methiocarb), and insecticide (Triazophos) on white clover (*Trifolium repens*) establishment, herbage yield, and sward botanical composition. *Crop Protection*, **13**, 429–432.
- Strong, D.R., Lawton, J.H. & Southwood, T.R.E. (1984) *Insects on Plants: Community Patterns and Mechanisms*. Blackwell Scientific Publications, Oxford.
- Tscharntke, T. & Greiler, H.J. (1995) Insect communities, grasses, and grasslands. *Annual Review of Entomology*, **40**, 535–558.
- Wall, D.H. & Reichman, O.J. (2000) Biotic manipulations involving belowground animals. *Methods in Ecosystem Science* (ed. by O. E. Sala, R. B. Jackson, H. A. Mooney and R. W. Howarth), pp. 321–329. Springer-Verlag, New York.
- Wallace, M.M.H. & Mahon, J.A. (1952) Webworm damage to pastures in the south-west of Western Australia. *Journal of the Australian Institute of Agricultural Science – June*, **1952**, 91–94.
- White, J.H. & French, N. (1968) Leatherjacket damage to grassland. *Journal of the British Grassland Society*, **23**, 326–329.
- Wilson, K., Gunn, A. & Cherrett, J.M. (1995) The application of a rhizotron to study the subterranean effects of pesticides. *Pedobiologia*, **39**, 132–143.

Accepted 1 June 2003

Appendix 1: literature search criteria

For Web of Science searches, the following key word combinations were used: insect herbivory and biomass, insect herbivory and diversity, insecticide and biomass, insecticide and herbivory, herbivory and diversity, insect herbivory and succession, insecticide and succession, insect herbivory and insecticide, insect herbivory and grassland, insect herbivory and

root, pesticide and grassland, and insect and grassland.

Searches through the literature of the following authors was conducted: Brown, V.K., Cain, M.L., Cantlon, J.E., Carson, W.P., Clements, R.O., Gange, A.C., Lawton, J.H., Louda, S., Maron, J.L., Masters, G.J., Olf, H., Ritchie, M.E., Root, R.B., Seastedt, T.R., Siemann, E., and Tilman, D.

Appendix 2: All experiments used in the study with a summary of habitat characteristics, primary production, a potential non-target effect, and study duration

Source	Habitat	<i>n</i>	Outbreak status	Plant species richness	Control plot phytomass (g m ⁻²) ± SE†	Sprayed plot phytomass (g m ⁻²) ± SE†	Potential earthworm or nematode exclusion‡	Seasons from first spray until phytomass measurements§
Standing crop measured								
Blackshaw, 1984; table 2: site 1	Mature pasture	6	No		195.8 ± 12.8	255.5 ± 12.8	No	0.5
Bowers, 1976; fig. 10	Mature pasture	5	No		346.7	448.6	Yes	0.5
Brown <i>et al.</i> , 1987; table 1	Young field	10	No	5	414.2 ± 77.5	417.7 ± 79.3	No	1
Carson & Root, 1999; fig. 3	Young field	30	No	22	499 ± 26.8	473 ± 26.0	No	1
Carson & Root, 2000; fig. 7	Forb dominated	15	Yes	19	429 ± 12.8	727 ± 40.0	No	6
Coupe & Cahill, 2001, unpublished	Native grassland	10	No	53	214 ± 12.9	221 ± 13.6	No	0.5
Dondale, 1972; table 3: field 1	Young pasture	7	No		5940¶	6820	No	0.25
Dondale, 1972; table 3: field 2	Young pasture	7	No		5980	6400	No	0.25
Dondale, 1972; table 3: field 3	Young pasture	7	No		3800	5300	No	0.25
Ellis <i>et al.</i> , 1990; table 6: North Wyke	Mature pasture	5	No		147	163	No	0.5
Fraser & Grime, 1997; fig. 1: site 1	Forb dominated	10	No	1	10 ± 1.0	10 ± 1.0	No	1
Fraser & Grime, 1997; fig. 1: site 2	Native grassland	10	No	5	57.5 ± 0.8	57.5 ± 1.3	No	1
Fraser & Grime, 1997; fig. 1: site 3	Forb dominated	10	No	27	125 ± 4.0	245 ± 6.7	No	1
Fraser & Grime, 1997; fig. 1: site 4	Forb dominated	10	No	22	225 ± 4.7	355 ± 2.9	No	1
Fraser & Grime, 1997; fig. 1: site 5	Forb dominated	10	No	1	625 ± 7.2	645 ± 6.8	No	1
Fraser & Grime, 1997; fig. 1: site 6	Forb dominated	10	No	1	107 ± 2.6	112 ± 2.4	No	1
Gibson <i>et al.</i> , 1990, unpublished data	Native grassland	8	No	54	441.0 ± 17.5	482.6 ± 27.3	No	2
Goldson & Trought, 1977	Young pasture	7	Yes		136.6	189.5	No	0.5
Martin, 1974; table 5	Young pasture	4	No	22	120	120	No	1
Newbold, 1981; table 1: Burrowland	Young pasture	5	No		195	212.7	No	0.5
Newbold, 1981; table 1: Grange of Cree	Young pasture	5	No		90.2	113.4	No	0.5
Shure, 1971; fig. 4	Young field	2	No	11	242 ± 32.9	286 ± 33.2	No	1
Wallace & Mahon, 1952; table 1	Young pasture	5	Yes	7	252.6	489.9	No	1
White & French, 1968; table 6: Mitford	Young pasture	6	Yes	2	185	321	No	1
White & French, 1968; table 3: Blagdon	Young pasture	6	Yes	6	367	465	No	1
Annual yield measured								
Barker, 1984; table 2	Young pasture	4	No	4	628.2	742.3	No	1
Clements <i>et al.</i> , 1982; table 2: Pwllpeiran High	Mature pasture	4	No		460	470	Yes	2
Clements <i>et al.</i> , 1982; table 2: Liscombe High	Mature pasture	4	No	7	290	240	Yes	2
Clements <i>et al.</i> , 1982; table 2: Corwen	Mature pasture	4	No	10	360	380	Yes	2
Clements <i>et al.</i> , 1982; table 2: Macclesfield	Mature pasture	4	No	8	380	330	Yes	2
Clements <i>et al.</i> , 1982; table 2: Oestwaldtwistle	Mature pasture	4	No	10	410	490	Yes	2
Clements <i>et al.</i> , 1982; table 2: Redesdale	Mature pasture	4	No	11	450	400	Yes	2
Clements <i>et al.</i> , 1982; table 2: Penrith	Mature pasture	4	No	8	490	600	Yes	2
Clements <i>et al.</i> , 1982; table 2: Brecon	Mature pasture	4	No	5	500	500	Yes	2
Clements <i>et al.</i> , 1982; table 2: Pwllpeiran Low	Mature pasture	4	No	8	540	510	Yes	2
Clements <i>et al.</i> , 1982; table 2: Llysfasi	Mature pasture	4	No	7	570	560	Yes	2
Clements <i>et al.</i> , 1982; table 2: Liscombe Low	Mature pasture	4	No	5	610	510	Yes	2
Clements <i>et al.</i> , 1982; table 2: Clunton	Mature pasture	4	No	11	610	680	Yes	2
Clements <i>et al.</i> , 1982; table 2: Selside	Mature pasture	4	No	8	660	650	Yes	2

Clements <i>et al.</i> , 1987; table 2: Level Crossing	Mature pasture	5	No	19	513	521	Yes	1
Clements <i>et al.</i> , 1987; table 2: Canal	Mature pasture	5	No	12	694	716	Yes	1
Clements <i>et al.</i> , 1990; table 2: Exminster	Mature pasture	4	No		680	760	Yes	1
Clements <i>et al.</i> , 1990; table 2: Highclere	Mature pasture	4	No		710	890	Yes	1
Clements <i>et al.</i> , 1990; table 2: Great Aine	Mature pasture	4	No		720	760	Yes	1
Clements <i>et al.</i> , 1990; table 2: Pant-y-dwr	Mature pasture	4	No		940	1070	Yes	1
Clements <i>et al.</i> , 1990; table 2: Barnard Castle	Mature pasture	4	No		1030	1100	Yes	1
Clements <i>et al.</i> , 1990; table 2: Winterburn	Mature pasture	4	No		1030	1110	Yes	1
Clements <i>et al.</i> , 1990; table 2: Ponterwyd	Mature pasture	4	No		1100	1090	Yes	1
Ellis <i>et al.</i> , 1990; table 6: Tadcaster	Mature pasture	5	No		142	178	No	0.5
Henderson & Clements, 1974; table 2	Mature pasture	4	No		719	740	No	1
Henderson & Clements, 1977; table 1: Devon	Young pasture	6	No		685.5	849.7	Yes	1
Henderson & Clements, 1977; table 1: Essex	Young pasture	6	No		875.5	858.7	Yes	1
Henderson & Clements, 1977; table 1: Lancashire	Young pasture	6	No		915	1016	Yes	1
Henderson & Clements, 1977; table 2: Leicestershire	Young pasture	6	No		918.9	934	Yes	1
Henderson & Clements, 1977; table 2: Kent	Young pasture	4	No		962.3	1020.5	Yes	1
Henderson & Clements, 1977; table 2: Yorkshire	Young pasture	6	No		1041.4	1042.9	Yes	1
Henderson & Clements, 1977; table 2: Northamptonshire	Young pasture	6	No		1089.8	1118.8	Yes	1
Henderson & Clements, 1977; table 2: Wiltshire	Young pasture	4	No		1163.4	1301.6	Yes	1
Henderson & Clements, 1977; table 2: Somerset	Young pasture	6	No		1165.2	1309.5	Yes	1
Henderson & Clements, 1977; table 2: Herefordshire	Young pasture	6	No		1211.8	1284.2	Yes	1
Henderson & Clements, 1977; table 2: Cheshire	Young pasture	6	No		1262.9	1282.7	Yes	1
Henderson & Clements, 1977; table 2: Shropshire	Young pasture	4	No		1289.6	1411.4	Yes	1
Henderson & Clements, 1977; table 2: Lincolnshire	Young pasture	6	No		1335.4	1442.9	Yes	1
Henderson & Clements, 1977; table 2: Gloucestershire	Young pasture	4	No		1480.7	1649.8	Yes	1
Standell & Clements, 1994; table 4: Long Ashton	Young pasture		No		1050	960	No	1
Wilson <i>et al.</i> , 1995; table 3	Young pasture	5	No	15	477 ± 32.2	625 ± 25.7	No	3

†When available. Weighted meta-analysis was conducted on standard deviation and phytomass at the 0.2 m² scale (the modal sampling area).

‡The insecticides used above with this non-target effect are aldicarb, methiocarb, and Temik.

§Assumes a 4-month growing season. Figures are approximate because precise sampling dates were often not provided.

¶Standing crop values from Dondale (1972) were not used in productivity-effect size analysis due to low drying temperature of vegetation samples.