

## THE IMPACT OF HERBIVORY ON PLANTS IN DIFFERENT RESOURCE CONDITIONS: A META-ANALYSIS

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**Abstract.** Understanding how plant recovery from herbivory interacts with the resource environment is necessary to predict under what resource conditions plants are most affected by herbivory, and ultimately how herbivory impacts plant population dynamics. It has been commonly assumed that plants are generally best able to recover from herbivory when growing in high resource conditions, an assumption which is supported by some models (e.g., the continuum of responses model) but opposed by others (e.g., the growth rate model). The validity and generality of any effects of resources (light, nutrients, and water) on plant recovery from herbivory were tested with mixed-model, factorial meta-analyses using a log response ratio metric applied to plant growth and reproduction data from the ecological literature. In total, 81 records from 45 studies were included in the growth meta-analysis, and 24 records from 14 studies in the reproduction meta-analysis. High resource levels and the absence of herbivory both strongly increased plant growth and reproduction. There was no significant overall interaction between growth or reproduction after herbivory and resource conditions, but the interaction terms were significant for each plant functional group in the growth meta-analysis. Basal meristem monocots grew significantly more after herbivory in high resources, while both dicot herbs and woody plants grew significantly more after herbivory in low resources. A similar result was found in the 34.6% of growth records where exact- or overcompensation occurred. Overcompensation was more likely in high resources for monocots and in low resources for dicot herbs. The reproduction data set was too small to subdivide. These qualitative differences between monocot and dicot herbs and woody plants explain many of the contradictory results in the literature and show that no single current model can account for the responses of all plants to herbivory.

**Key words:** *compensation; continuum of responses model; defoliation; effect size; growth rate model; herbivory; log response ratio; meta-analysis; plant growth and reproduction; plant–herbivore interactions; overcompensation; resources.*

### INTRODUCTION

While for the great majority of cases herbivory is detrimental to plants (e.g., Belsky 1986, Crawley 1997, Bigger and Marvier 1998), it has been suggested repeatedly that plants can sometimes increase fitness after herbivory through compensatory growth or reproduction (e.g., Owen and Weigert 1976, Dyer et al. 1982, McNaughton 1983, Maschinski and Whitham 1989, Vail 1992). Compensation is defined generally as a positive response of plants to injury (Belsky 1986), in which damaged plants alter their resource allocation, physiology, and/or phenology to reduce the impacts of damage on their growth and reproduction relative to undamaged plants. In many circumstances, it is difficult to distinguish undercompensation from no compensation; both are viewed more simply as a negative effect of herbivory on plants. (Note that we follow Trumble

et al. [1993] in restricting our use of the word “compensation” to Belsky’s [1986] exact- and overcompensation.) Overcompensation has been demonstrated in several cases, especially among plants in cultivation and greenhouse studies (e.g., McNaughton et al. 1983, Paige and Whitham 1987, Dyer et al. 1991, Paige 1999), though no field demonstrations are without controversy (see Belsky 1986, Bergelson and Crawley 1992, Marquis 1992, Crawley 1997).

Resources are one factor that can influence the degree to which plants recover from herbivory. It has been commonly assumed that plants growing in high resource conditions are best able to compensate for or tolerate herbivory (Bryant et al. 1983, Coley et al. 1985, Chapin and McNaughton 1989, Maschinski and Whitham 1989, Louda et al. 1990, Belsky et al. 1993, Rosenthal and Kotanen 1994, Bazzaz 1996, Irwin and Aarsen 1996, Crawley 1997; but see Hilbert et al. 1981), in part because replacing a fixed amount of eaten tissue requires a larger fraction of the net production of a plant growing in low resources than high resources (Coley et al. 1985). Experimental support, however, remains equivocal (e.g., McNaughton et al. 1983, Coughenour et al. 1985, Verkaar et al. 1986, and Mas-

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chinski and Whitham 1989 are pro; whereas McNaughton and Chapin 1985, Stafford 1989, Van Auken and Bush 1989, Schmid et al. 1990, and Meyer and Root 1993 are con).

Several plant–herbivore theories, including the continuum of responses model (Maschinski and Whitham 1989) and the growth rate model (Hilbert et al. 1981), make conflicting predictions about how plants respond to herbivory under different resource conditions. The continuum of responses model (Maschinski and Whitham 1989), for example, predicts that the probability of compensation for herbivory increases with increasing resources levels. This graphical model assumes that at high nutrient levels, tissues can be replaced more easily and plants can grow faster so as to recover more rapidly from damage. In contrast, the growth rate model (Hilbert et al. 1981) predicts that damaged plants will recover from tissue removal more fully in low than high resources. This mathematical model concluded that when plants are growing below their potential maximum relative growth rate (RGR) in stressed conditions such as low resource levels, they require only small changes in RGR to compensate for herbivory, especially when damage is minor. Plants growing in high resource conditions are more likely to be growing at or near their potential maximum RGR, so that any increase in RGR can only be small and probably insufficient for compensation to occur.

We used meta-analyses to assess how plants respond to herbivory in growth and reproduction under different resource levels. Meta-analysis is a statistical technique that synthesizes results from many independent studies to determine the consistency of the direction of those results and to estimate the overall size of the effect of interest (Gurevitch et al. 1992). Traditionally utilized in medical and social sciences (Gurevitch et al. 1992), meta-analysis is becoming more widely used in ecology (e.g., Jarvinen 1991, Gurevitch et al. 1992, Vander Werf 1992, Fernandez-Duque and Voleggia 1994, Tohansca and Byrne 1994, Wooster 1994, Curtis 1996, Hechtel and Juliano 1997, Bigger and Marvier 1998, Møller and Thornhill 1998, Downing et al. 1999). With its rise in application to ecological problems, meta-analysis has also met with criticism, warnings, and suggestions for improvement (Wachter 1988, Finney 1995, Osenberg et al. 1997, Petraitis 1998, Palmer 1999), which we have taken into account where possible.

The two separate meta-analyses presented here utilize a factorial design to examine the main effects and the interaction of resources and herbivory on two dependent variables: plant growth and reproduction. We further focused on how plant responses differed among three groups: dicot herbs, woody plants, and monocot herbs. Because these groups generally differ in their patterns of growth and morphology, we expected potential functional differences in their responses to herbivory and resources (e.g., Harper 1977, Belsky 1986, Abrahamson 1989, Irwin and Aarssen 1996).

## METHODS

### *Literature survey*

In our review of the literature, we included data from all published studies we could find that met our predetermined requirements. We used four electronic databases: BIOSIS for 1991–1999, Current Contents for 1988–1998, ISI Science Citation Database for 1988–1999, and AGRICOLA for 1979–1999. Titles and abstracts were searched with the following set of keywords: plant and (herbiv\$ or defoli\$ or clip\$) and (resource\$ or light or shad\$ or water or nutrient\$ or phosphorus or nitrogen or fertiliz\$), where “\$” indicates a wildcard for the remainder of the word. We also manually searched titles and abstracts for these same keywords for the years 1980 to 1987 from the following eight journals: American Journal of Botany, American Midland Naturalist, American Naturalist, Ecology, Functional Ecology, New Phytologist, Oecologia, and Oikos. From the articles that met our search criteria we further searched the titles of their cited references for the above keywords. In the growth meta-analysis, we included 81 records from a total of 45 studies by 41 different primary authors in 27 journals spanning the years 1983–1999 (Table 1). The reproduction meta-analysis was based on 24 records from 14 studies by as many different primary authors in 10 journals published between 1988 and 1998 (Table 2).

### *Criteria for inclusion*

We set specific requirements for inclusion prior to searching to avoid bias in selection. We chose studies that compared plant responses to herbivory vs. no herbivory under elevated resources and a control. Within this design, the following six conditions were also applied.

First, the study organism was a vascular plant. Second, the resource manipulated was light, water, or nutrients. The control for resource level was unmanipulated, reduced, or low resources, while the experimental treatment involved an addition or high level of resources. We termed the former “low” and the latter “high” resource levels. Third, equivalent amounts of artificial or natural herbivory were applied to plants in the high and low resource groups. We rejected studies where herbivory levels were not reported, ambient, or uncontrolled such that high nutrient plants might have been eaten more.

Fourth, the response variables were a designated measurement of reproduction and/or growth. Acceptable measures of reproduction were, in order of preference, the biomass or number of seeds, then fruit, then flowers. Growth measurements were biomass, height, leaf area, and number of branches. Our preference was for a measure of either total or aboveground biomass because these variables are most often reported and are generally used to define compensation. When separate above- and belowground biomass measures were re-

ported, we used total biomass but also recorded all values for a separate above- vs. belowground analysis. A measure of biomass was reported and used for 82.7% of the growth records. Six studies (see Table 1) included clipped biomass or "offtake" in their estimates of final biomass. Inclusion of clipped biomass should not alter the relative differences among treatments, but may change the overall magnitudes of the herbivory and resource effects (e.g., Dyer et al. 1991, Hicks and Reader 1995, Houle and Simard 1996). When biomass was not reported, another acceptable measure was used (if more than one was available, we chose randomly). Although plant size is not a direct measure of fitness, larger plant sizes have been shown to correlate positively with greater plant reproduction (Harper 1977).

Fifth, means, sample sizes, and some measure of variation from which either standard deviations or the mean square error could be calculated were reported in either numerical or graphical form for each of the four treatment groups (herbivory-high resources, no herbivory-high resources, herbivory-low resources, and no herbivory-low resources). For studies in which some or all of this information was unreported, we attempted to contact the author(s) when the data were published after 1989. Articles presenting data in graphical form were scanned with a Hewlett Packard ScanJet IIc (Hewlett Packard, Palo Alto, California, USA) and the freeware program DataThief II (Tummers 1999) was used to estimate the  $x$ ,  $y$  coordinates of the data. Values obtained in this manner were highly repeatable, with an error of <0.2%.

Sixth, when more than one record from a given study was appropriate for this meta-analysis, the additional records were included only when the measurements were made on different groups of both experimental and control plants. If measurements were made on the same plants, we selected the record that most closely matched our above criteria or, when records were equally suitable, we chose randomly.

More than 100 records were rejected, most because the study was missing a treatment, usually the undefoliated control. Only 11 records were rejected for not reporting the necessary data in the paper or through correspondence with the author(s) despite an appropriate experimental design.

#### Attribute coding

We classified each record by a suite of variables that could potentially influence plant response to combinations of herbivory and resource treatments. These variables were: plant functional groups, resource manipulated, type of herbivory, and location and duration of experiment (see Table 1). We chose to use the functional group variable (dicot herbs, woody plants, monocot herbs) as a class variable in the meta-analysis because we believed the growth and morphological differences among these groups would explain many of the differences in plant response to herbivory observed

in the literature (Harper 1977, Belsky 1986, Abrahamson 1989, Irwin and Aarssen 1996).

#### Numerical methods

For meta-analyses of growth and reproduction measurements, we chose the log response ratio as an index of effect size and used a factorial design, mixed effects model (see Gurevitch and Hedges 1993 for mixed model, Hechtel and Juliano 1997 for factorial design, and Hedges et al. 1999 for single factor log response ratio) to examine plant response to herbivory, resources, and their interaction. The log response ratio was selected because (1) it quantifies proportionate changes, thereby eliminating differences due to plant size, (2) its calculations were meaningful summaries for our questions, and (3) our data met the sample size requirements described by Hedges et al. (1999). Class subdivisions were used only in the growth meta-analysis; the reproduction meta-analysis did not contain enough records to do so. Calculations were completed in Microsoft Excel workbooks (Microsoft 1998).

For every record, the effect sizes for each main effect and the interaction were calculated as:

$$L_{\text{herbivory}} = [\ln(\bar{Y}_{e,h}) + \ln(\bar{Y}_{e,l})] - [\ln(\bar{Y}_{p,h}) + \ln(\bar{Y}_{p,l})]$$

$$L_{\text{resources}} = [\ln(\bar{Y}_{p,h}) + \ln(\bar{Y}_{e,h})] - [\ln(\bar{Y}_{p,l}) + \ln(\bar{Y}_{e,l})]$$

$$L_{\text{interaction}} = [\ln(\bar{Y}_{e,h}) - \ln(\bar{Y}_{p,h})] - [\ln(\bar{Y}_{e,l}) - \ln(\bar{Y}_{p,l})]$$

where  $\bar{Y}$  represents the sample mean, the subscripts "e" and "p" refer to herbivory (eaten) and no herbivory (protected), respectively, and the subscripts "h" and "l" refer to high and low resource levels, respectively. Note that the interaction term can also be expressed as a more traditional interaction:

$$L_{\text{interaction}} = [\ln(\bar{Y}_{p,l}) + \ln(\bar{Y}_{e,h})] - [\ln(\bar{Y}_{p,h}) + \ln(\bar{Y}_{e,l})]$$

but we find the former arrangement more meaningful than the latter for understanding the underlying causes of our results.

A single variance estimate was calculated for each record,

$$v = \frac{s_{e,h}^2}{n_{e,h} \bar{Y}_{e,h}^2} + \frac{s_{p,h}^2}{n_{p,h} \bar{Y}_{p,h}^2} + \frac{s_{e,l}^2}{n_{e,l} \bar{Y}_{e,l}^2} + \frac{s_{p,l}^2}{n_{p,l} \bar{Y}_{p,l}^2}$$

where  $s$  is the standard deviation or mean square error term and  $n$  is the sample size for each treatment group. This was the most conservative extrapolation of the single factor variance estimate in Hedges et al. (1999).

Following Gurevitch et al. (1992), we also calculated the statistic,  $Q_B^*$ , to estimate the heterogeneity among classes in our effect size comparisons. This statistic tests the null hypothesis of common effect size against the alternative of at least one effect size that differs from the rest.  $Q_B^*$  has a chi-squared distribution with degrees of freedom equal to one less than the number of classes.

The sign of the log response ratio reflects the un-

TABLE 1. Growth meta-analysis records with authors, focal species, attribute coding, and effect sizes for each study.

Citation	Species	FG	HT	EL	RM
Alward and Joern (1993)	<i>Bouteloua gracilis</i> no neighbors	M	R	F	H
	<i>Bouteloua hirsuta</i> no neighbors	M	R	F	H
	<i>Bouteloua gracilis</i> with neighbors	M	R	F	H
	<i>Bouteloua hirsuta</i> with neighbors	M	R	F	H
Beaulieu et al. (1996)	<i>Dupontia fisheri</i>	M	R	F	N
	<i>Eriophorum scheuchzeri</i>	M	R	F	N
Bergelson and Crawley (1992)	<i>Ipomopsis aggregata</i>	D	A	F	P
Borowicz (1993)	<i>Lotus corniculatus</i> with conspecifics, h1	D	A	G	N
	<i>Lotus corniculatus</i> with <i>Brassica napus</i> , h1	D	A	G	N
	<i>Lotus corniculatus</i> with conspecifics, h2	D	A	G	N
	<i>Lotus corniculatus</i> with <i>Brassica napus</i> , h2	D	A	G	N
	<i>Lotus corniculatus</i> with conspecifics, h3	D	A	G	N
	<i>Lotus corniculatus</i> with <i>Brassica napus</i> , h3	D	A	G	N
Borowicz and Fitter (1990)	<i>Lotus corniculatus</i> genetic cross 1	D	A	G	N
	<i>Lotus corniculatus</i> genetic cross 2	D	A	G	N
	<i>Lotus corniculatus</i> genetic cross 3	D	A	G	N
Briggs (1991)	<i>Lotus corniculatus</i>	D	R	G	N
Busso et al. (1989)	<i>Agropyron desertorum</i> 1986	M	A	F	H
	<i>Agropyron spicatum</i> 1986	M	A	F	H
	<i>Agropyron desertorum</i> 1987	M	A	F	H
	<i>Agropyron spicatum</i> 1987	M	A	F	H
Fay et al. (1996)	<i>Silphium integrifolium</i> low water group	D	R	C	H
	<i>Silphium integrifolium</i> high water group	D	R	C	H
Gange and Brown (1989)	<i>Capsella bursa-pastoris</i>	D	R	G	H
Gertz and Bach (1994)	<i>Lycopersicon esculentum</i>	D	R	G	P
Hansson (1994)	<i>Anthriscus sylvestris</i> 1989	D	A	C	N
	<i>Anthriscus sylvestris</i> 1990	D	A	C	N
Hartley and Amos (1999)	<i>Calluna vulgaris</i>	W	A	G	N
	<i>Nardus stricta</i>	M	A	G	N
Hartvigsen et al. (1995)	<i>Populus deltoides</i>	W	A	G	N
Hatcher et al. (1997)	<i>Rumex obtusifolius</i>	D	R	C	N
Hicks and Reader (1995)	<i>Poa compressa</i>	M	A	G	N
	<i>Poa pratensis</i>	M	A	G	N
	<i>Dactylis glomerata</i>	M	A	G	N
Houle and Simard (1996)	<i>Salix plantifolia</i>	W	A	G	N
Irwin and Aarssen (1996)	<i>Epilobium ciliatum</i> ssp. <i>glandulosum</i> alone	D	A	G	N
	<i>Epilobium ciliatum</i> ssp. <i>glandulosum</i> comp.	D	A	G	N
Juenger and Bergelson (1997)	<i>Ipomopsis aggregata</i> 1994 pollen control	D	A	G	N
	<i>Ipomopsis aggregata</i> 1994 hand pollinated	D	A	G	N
	<i>Ipomopsis aggregata</i> 1995 pollen control	D	A	G	N
	<i>Ipomopsis aggregata</i> 1995 hand pollinated	D	A	G	N
Lentz and Cipollini (1998)	<i>Scirpus ancistrochaetus</i>	M	A	C	P
Lim and Turner (1996)	<i>Dillenia suffructiso</i>	W	A	G	N
	<i>Trema tomentosa</i>	W	A	G	N
	<i>Macaranga heynei</i>	W	A	G	N
Lortie and Aarssen (1997)	<i>Verbascum thapsus</i> population A	D	A	F	N
	<i>Verbascum thapsus</i> population B	D	A	F	N
Maybry and Wayne (1997)	<i>Abutilon theophrasti</i>	D	A	G	P
McGraw et al. (1990)	<i>Quercus rubra</i>	W	A	G	P
Mulder and Ruess (1998)	<i>Triglochin palustris</i>	M	A	F	N
Mutikainen and Walls (1995)	<i>Urtica</i> spp.	D	A	G	N
Ovaska et al. (1993)	<i>Betula pendula</i>	W	A	G	N
Pierson et al. (1990)	<i>Bromus tectorum</i>	M	A	G	P
Reich et al. (1993)	<i>Pinus resinosa</i>	W	A	G	N
Ruess et al. (1997)†	<i>Carex ramenskii</i> lab, no salt	M	A	G	N
	<i>Carex ramenskii</i> 1991 field	M	A	G	N
	<i>Carex ramenskii</i> 1992 field	M	A	G	N
	<i>Carex ramenskii</i> 1993 field	M	A	G	N
Ruess et al. (1983)‡	<i>Kyllinga nervosa</i> ammonium	M	A	G	N
	<i>Kyllinga nervosa</i> nitrate	M	A	G	N
Ruohomaki et al. (1996)	<i>Betula pubescens</i>	W	A	G	N
Sadras et al. (1998)	<i>Gossypium hirsutum</i>	D	R	F	H
Schaeffer and Mason (1990)	<i>Guaiacum sanctum</i>	W	R	G	P
Simms (1985)	<i>Zenobia pulverulenta</i>	W	A	F	N
	<i>Lyonia lucida</i>	W	A	F	N
Singh and Sale (1997)†	<i>Trifolium repens</i>	D	A	F	N
Stafford (1989)†	<i>Abutilon theophrasti</i>	D	A	G	N
Sugiyama and Nakashima (1995)	<i>Festuca arundinacea</i>	M	A	G	N
VanAuken and Bush (1989)†	<i>Bouteloua curtipendula</i> alone	M	A	G	N
Wait (1997)	<i>Populus deltoides</i>	W	A	F	N
Wegener and Odasz (1997)†	<i>Dupontia fisheri</i>	M	A	G	N



TABLE 1. Extended.

ED	$L_{\text{herb}}$	$L_{\text{res}}$	$L_{\text{int}}$	X
425	-0.602	0.819	0.111	
425	-0.707	2.047	0.956	
425	-1.334	1.193	-0.168	X
425	0.489	1.148	0.223	X
60	-0.229	-0.269	0.282	
60	-1.063	-0.179	-0.036	X
117	1.716	1.560	-1.324	X
55	-2.166	1.754	-0.203	X
86	-0.661	1.163	-0.934	X
68	-1.618	0.602	-0.206	
55	-0.658	0.180	-0.152	
68	-1.301	0.520	0.896	
86	0.119	1.429	-0.255	
46	-0.226	1.092	-0.097	X
46	-0.346	0.149	-0.346	
46	-0.483	0.453	-0.269	
47	-0.194	0.583	0.038	
1270	-3.000	0.927	0.121	
2365	-2.480	1.655	0.914	
1270	-3.021	0.016	-0.716	
2365	-3.386	-0.067	-0.274	
37	-1.083	0.428	-0.018	
38	-0.689	1.230	0.198	
182	-0.264	0.349	0.019	
28	-0.779	2.685	-0.459	
425	-0.086	0.866	0.012	X
120	-0.014	1.232	-0.014	
540	-0.845	1.535	-0.013	
666	-0.764	2.206	0.215	
35	-2.416	0.251	-0.659	
150	-1.114	0.709	0.001	
60	-0.941	0.941	0.037	
60	-0.972	0.841	-0.133	
60	-0.756	0.527	0.063	
35	-0.246	0.130	0.118	
109	-0.173	6.140	0.433	X
109	-0.514	5.431	-1.078	X
150	0.469	0.369	-0.521	X
150	0.691	0.742	-0.547	X
150	1.486	1.418	-0.520	X
150	1.973	0.050	0.465	X
120	-0.013	3.276	0.736	X
63	-0.622	0.550	-0.119	X
63	-0.020	1.172	0.020	
63	-0.006	1.113	-0.354	X
140	-0.528	0.211	-0.074	
140	-0.574	0.199	-0.140	
100	-0.433	0.150	0.107	
120	-2.216	1.626	0.248	
44	-0.661	-0.049	-0.139	
49	-0.158	2.319	0.087	
14	-0.682	0.143	-0.044	
180	-0.915	3.146	0.737	
183	0.476	0.256	-0.058	X
84	0.017	0.908	0.222	X
84	-0.556	0.993	0.206	
84	-1.205	1.108	0.326	X
84	0.204	1.575	0.204	
63	-1.255	-0.610	-0.147	
63	-0.922	1.504	-0.085	
2113	-0.342	0.433	0.046	
145	-1.416	0.187	-0.499	
288	-1.521	0.564	-0.772	
210	0.237	1.117	-0.350	X
210	1.460	1.176	0.073	X
36	-0.852	2.220	-0.262	
35	-1.451	1.287	-0.364	
44	-2.353	1.858	0.571	
126	-2.578	2.478	-0.477	X
60	-0.174	0.048	0.406	X
158	-1.057	2.034	-0.756	

derlying qualitative patterns of plant growth or reproduction. If plants in high resources are larger or reproduce more than those in low resources,  $L_{\text{resource}}$  will be positive (and vice versa). If herbivory decreases plant size or reproduction relative to protected plants,  $L_{\text{herbivory}}$  will be negative (and vice versa). For the interaction effect size, positive and negative directionality can result from two different scenarios: plants can have greater overcompensation or can be less detrimentally affected by herbivory under one resource level than another (Fig. 1). We defined compensation as occurring in those cases where plants that experienced herbivory equaled or surpassed control plants in size or reproductive output in either resource treatment.

To understand how the interaction effect sizes of our individual studies were distributed among these possibilities, we examined the two components of the equation for  $L_{\text{interaction}}$ :  $L_H = \ln(\bar{Y}_{e,h}) - \ln(\bar{Y}_{p,h})$  and  $L_L = \ln(\bar{Y}_{e,l}) - \ln(\bar{Y}_{p,l})$ . A positive  $L_H$  or  $L_L$  indicates that plants overcompensated for herbivory in high or low resource levels, respectively. A negative  $L_H$  or  $L_L$  indicates a detrimental effect of herbivory in high or low resource levels, respectively (partial or undercompensation sensu Belsky 1986). How plant responses to herbivory compare between the two resource levels determines the overall effect size.

In this meta-analysis, a significant effect of herbivory and resource level on the response variable (growth, reproduction) occurred when 95% confidence intervals around weighted means (Hedges et al. 1999) of the log response ratio (class or overall) did not overlap zero. If the 95% confidence intervals around two mean effect sizes did not overlap, then the groups were considered to have significantly different responses. Confidence intervals were calculated as  $L \pm 1.96s$ , where  $L$  is either the class or overall weighted mean of the log response ratio and  $s$  is the standard error for that effect size. Throughout the manuscript, we report  $L \pm 1.96s$ .

To further understand the interaction of resources and herbivory, we also examined the weighted means of the log response ratio interaction term of resource manipulated (light, nutrients, water) as a nested factor within the functional groups (see Curtis 1996). Because our sample size did not permit additional nested divisions, the type of herbivory (artificial, natural) and experiment location (field, greenhouse, common garden) were separately checked as nested factors within the functional groups. We additionally tested the idea that compensation differs by experiment location with a chi-square test. Confidence intervals and significance levels were corrected for multiple comparisons by the Dunn-Sidak method (Sokal and Rohlf 1995). The duration of experiment was plotted against the interaction term to check for a reduction in variance of effect size with time (Gurevitch et al. 1992, Maurer 1999).

TABLE 1. Continued.

Citation	Species	FG	HT	EL	RM
Welker and Menke (1990)	<i>Quercus douglasii</i>	W	A	G	H
Willis et al. (1993)	<i>Hypericum gramineum</i>	D	R	G	H
	<i>Hypericum perforatum</i>	D	R	G	H
Willis et al. (1995)	<i>Hypericum gramineum</i>	D	R	G	N
	<i>Hypericum perforatum</i>	D	R	G	N
Willis et al. (1998)	<i>Hypericum gramineum</i>	D	R	G	N
	<i>Hypericum perforatum</i>	D	R	G	N
	<i>Hypericum gramineum</i>	D	R	F	N
	<i>Hypericum perforatum</i>	D	R	F	N
Wright et al. (1989)	<i>Quercus rubra</i>	W	A	G	H

Notes: Codes are: FG = functional group (D = herbaceous dicot, W = woody, M = herbaceous monocot); HT = type of herbivory (A = artificial herbivore, R = natural herbivory); EL = experiment location (G = greenhouse, C = common garden, F = field); RM = resource manipulated (P = light, H = water, N = nutrients); ED = experiment duration (days, estimated from month and year measures in some studies);  $L_{\text{herb}}$  = log response ratio for herbivory;  $L_{\text{res}}$  = log response ratio for resources;  $L_{\text{int}}$  = log response ratio for the interaction; X = records where some exact- or overcompensation occurred.

† Offtake included in growth measurements.

‡ Offtake may have been included in growth estimates.

### Methodological considerations

For comparison, we also recalculated the growth meta-analyses with the more commonly used standardized difference  $d$  statistic as an index of effect size. The  $d$  statistic differs from the log response ratio in that it calculates the difference between the treatment and control groups. This difference is divided by the pooled standard deviation and multiplied by a term that adjusts for sample size (for formulae see Gurevitch and Hedges 1993, Hechtel and Juliano 1997).

## RESULTS

### Meta-analyses outcomes

There were significant main effects of herbivory and resource levels on plant biomass both overall and for all three functional groups (Figs. 2 and 3). Plants grew more in the absence of herbivory and with higher resource levels. The response of plant reproduction to the main effects of resources and herbivory was consistent with the growth response: plants reproduced more with no herbivory and higher resource levels (Fig. 2).

There were differences among functional groups in their growth responses to resources and herbivory. The main effect of herbivory was significantly more negative for monocot herbs than dicot herbs or woody plants ( $Q_B^* = 11.43$ ,  $df = 2$ ,  $P < 0.01$ ). The main effect of resources was slightly greater for dicot herbs than monocot herbs and woody plants ( $Q_B^* = 6.12$ ,  $df = 2$ ,  $P < 0.05$ ).

The overall interaction of herbivory and resources was not significantly different from zero in either the growth ( $L_{\text{interaction}} = -0.047 \pm 0.067$ ,  $n = 81$ ; Fig. 2) or reproduction meta-analyses ( $L_{\text{interaction}} = 0.144 \pm 0.244$ ,  $n = 24$ ; Fig. 2). The interaction term in both cases was smaller in magnitude than the main effects. However, the growth response of monocot herbs to the interaction was significantly different from those of dicot herbs and woody plants (woody dicots = 16, woody gymnosperms = 1) and each class significantly

differed from zero (Fig. 3,  $Q_B^* = 15.43$ ,  $df = 2$ ,  $P < 0.001$ ). Monocot growth, with a significantly positive log response ratio, was less detrimentally affected by and/or overcompensated more for herbivory in high resource conditions. Growth of dicot herbs and woody plants responded in the opposite manner, with significantly negative log response ratios indicating that plants were less negatively affected by and/or overcompensated more for herbivory in low resource conditions.

### Incidence of compensation

The great majority of plants in the growth meta-analysis were instances in which plants were detrimentally affected by herbivory in one or both resource conditions (Fig. 4). Exact- or overcompensation for herbivory occurred in at least one resource treatment in 34.6% of all cases ( $n = 81$ ), 26.9% of monocot records ( $n = 26$ ), 33.3% of dicot herb records ( $n = 39$ ), and 43.8% of woody records ( $n = 16$ ; Fig. 4). The exclusion of those records where clipped biomass was included in final biomass did not qualitatively alter the observed levels of compensation, which were changed quantitatively by only 0–5 percentage points. In the reproduction meta-analysis (23 herbaceous dicot records and one woody plant record), exact- or overcompensation for herbivory occurred in 29.2% of records. These short-term observations of overcompensation, however, are not necessarily a reflection of long-term fitness benefits (Belsky et al. 1993, Crawley 1997, Simons and Johnston 1999).

As expected from the nonsignificant  $L_{\text{interaction}}$  term in the growth meta-analysis, there were almost equal numbers of records in which plants exactly or overcompensated for herbivory in only low ( $n = 10$ ), only high ( $n = 9$ ), or both high and low resource treatments ( $n = 8$ ; Fig. 4). The absence of an overall trend in compensatory growth was driven by the different responses of monocot herbs, dicot herbs, and woody plants (Fig. 4).

TABLE 1. Continued, extended.

ED	$L_{\text{herb}}$	$L_{\text{res}}$	$L_{\text{int}}$	X
1018	-0.046	0.939	-0.151	X
100	-2.086	2.568	-1.450	
100	-3.597	2.815	0.858	
168	-0.584	1.462	0.182	
168	-0.813	1.438	-0.071	
240	-0.063	2.164	0.075	X
240	-0.515	2.578	-0.154	
240	-0.768	1.731	0.435	X
240	1.921	1.408	-2.875	
127	0.075	-0.022	0.081	X

Exact- and overcompensation were more likely and more pronounced in high resources for monocots and in low resources for dicot herbs (Fig. 4). In monocots, the seven cases of exact- or overcompensation all showed greater relative growth in high resource conditions: exact- or overcompensation in monocots occurred in the high resource treatment only ( $n = 5$ ) or involved greater overcompensation in the high than low resource treatment ( $n = 2$ ). In contrast, 10 of the 13 dicot herb records with exact- or overcompensation showed greater relative growth in low resource conditions. Of these ten records, exact- or overcompensation occurred in only the low resource treatment ( $n = 7$ ) or involved greater overcompensation in the low than high resource treatment ( $n = 3$ ). Of the seven cases of exact- or overcompensation in woody plants, four showed greater relative growth in low resource conditions and three showed relatively greater growth in high resource conditions.

#### Further growth meta-analysis subdivisions

Comparisons of mean  $L_{\text{interaction}}$  among subdivisions of the functional groups (type of resource manipulated, type of herbivory, and duration and location of experiment) provided no additional understanding of the variation in plant growth response. The weighted means of  $L_{\text{interaction}}$  for light, nutrients, and water within each functional group had the same direction as their respective functional groups and did not significantly differ from each other (Fig. 5). Only light within monocots did not overlap zero, but this group contained only two records and overlapped the confidence intervals of the other resource categories. Type of herbivory (real vs. artificial) and experiment location (field vs. greenhouse vs. common garden) followed the same pattern, i.e., their 95% confidence intervals all overlapped within each plant group. Experiments occurring over longer time scales did not have interaction effect sizes that were less variable than experiments done over shorter time periods (cf., Gurevitch et al. 1992, Maurer 1999).

There was no significant effect of study location—field studies vs. greenhouse/common garden studies—on the overall likelihood of a record containing exact- or overcompensation in plant growth ( $\chi^2 = 0.289$ ,  $df = 3$ ,  $P = 0.96$ ). Compensation in growth occurred in 38.1% of field records and 31.7% of greenhouse/common garden records ( $n = 21$  and 60 respectively). This result is contrary to an observation by Marquis (1992) that overcompensation is “much more frequent” in plants in cultivation and greenhouse studies than in field studies.

Plant growth above- and belowground in response

TABLE 2. Reproduction meta-analysis records with authors, focal species, attribute coding, and the effect sizes for each study.

Citation	Species	FG	$L_{\text{herb}}$	$L_{\text{res}}$	$L_{\text{int}}$	X
Benner (1988)	<i>Thlaspi arvense</i>	D	0.459	0.428	0.178	X
Bergelson and Crawley (1992)	<i>Ipomopsis aggregata</i>	D	-0.594	0.673	0.179	
Briggs (1991)	<i>Lotus corniculatus</i>	D	-1.931	0.513	-0.121	
Fay et al. (1996)	<i>Silphium integrifolium</i>	D	-0.206	0.206	-0.075	
Fernandez and Pritts (1996)	<i>Rubus idaeus</i>	W	0.348	0.405	0.231	X
Gange and Brown (1989)	<i>Capsella bursa-pastoris</i>	D	-0.330	-0.090	0.578	X
Hansson (1994)	<i>Anthriscus sylvestris</i>	D	2.673	2.546	-0.010	X
Irwin and Aarssen (1996)	<i>Epilobium ciliatum</i> ssp. <i>glandulosum</i>	D	0.074	5.504	0.429	X
Juenger and Bergelson (1997)	<i>Ipomopsis aggregata</i>	D	-2.599	-0.122	0.122	
	<i>Ipomopsis aggregata</i>	D	-1.588	0.888	-0.008	
	<i>Ipomopsis aggregata</i>	D	-1.693	1.271	-0.082	
	<i>Ipomopsis aggregata</i>	D	-2.812	0.503	-0.122	
Mabry and Wayne (1997)	<i>Abutilon theophrasti</i>	D	-0.775	0.615	0.451	
Machinski and Whitham (1989)	<i>Ipomopsis arizonica</i> open fert, 1985	D	-1.357	0.658	1.085	
	<i>Ipomopsis arizonica</i> open fert, 1986	D	-0.932	2.070	0.264	
	<i>Ipomopsis arizonica</i> open fert, 1987	D	-0.290	2.678	0.699	X
	<i>Ipomopsis arizonica</i> grass fert, 1985	D	-1.768	0.523	-0.430	
	<i>Ipomopsis arizonica</i> grass fert, 1986	D	-1.412	0.940	1.153	
	<i>Ipomopsis arizonica</i> grass fert, 1987	D	-0.650	2.204	0.544	
	<i>Ipomopsis arizonica</i> open water, 1985	D	-2.054	0.143	0.388	
	<i>Ipomopsis arizonica</i> open water, 1986	D	-0.896	1.176	0.299	
Mutikainen and Walls (1995)	<i>Urtica</i> spp.	D	-0.087	1.767	-0.087	X
Sadras et al. (1998)	<i>Gossypium hirsutum</i>	D	-2.212	-0.653	-1.147	
Shimada et al. (1992)	<i>Glycine max</i>	D	-0.515	1.468	-0.237	

Note: Codes are the same as those in Table 1.

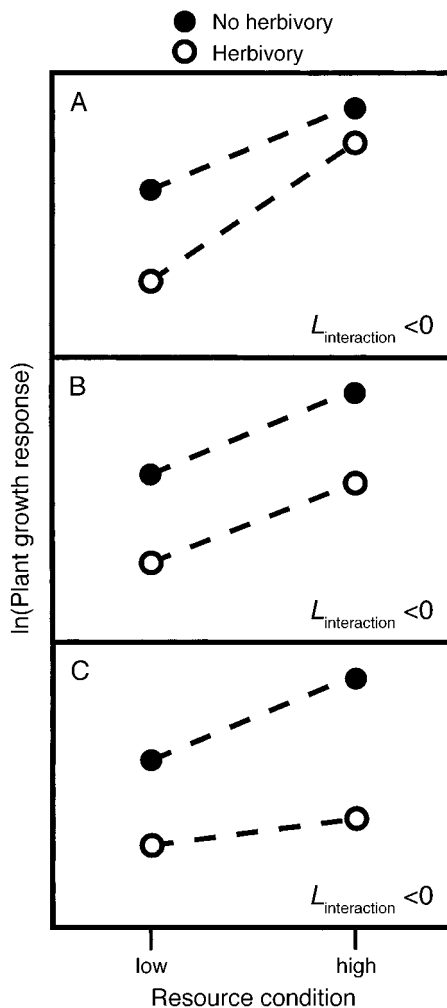


FIG. 1. Possible responses of plants to herbivory in different resource conditions.  $L_{\text{interaction}}$  is the log response ratio metric for the interaction of resource level and herbivory in the growth meta-analysis. The sign of  $L_{\text{interaction}}$  is determined solely by the relative slopes of the “herbivory” and “no herbivory” lines. Cases of exact or overcompensation will show “herbivory” points at or above “no herbivory” points, but the sign of  $L_{\text{interaction}}$  will be unchanged unless the relative slopes of the lines are qualitatively altered.

to the interaction of herbivory and resources was qualitatively the same in 76% of those records which provided separate above- and belowground measurements ( $n = 38$ ). Our choice in the overall meta-analysis of aboveground biomass when total biomass was not available should therefore produce qualitatively consistent results.

#### Methodological considerations

Use of the standardized difference effect size produced results that were similar to, though larger in magnitude than, the log response ratio in the growth meta-analysis. However, unlike the log response ratio results, the standardized difference for the interaction

was negative for monocots and not significantly different from zero.

This discrepancy between the log response ratio and the standardized difference interaction terms is due to a negative bias in the latter as pertains to our question. Because the standardized difference utilizes absolute rather than proportional changes, it assumes that plants in high and low resource conditions share a common linear growth trajectory. If this is not the case and plants in low resource conditions, for example, grow at a slower rate than plants in high resource conditions, then the interaction term of the standardized difference will actually be slightly negative when resources have no influence on plant response to herbivory.

Consider an example in which plants do not alter their growth following herbivory, but plants growing in high resources quadruple their biomass per unit time while plants in low resources only double their biomass. In this case, there is a main effect of resources but no effect of the interaction of resources and herbivory on plant growth. An experiment involving the removal of half of the biomass from plants initially one unit in mass will give results proportional to  $\bar{Y}_{e,h} = 2$ ,  $\bar{Y}_{p,h} = 4$ ,  $\bar{Y}_{e,l} = 1$ ,  $\bar{Y}_{p,l} = 2$ . The standardized difference in this case (numerator =  $(\bar{Y}_{e,h} - \bar{Y}_{p,h}) - (\bar{Y}_{e,l} - \bar{Y}_{p,l}) = -1$ ) is a negative number, whereas the log response ratio accurately reports zero.

#### DISCUSSION

The evidence presented here does not support the hypothesis that plants growing in high resource environments can better compensate for or better tolerate herbivory than plants growing in low resource environments. Our analyses confirm that plants generally

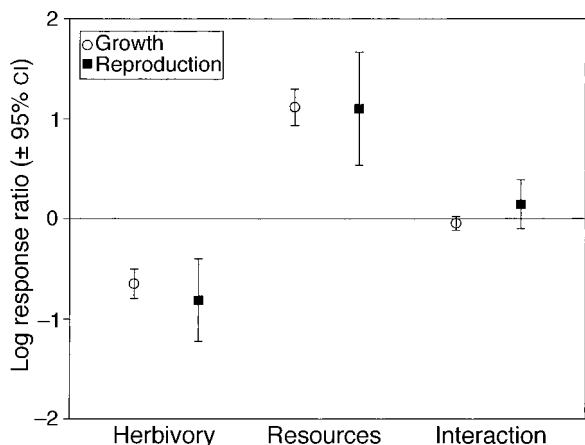


FIG. 2. The overall weighted mean of the log response ratio metric for the herbivory and resource treatments and their interaction, for the growth ( $n = 82$  records) and reproduction ( $n = 24$  records) meta-analyses. Bars represent 95% confidence intervals. It can be seen that plants grew and reproduced significantly worse with herbivory and significantly better with resource addition, but across all records there were no significant interactions between herbivory and resource.



FIG. 3. The log response ratios for classes (functional groups) in the growth meta-analysis. Bars represent 95% confidence intervals. Note that monocot herbs have a significantly positive  $L_{\text{interaction}}$  and that dicot herbs and woody plants have significantly negative  $L_{\text{interaction}}$  values.

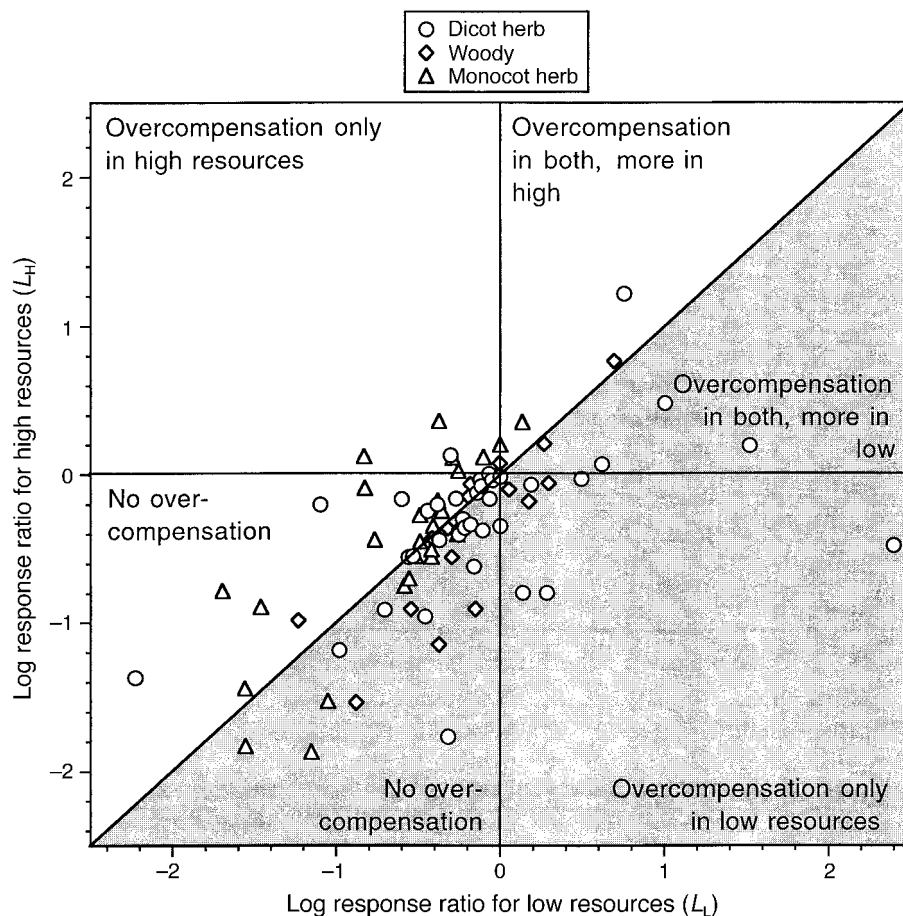
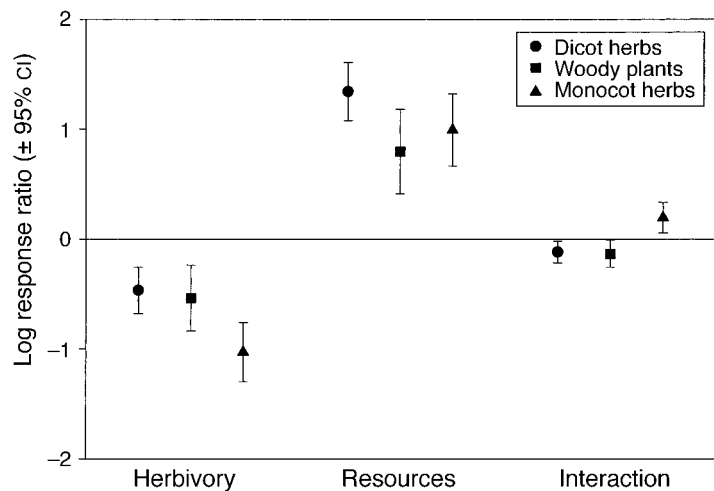


FIG. 4. High ( $L_H$ ) vs. low ( $L_L$ ) resource components of the interaction log response ratio for all 82 records in the growth meta-analysis. Since  $L_{\text{interaction}} = L_H - L_L$ , points on the diagonal line ( $L_H = L_L$ ) represent  $L_{\text{interaction}} = 0$ , points above this line (unshaded area) are records with positive  $L_{\text{interaction}}$  terms, and points below this line (shaded area) are records with negative  $L_{\text{interaction}}$  terms. Most points fall in the lower left-hand quadrant. These are cases of no overcompensation where plants are either less detrimentally affected in high (above the diagonal line) or low (below the line) resources.

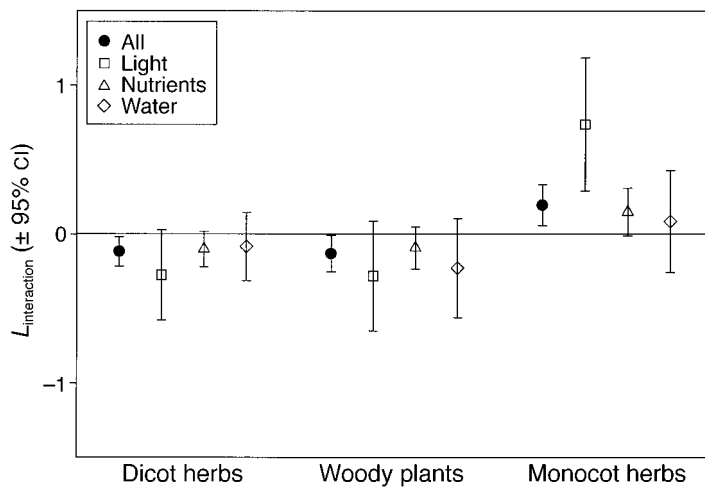


FIG. 5. Growth meta-analysis interaction log response ratio ( $L_{\text{interaction}}$ ) for resource manipulated (light, nutrients, water) within functional groups (dicot herbs, woody plants, monocot herbs). "All" is the overall  $L_{\text{interaction}}$  value for each plant functional group without subdivision by resource type. Bars represent 95% confidence intervals.

do grow and reproduce better in situations with either high resources or no herbivory, but the interaction of these factors is complex. It is commonly assumed that plants growing in high resource conditions are best able to compensate for or tolerate herbivory (Bryant et al. 1983, Coley et al. 1985, Bazzaz 1996, Crawley 1997). Yet monocots were the only group that grew more after herbivory in high resource conditions. Dicot herbs and woody plants, on the other hand, recovered significantly better from herbivory in low resource conditions.

These results imply that the different models of plant response to herbivory may apply to different groups of plants and probably work through different mechanistic pathways (see also Alward and Joern 1993, Meyer and Root 1993, Gertz and Bach 1994, Hicks and Reader 1995). We found support for both the continuum of responses model (Maschinski and Whitham 1989) and the growth rate model (Hilbert et al. 1981)—the responses of monocots are consistent with the former hypothesis and dicot herbs and woody plants with the latter. The fundamental differences in how plants in these functional groups grew after herbivory may be driven by the location of meristematic tissue. All of the monocots included in this analysis were herbaceous grasses, sedges, and rushes with basal meristems. In contrast, almost all of the dicot herbs and woody plants have apical meristems. The architectural and physiological consequences of meristem location are likely to set these groups apart with regard to herbivory (Abrahamson 1989, Irwin and Aarssen 1996).

The basal meristem habit of monocots often is an adaptation to grazing, and many grasses especially have evolved in the presence of strong ungulate grazing (Stebbins 1981). The basal meristem architecture together with the lack of leaf abscission in most grasses, sedges, and rushes can result in limited herbivory increasing net photosynthesis by removing old leaf tissue and increasing light levels to new tissues (Vickery

1972, McNaughton 1979, Owen and Wiegart 1981, Knapp and Seastedt 1986, McNaughton 1992, Hamilton et al. 1998). Reduced self shading after herbivory is likely to be more prevalent in high nutrient conditions where there is extensive aboveground growth. Furthermore, Hamilton et al. (1998) found that compensation for herbivory in a Serengeti Plains grass species occurred only above a critical tissue nitrogen concentration, a result that may apply to basal meristem monocots generally. For these reasons, monocots with basal meristems may be most likely to recover best from herbivory in high resource conditions and conform to the continuum of responses model (Maschinski and Whitham 1989).

In contrast to monocots with basal meristems, our results suggest that dicot herbs and woody plants may be best able to increase their relative growth rates (RGR) after herbivory in low resource conditions as expected under the growth rate model (Hilbert et al. 1981). Hilbert et al. (1981) proposed that plants grow further below their potential maximum RGR in stressed conditions or low resource levels than in normal or enriched resource conditions. Low resource plants will therefore require smaller changes in RGR than high resource plants to compensate for herbivory. It is not clear why this should occur with dicot herbs and woody plants but not with basal meristem monocots.

The patterns we observed could be explained if monocots differ from woody plants and dicot herbs in their carbon limitation after herbivory (Bryant et al. 1983, Meyer and Root 1993). From their work with the dicot herb *Solidago altissima*, Meyer and Root (1993) suggested that plants with abundant nutrients are more likely to be carbon limited than plants in low nutrient conditions. Carbon-limited plants will be more detrimentally affected by leaf herbivory because the loss of leaf tissue primarily increases carbon limitation. Herbivory may not cause carbon limitation in grazing-adapted basal meristem monocots, however, because

grazing can disproportionately remove old leaves and reduce self shading of the younger leaves. Growth after herbivory, and whether a plant is carbon limited or has an excess of carbon as a result of herbivory, will also depend on whether a plant has reserves and where they are stored (Tuomi et al. 1984).

Other hypotheses also suggest that resource levels alone are not driving patterns of recovery from herbivory across resource gradients, but rather the interactions of resource level with plant growth rate trajectory (Wait 1997) or competitive environment (Irwin and Aarssen 1996). Wait (1997) extends the growth rate model of Hilbert et al. (1981), suggesting that the response of plants to herbivory is dependent not on relative growth rates per se but rather on growth rate trajectory. Plants with a negative growth rate trajectory are predicted to be less able to compensate for herbivory than plants with a constant or positive growth rate trajectory. A positive growth rate trajectory is expected in plants that have a greater resource supply than demand, but this can occur under any resource level. Wait (1997) found that, for *Populus deltoides* saplings, equal compensation occurred at all resource levels when growth rates were increasing, but undercompensation occurred at high resource levels when growth rates were declining. For this hypothesis to be in accordance with the results of our meta-analysis, a positive growth rate trajectory would be more likely under high resource conditions only for monocots. In contrast, it would be far less probable for dicot herbs and woody plants to have positive growth rate trajectories more often under low resource conditions.

The light competition hypothesis (Irwin and Aarssen 1996) presents two scenarios in which apical meristem plants will recover better from apical herbivory in low resource than high resource conditions. In the presence of competitors, they predict that apical meristem plants suffering herbivory are more likely to be shaded by neighbors in high resources than low resources, as growth of neighbors is greatest in high resources. In the absence of competitors, Irwin and Aarssen (1996) predict that plant recovery from herbivory will be greatest at intermediate resource levels because apical herbivory releases the plant from apical dominance and resources are sufficient to allow extensive growth to occur. High resources are thought to weaken apical dominance and cause extensive lateral growth even without apical herbivory. At very low resource levels, there may be insufficient resources to fuel lateral growth after herbivory. To be consistent with the light competition hypothesis, dicot herbs and woody plants grown without competitors in our growth meta-analysis would need to have perceived their "low" resource treatments as closer to biologically intermediate than biologically low.

In summary, our growth meta-analysis suggests that there is a functional split between basal meristem monocots and dicot herbs/woody plants in how re-

sources influence plant recovery from herbivory. This functional split is not predicted by the continuum of responses model (Maschinski and Whitham 1989) or the growth rate model (Hilbert et al. 1983), but can potentially be explained by the concept of self-shading growth limitation in ungrazed basal meristem monocots (e.g., McNaughton 1992), together with the carbon-nutrient balance hypothesis (Bryant et al. 1983, Meyer and Root 1993) and the light competition hypothesis (Irwin and Aarssen 1996) applied to apical meristem dicot herbs and woody plants. Although each of these hypotheses was largely designed for soil nutrient gradients, they may also apply to gradients of water and light (no significant differences were found among these resource groups in our growth meta-analysis; Fig. 5).

Despite these overall patterns, there was a great deal of variability within this meta-analysis. Many individual records of dicot herbs, woody plants, and monocot herbs had interaction log response ratios qualitatively opposite from their overall class responses (14/39 positive dicot herbs, 7/16 positive woody, 9/26 negative monocots). Over one-third of dicot herbs grew more in high resource conditions after herbivory, consistent with Maschinski and Whitham (1989) whose continuum of responses model was based on a study of reproduction in the dicot herb *Ipomopsis arizonica*. Removal of the apical meristem in *I. arizonica* results in branching, the degree of which they suggest to be dependent on availability of both carbohydrate reserves and nutrients in soil (Paige and Whitham 1987, Maschinski and Whitham 1989). This response agrees with the prediction of Irwin and Aarssen (1996) that lateral branching after the disruption of apical dominance is less likely to take place in low resources. Similarly, over one-third of monocots grew more in low resources after herbivory, consistent with the growth rate model of Hilbert et al. (1981).

The resource environment of plants is only one of many variables known or predicted to influence plant recovery from herbivory (e.g., McNaughton 1983, Richards 1993, Trumble et al. 1993), and hypotheses which rely solely on plant resources to predict these responses are likely to have limited predictive power. High and low resource environments will certainly play a role in how plants respond to damage of any sort, but a better understanding of this role will only come from going beyond the study of patterns to attempt to elucidate the fundamental physiological and developmental processes responsible for the observed plant responses.

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