

THE CONTINUUM OF PLANT RESPONSES TO HERBIVORY:
THE INFLUENCE OF PLANT ASSOCIATION, NUTRIENT
AVAILABILITY, AND TIMING

JOYCE MASCHINSKI AND THOMAS G. WHITHAM

Department of Biological Sciences, Northern Arizona University, Flagstaff, Arizona 86011

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The recent controversy over the impact that herbivores have on the plants they eat is polarized into two camps (Belsky 1986; McNaughton 1986). At one extreme, it has been suggested that herbivores benefit the plants they eat by increasing fruit and seed production (Hendrix 1979; Janzen 1979; Hendrix and Trapp 1981; Paige and Whitham 1987*a*; but see Hendrix 1984), increasing biomass production (McNaughton 1976, 1979; Savory 1983; Cargill and Jefferies 1984), increasing shoot production (Heichel and Turner 1983), increasing rosette production (Inouye 1982), increasing prop roots and tiller production (Simberloff et al. 1978; Caldwell et al. 1981), or increasing nutrient supply (Owen and Wiegert 1976; Owen 1980).

At the other extreme, many studies of agricultural systems and fewer studies of natural systems support the widely held view that plants are negatively affected by herbivores. These studies have shown that herbivores can limit plant distribution (Harper 1977; Parker and Root 1981; Louda 1983), reduce reproductive potential (Rockwood 1973; Inouye 1982; Louda 1984; Edwards 1985; Whitham and Mopper 1985), and modify competitive ability (Harper 1977; Dirzo and Harper 1982).

Between these extremes lie studies reporting that herbivores have no effect on the plants they eat (Lee and Bazzaz 1980; Heichel and Turner 1983; Fowler and Rausher 1985; McNaughton and Chapin 1985; Julien and Bourne 1986; Karban and Courtney 1987). Such neutral effects of herbivory may be due to the ability of plants to replace certain tissues, such as meristematic tissue and young leaves.

Although these studies appear contradictory, here we present experiments showing that a plant's response to herbivory is plastic and varies according to the conditions it experiences. Because the effects of herbivory are governed by interactions between the environment and the affected plant (McNaughton 1986), plant responses vary according to prevalent biotic and abiotic conditions. Consequently, these studies, rather than being in opposition, represent different extremes of the same continuum. Herbivory can be detrimental, of no consequence, or even beneficial, depending on the conditions governing a plant's ability to replace tissue consumed by herbivores.

Factors known to influence the degree of compensatory growth include timing and intensity of grazing (Harper 1969, 1977; Mueggler 1970, 1972; Crawley 1983;

Olson and Richards 1988), water availability (Cox and McEvoy 1983), nutrient availability (Bryant et al. 1983; McNaughton and Chapin 1985), history of defoliation (Olson and Richards 1988), and type (Inouye 1982) and age of tissue eaten (Milthorpe and Davidson 1965; Crawley 1983). Collectively, these factors influence a plant's physiological state and its ability to compensate for herbivory. Although the interactive effects of any of these factors can also influence plant growth and reproduction (Berendse 1985; Brunsting and Heil 1985; Fowler and Rausher 1985), empirical tests are still needed to demonstrate how interactive effects influence plant compensation for herbivory.

Further, conditions favoring the range in compensatory responses a given species may experience are not well known. For example, Belsky (1986, 1987) suggested that overcompensation most probably occurs in moderately grazed wetlands where water and nutrients are abundant, soils are not compacted by large mammals, and species grow in monoculture free of interspecific competition. However, empirical tests substantiating this supposition are still lacking.

In this study we examined the single and interactive effects of plant association, nutrient availability, and timing of herbivory on the relative fitness of an herbaceous biennial, *Ipomopsis arizonica*. In addition, we sought to determine how herbivory affects the natural population and whether plants compensate for herbivory in a predictable manner.

Compensatory ability as defined here can be divided into three classes: overcompensation, equal compensation, and undercompensation. Overcompensation, whereby herbivory is beneficial, occurs when grazed plants produce significantly greater numbers of fruits and seeds than control, ungrazed plants. Equal compensation occurs when grazed plants produce equal numbers of fruits and seeds as controls and are not affected by herbivores. Undercompensation, whereby herbivory is detrimental, occurs when grazed plants produce significantly fewer fruits and seeds than controls.

METHODS

Organisms and Study Sites

We conducted this study in the summers of 1985 through 1987 near Sunset Crater National Monument, Flagstaff, Arizona (elevation, 2300 m). *Ipomopsis arizonica* (Polemoniaceae) grows at this site among stands of ponderosa pine, *Pinus ponderosa*, in soils largely consisting of volcanic cinder (68% of the mass per sample is made up of particles larger than 2 mm in diameter). *I. arizonica* is a monocarpic herb, closely related to *Ipomopsis aggregata* (Grant and Wilken 1986). The two species share similar flower color, vegetative form, and flowering pattern (see Paige and Whitham 1987a,b) but differ in habitat, size, average fruit production, and resource-allocation patterns (Maschinski and Paige, unpubl. data). *I. arizonica* has an indeterminate vegetative phase as a rosette but typically elongates and flowers in its second year from late June through late September. Plants usually die after flowering, but under conditions that may include extreme pollinator limitation, a few persist another year (see Paige and Whitham 1987b).

At Sunset Crater, approximately 45%–66% of the *I. arizonica* population is grazed by vertebrates such as rock squirrels (*Spermophilus variegatus grammurus*) and mule deer (*Odocoileus hemionus*). Rodent grazing occurs from January through September on rosettes, whereas deer herbivory occurs in the late spring and early summer on plants that have begun to elongate flowering stalks. Vertebrate herbivores commonly remove the tender young leaves and meristematic tissue of *I. arizonica*, leaving 5%–25% of the aboveground biomass intact. Such meristem removal induces a compensatory response by the plant, causing a single-stalked plant to produce two or more shoots from the base of the rosette within 2 wk after being grazed (Paige and Whitham 1987a). Severe herbivory on rosettes may delay flowering for 2 yr or more (Maschinski, pers. obs.). Multiple bouts of vertebrate herbivory are rare, but vertebrates occasionally remove meristems from the lateral shoots of grazed plants, causing *I. arizonica* to again compensate by producing multiple lateral branches along the entire length of a lateral shoot.

Experimental Design

Our experimental units (here, “triplets”) consisted of three independent rosettes of equal size growing within 1 m of each other. We selected 76 triplets in 1985, 92 triplets in 1986, and 80 triplets in 1987. Within each triplet, one rosette had previously been grazed by vertebrates, one was experimentally clipped at its base to simulate herbivory, and one received no treatment to serve as a control. Clipped plants had 95% of aboveground biomass removed. We estimated the size of each rosette by measuring the diameter of the basal stem. Because vertebrate herbivores graze plants in a wide range of size classes that were matched in size to ungrazed triplet members, grazed plants did not begin the experiment with a size advantage. All plants, including naturally grazed plants, were beginning to elongate flowering stalks at the time they were selected as triplet members. No triplet members were subterraneously connected.

We did not protect triplet members from subsequent herbivory by vertebrates or insects. In our 3-yr study, repeated bouts of vertebrate herbivory were rare. Although various insect herbivores feed on *I. arizonica* at Sunset Crater, insect herbivory did not significantly affect fruit set of the experimental plants in this study (Maschinski and Whitham, unpubl. data). (Compensatory responses to insect herbivory shall be covered elsewhere.)

To address how plant association interacted with vertebrate herbivory in affecting plant growth and reproduction, we selected triplets that were growing in proximity with other plant species. In 1985, 27 triplets were growing within 2 m of ponderosa pine (*Pinus ponderosa*), 29 triplets were growing within 10 cm of the bunchgrass *Muhlenbergia montana*, and 20 triplets were growing in the open (>10 cm from the root system of grasses and other herbaceous neighbors, >1 m beyond the dripline of a ponderosa pine) where potential interspecific competition could be eliminated as a variable. In 1986, we repeated the experiments by selecting 31 triplets near pines, 29 triplets growing with grass, and 32 triplets growing in the open. In 1987, we selected 20 triplets near pines, 29 triplets near grass, and 31 triplets growing in the open. Each year we attempted to get the largest sample size

possible. Differences in the numbers of triplets per group varied among years because of the limited availability of equally sized plants growing in each plant association.

To examine the interaction of water and nutrient levels with herbivory and/or plant association, we supplemented water and fertilizer to some triplets. We randomly assigned triplets growing in the three associations to one of three treatments: (1) water and fertilizer, (2) water, or (3) control (no water or fertilizer). From June 1 through July 31, 1985, and from June 14 through August 9, 1986, treatment plants weekly received 250 ml of water or 250 ml of 0.02 M solution of Peter's Professional fertilizer T (20-20-20). In 1987, we omitted the water treatment but fertilized plants from May 2 through July 18.

From August 27 through September 15, we counted total fruit set. In 1985 and 1986, we weighed and counted the number of seeds per fruit from the three most mature fruits from each triplet member. We eliminated plants that had only immature, damaged, or dehiscent fruit from the seed analysis. We assessed whole-plot differences between triplets using an analysis of covariance (ANCOVA) with two treatment factors (plant association and nutrient treatment), one blocking factor (year), and one nested factor (grazing level: ungrazed, grazed, or clipped) (Snedecor and Cochran 1980). Basal-stem diameter, our size estimate, was a covariate to adjust for the effects of plant size on yield. We adjusted alpha levels for the three variables measured using a Bonferroni adjustment.

To make multiple comparisons of whole-plot plant association, nutrient treatment, and timing of herbivory groups, we used a Student-Newman-Keuls test (Zar 1984). First, we determined whether fruit set differed across the three plant associations and across the three nutrient groups. In addition, to determine whether compensatory ability was influenced by plant association and nutrient availability, we compared within-triplet fruit set of grazed and clipped plants with that of ungrazed plants in each of the nine combinations of plant association and nutrient treatment, using a one-tailed Dunnett's test (Zar 1984).

To determine how early- and late-season herbivory influenced fruit set and compensatory ability, we examined between-year differences and within-year differences of clipped-plant response. Each year we compared the fruit set of clipped plants, for which we knew the exact time and intensity of herbivory, with the fruit set of ungrazed and naturally grazed plants that were grazed approximately 1–8 mo earlier than clipped plants. For 3 yr we simulated herbivory, removing 95% of aboveground biomass on dates that reflect the range in the timing of natural herbivory. In 1985, we clipped plants on May 30; in 1986, on June 12; and in 1987, on May 2. Because clipped plants had an architecture indistinguishable from naturally grazed plants, clipping accurately reflected the intensity of natural herbivory. Comparison across years of the performance of clipped plants with that of naturally grazed plants reflects the effect of differential timing, rather than the intensity, of herbivory.

Because approximately 18% of the natural population is grazed as late as July, we implemented a second experiment in 1986 to measure within-year response to early- and late-season clipping and to determine whether the effects of late-season

TABLE 1
ANALYSES OF COVARIANCE OF COMPENSATION IN *IPOMOPSIS ARIZONICA*

Source of Variation	df	Fruit Set ^a	Seeds/ Fruit	Seed Weight (mg)
Plant association	2	65677*	17.95	25.5
Nutrient treatment	2	492983****	63.99	21
Plant association × Nutrient treatment	4	39475	41.82	64
Stem diameter ^b	1	795821****	92.53	25
Year	2/1	574610****	0.11	—
Error ^c	236/71/50	14648	25.49	50
Grazing level	2	28422**	59.15	1.08
Grazing × Plant association	4	7624	12.87	1.42
Grazing × Nutrient treatment	4	3990	8.99	0.96
Grazing × Plant association × Nutrient treatment	8	5550	3.96	0.8
Error ^c	478/146/100	5057	18.28	2

NOTE.—Mean squares of ANCOVA's for fruit set, seeds per fruit, and seed weight are reported.

^a *P* values are of the *F* ratios. Alpha levels reflect Bonferroni adjustment.

^b Covariate.

^c For the three characters, respectively.

* *P* < 0.05.

** *P* < 0.01.

**** *P* < 0.0001.

herbivory could be overcome by nutrient supplements. Using a 2 × 2 factorial design, we imposed two different times of herbivory and two different fertilizer treatments on 110 ungrazed plants. We clipped 24 plants on June 12 to simulate early-season herbivory and fertilized them weekly until August 27. We clipped 31 plants on July 24 to simulate late-season herbivory and fertilized them weekly. For control plants, 53 received no fertilizer but were clipped on the same dates as the fertilized groups. On September 11, we counted the total numbers of fruits and flowers each plant produced. We analyzed these data using a two-way ANCOVA with stem diameter as the covariate.

RESULTS

Fruit Set as a Measure of Plant Fitness

Fruit quality as measured by the numbers of seeds per fruit and seed weight (table 1) did not vary in response to plant association ($F = 0.70$, $P = 0.49$; $F = 0.51$, $P = 0.60$, respectively) or nutrient treatment ($F = 2.51$, $P = 0.09$; $F = 0.41$, $P = 0.66$, respectively). Similarly, neither natural nor simulated herbivory affected the number of seeds produced per fruit or seed weight ($F = 3.28$, $P = 0.12$; $F = 0.54$, $P = 0.58$, respectively; see also table 2). Therefore, fruit set of *Ipomopsis arizonica* effectively reflects relative plant fitness (as was found in Paige and Whitham 1987a for *I. aggregata*) and provides our basis for comparison of plant performance in the discussion that follows.

TABLE 2
FRUIT SET AND SEED CHARACTERS OF THREE GRAZING LEVELS

CHARACTER*	GRAZING LEVEL		
	Ungrazed	Vertebrate-Grazed	Clipped
1985			
Fruit set (60)	40.7 ± 3.9 ^a	37.4 ± 3.9 ^a	24.5 ± 3.9 ^b
Seeds/fruit (23)	10.8 ± 2.5 ^a	10.0 ± 2.5 ^a	8.7 ± 2.5 ^a
1986			
Fruit set (88)	75.1 ± 5.2 ^a	74.6 ± 5.2 ^a	50.1 ± 5.2 ^b
Seeds/fruit (59)	11.4 ± 1.9 ^a	11.1 ± 1.9 ^a	9.8 ± 1.9 ^a
Seed mass, in mg (59)	9.7 ± 1.0 ^a	8.9 ± 1.0 ^a	9.6 ± 1.0 ^a
1987			
Fruit set (97)	157.3 ± 11.4 ^a	167.5 ± 11.4 ^a	138.6 ± 11.4 ^a

NOTE.—Values are means ± one standard error. Different letters within a row indicate significant differences as measured by the Student-Newman-Keuls test ($P < 0.05$).

* Sample size is in parentheses.

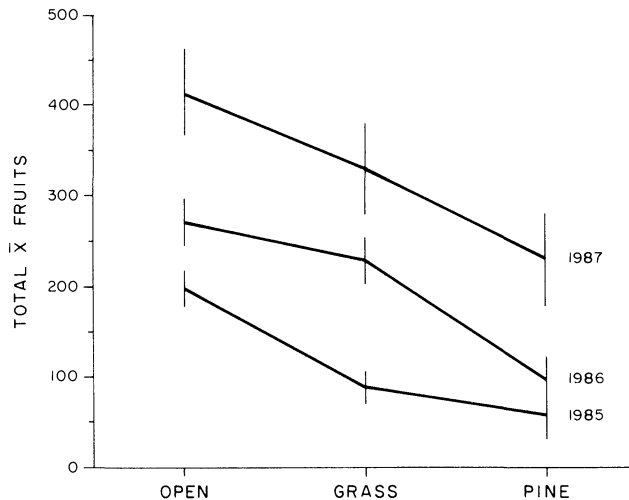


FIG. 1.—Comparison of total fruit set ($\bar{X} + 1$ SE) across three plant associations. Analysis of covariance indicates that plant association significantly affected fruit set ($F = 4.48$, $P = 0.03$ after Bonferroni adjustment). All pair-wise differences are significant for all years as measured by Student-Newman-Keuls test ($P < 0.05$).

Influence of Plant Association and Nutrient Treatment on Fruit Set

Both plant association and nutrient availability influenced the overall performance of *I. arizonica*. Before these factors could be examined for their impact on compensatory growth, we first examined how each individually affected relative plant fitness.

The association of *I. arizonica* with other plants significantly decreased fruit set ($F = 4.48$, $P = 0.03$; table 1; fig. 1). In all three years, plants growing in the

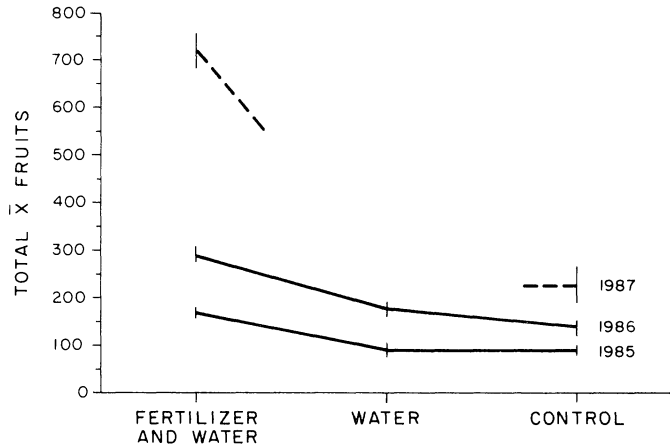


FIG. 2.—Comparison of total fruit set ($\bar{X} \pm 1$ SE) across the three nutrient treatments. Analysis of covariance indicates that treatment significantly influenced fruit set ($F = 33.66$, $P < 0.0001$). In 1985 through 1987, the differences between the fertilized group and the two other groups are significant (Student-Newman-Keuls test, $P < 0.05$). In 1985 and 1986, the water-treatment and control groups are not significantly different (SNK, $P > 0.05$). Water treatment was eliminated in 1987.

TABLE 3

PRECIPITATION IN MAY AND JUNE AT SUNSET CRATER NATIONAL MONUMENT, IN MILLIMETERS

Year	May	June	Total
1985	0.625	0.200	0.825
1986	1.075	1.950	3.025
1987	2.575	1.725	4.300

open set the highest numbers of fruit, plants growing with grasses set intermediate levels of fruit, and plants growing near ponderosa pine set the fewest fruits (e.g., 1985 open $\bar{X} = 197$, 1985 grass $\bar{X} = 94$, 1985 pine $\bar{X} = 62$; fig. 1).

Nutrient treatment significantly affected fruit set in all three years ($F = 33.66$, $P < 0.0001$; table 1; fig. 2). Triplets treated with fertilizer solution set significantly more fruits than either water-treated plants or controls (1985 fertilizer $\bar{X} = 160$, 1985 water $\bar{X} = 96$, 1985 control $\bar{X} = 97$; 1986 fertilizer $\bar{X} = 292$, 1986 water $\bar{X} = 165$, 1986 control $\bar{X} = 143$; 1987 fertilizer $\bar{X} = 742$, 1987 control $\bar{X} = 239$; $P < 0.05$ for all comparisons; fig. 2). Water treatment alone did not significantly increase fruit set in 1985 or 1986 (fig. 2).

In addition, average fruit set within a plant association or nutrient treatment significantly increased over the 3-yr period of this study ($F = 39.23$, $P < 0.0001$; table 1; figs. 1, 2). This year-to-year variation in fruit set coincides with the increased May–June precipitation from 1985 to 1987 (table 3). Since *I. arizonica* elongates and sets flower buds in May and June, precipitation during this period may be critical to ultimate fruit set for the season. For example, the fruit set of

TABLE 4
ANALYSIS OF COVARIANCE FOR FRUIT SET OF PLANTS RECEIVING
EARLY- AND LATE-SEASON HERBIVORY WITH AND WITHOUT
FERTILIZER SUPPLEMENTS

Source	df	Mean Square	F	P
Fertilizer	1	15869	16.09	0.0001
Time of clip	1	21620	21.92	0.00001
Fertilizer \times Time	1	5664	5.74	0.018
Diameter	1	21945	22.25	0.00001
Error	103	986		

plants growing in association with grass was 60% greater in 1986 than in 1985. Corresponding with this increase in fruit set in 1986 was a 70% increase in May–June rainfall. In 1987, the 32% increase in fruit set by plants associated with grass over the preceding year corresponded with a 28% increase in May–June rainfall.

Comparison of Grazed and Clipped Plants with Ungrazed Controls

In all three years, naturally grazed plants compensated equally, producing just as many fruits as ungrazed plants (table 2). However, differences in the degree of clipped-plant compensation varied according to the time of year of clipping. In 1985 and 1986, plants clipped in late May or mid-June undercompensated, producing significantly fewer fruits than ungrazed plants (table 2; 1985 ungrazed \bar{X} = 40.7, 1985 clipped \bar{X} = 24.5, q = 4.14, P < 0.05; 1986 ungrazed \bar{X} = 75.1, 1986 clipped \bar{X} = 50.1, q = 4.84, P < 0.05). However, in 1987, when plants were clipped in early May, there were no significant differences between the fruit set by ungrazed, grazed, or clipped plants (1987 ungrazed \bar{X} = 157.3; 1987 grazed \bar{X} = 167.5, q = 1.28, P > 0.05; 1987 clipped \bar{X} = 138.6, q = 1.79, P > 0.05). Therefore, a 3-wk difference in the timing of herbivory can affect whether a plant compensates equally or undercompensates for herbivory.

Our 1986 within-year clipping experiment further substantiates this finding (table 4). Plants clipped early in the season set greater numbers of fruits than plants clipped later in the season (controls, early-clipped \bar{X} = 32.9 vs. late-clipped \bar{X} = 18.0, q' = 5.18, P < 0.05; fertilized, early-clipped \bar{X} = 72.7 vs. late-clipped \bar{X} = 28.5, q' = 1.69, P < 0.01). Fertilizer supplements overcame the effects of late-season herbivory: plants fertilized and clipped late set the same numbers of fruits as control plants clipped early (28.5 vs. 32.9, q' = 0.50, P > 0.05). Thus, the timing of herbivory interacts with nutrient treatment to determine the degree to which plants can recover from herbivory.

Compensatory Response to Herbivory as a Function of Plant Association and Nutrients

The compensatory response of *I. arizonica* varied with plant association and nutrient treatment (fig. 3). In all 3 yr, the most common response to herbivory was equal compensation. All pine groups and all watered groups showed equal compensation across years, as did the grass-fertilized group.

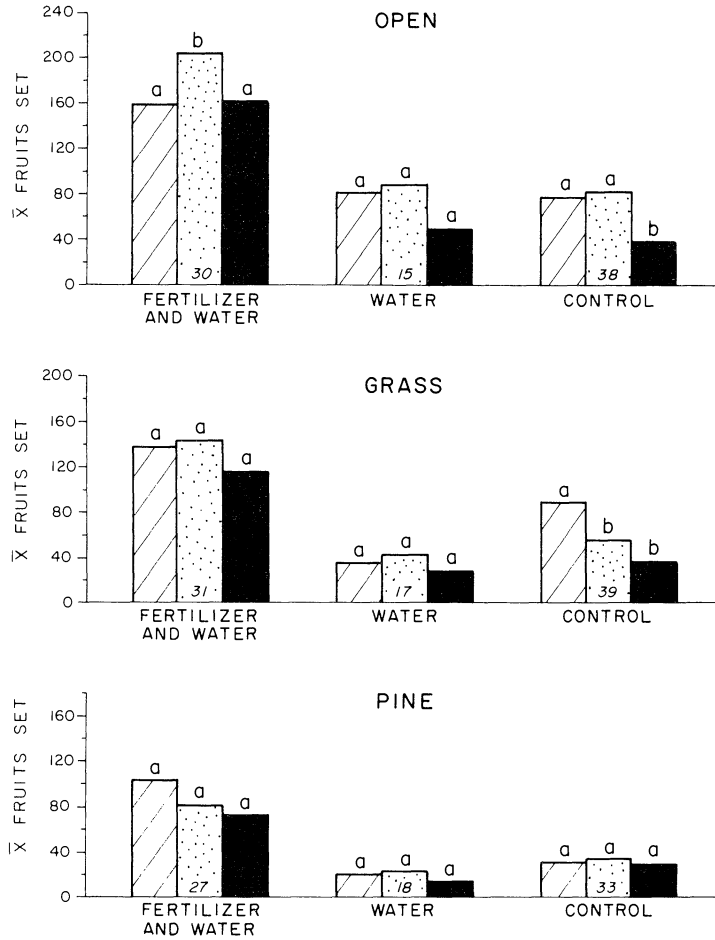


Fig. 3.—Comparison of mean triplet fruit set averaged across 1985, 1986, and 1987 (years are averaged for illustrative purposes only). Statistics were performed with year as a blocking factor. Significant differences between ungrazed plants and the grazed or clipped plants, determined using one-tailed Dunnett's tests, are indicated with letters above the columns. Sample sizes are indicated at the bottom of grazed columns. *Hatching*, Ungrazed; *stippling*, naturally grazed; *solid*, clipped.

When we examined the 3-yr average of compensatory responses, there were several notable exceptions to this pattern of equal compensation: undercompensation occurred in control groups for both open and grass associations; and overcompensation occurred in the open-fertilized group (fig. 3).

The year-to-year variation in compensatory responses further supports this pattern of a compensatory continuum. The five plant-association-nutrient-treatment groups that showed year-to-year variation are summarized in table 5. An association with grass decreased the chances of compensation for herbivory regardless of whether nutrients were supplemented to the *I. arizonica* plants growing in this association. Clipped plants undercompensated in the 1985 grass-

TABLE 5
 COMPENSATORY RESPONSES FOR NUTRIENT-TREATMENT-PLANT-ASSOCIATION GROUPS
 WITH YEAR-TO-YEAR VARIATION

NUTRIENT TREATMENT AND PLANT ASSOCIATION*	N†	YEAR	GRAZING LEVEL‡		
			Ungrazed	Grazed	Clipped
Open-fertilized	5	1985	63 ± 13.5	139 ± 13.5+	55 ± 13.5
	10	1986	148 ± 15.3	137 ± 15.3	106 ± 15.3
	15	1987	269 ± 18.5	359 ± 18.5+	330 ± 18.5+
Open-watered	5	1985	69 ± 13.5	56 ± 13.5	30 ± 13.5-
	10	1986	93 ± 15.3	119 ± 15.3	69 ± 15.3
Open-control	10	1985	78 ± 13.5	80 ± 13.5	23 ± 13.5-
	12	1986	60 ± 15.3	45 ± 15.3	33 ± 15.3
	16	1987	100 ± 18.5	119 ± 18.5	61 ± 18.5-
Grass-fertilized	7	1985	66 ± 11.4	36 ± 11.4	22 ± 11.4-
	10	1986	107 ± 15.3	122 ± 15.3	94 ± 15.3
	14	1987	250 ± 19.2	262 ± 19.2	237 ± 19.2
Grass-control	15	1985	41 ± 11.4	21 ± 11.4	21 ± 11.4
	9	1986	119 ± 15.3	59 ± 15.3-	33 ± 15.3-
	15	1987	109 ± 19.2	89 ± 19.2	60 ± 19.2-

NOTE.—Values are means ± one standard error.

* Groups not reported here had equal compensation across all three grazing levels in all three years.

† N, Sample size.

‡ , +, Significant overcompensation in comparison with ungrazed plant within the same nutrient-treatment-plant-association group; -, significant undercompensation. Numbers without symbols do not differ significantly as measured by one-tailed Dunnett's test, $\alpha = 0.05$.

fertilized group (ungrazed vs. clipped $q' = 2.27$, $P < 0.05$) and in the 1987 grass-control group (ungrazed vs. clipped $q' = 2.49$, $P < 0.05$). Both grazed and clipped plants in the grass-control group undercompensated in 1986 (ungrazed vs. grazed $q' = 3.06$, $P < 0.05$; ungrazed vs. clipped $q' = 4.44$, $P < 0.05$).

Plants clipped late in the growing season had a greater probability of undercompensating if nutrients were not supplemented. Clipped plants in the 1985 open-watered and the 1985 and 1987 open-control groups set significantly less fruit than controls (table 5; $q' = 2.01$, $P < 0.05$; $q' = 2.81$, $P < 0.05$; $q' = 2.95$, $P < 0.05$, respectively). Thus, cases of undercompensation were seen either when nutrients were absent or when neighbors were present.

At the opposite end of the spectrum, there were three cases of nutrient-dependent overcompensation (table 5). In 1985, naturally grazed plants in the open-fertilized group significantly overcompensated in response to herbivory, producing 2.2 times as many fruits as control, ungrazed plants ($q' = 3.93$, $P < 0.05$). The same pattern occurred in the 1987 open-fertilized group: naturally grazed plants produced 33% more fruit than ungrazed controls ($q' = 4.65$, $P < 0.05$). In addition, clipped plants in this group produced 23% more fruit than controls ($q' = 3.15$, $P < 0.05$). In 1986, this pattern of overcompensation was absent, possibly because of the increased vigor of ungrazed, control plants ($q' = 0.57$, $P > 0.05$). Thus, the interaction of weather, timing of herbivory, and the competitive and nutrient conditions faced by an individual plant determined the degree to which *I. arizonica* could compensate.

DISCUSSION

The controversy over the impact herbivores have on plants has thus far been centered around a deterministic or fixed-response approach to examining compensation (but see McNaughton 1983, fig. 1). The concern has been *whether* or not plants compensate rather than *when* plants compensate.

The response of *Ipomopsis arizonica* to herbivory in this study demonstrates the plasticity of compensatory growth within a single species. Rather than exhibiting a constant response, *I. arizonica* responds variably to different plant associations, nutrient regimens, and timing of herbivory. Depending on these variables, our experiments resulted in all three possible compensatory outcomes. Herbivory can benefit the plant, it can be of no consequence because the plant replaces tissue lost to herbivores, or it can be detrimental to the plant. Here we discuss the conditions that lead to this range of compensatory responses and propose a model to illustrate them.

Neutral to Negative Effects of Herbivory—The Range of Natural Responses

The most common response to natural levels of herbivory was equal compensation; 80% of the population compensated equally in response to natural herbivory (fig. 3). Conversely, 16% of plants studied undercompensated; all were growing in association with grasses. Thus, under natural conditions, the responses along the compensatory continuum that *I. arizonica* experienced ranged from neutral to negative. Overcompensation did not occur naturally; this response required nutrient supplementation.

By surveying the levels of herbivory and the distribution of *I. arizonica* in the natural population, we estimated the percentages of plants likely to equally compensate or undercompensate within a given year. In the 3 yr during which we studied this population, herbivory levels varied across years and there was no geographical area or plant-association group that was consistently or selectively grazed by the herbivores. For example, in 1987, approximately 50% of the plants growing in the open and in association with grasses were naturally grazed, whereas only 23% of the plants growing near pines were grazed. In contrast, herbivory levels in 1986 for plants growing in the open and in association with pines were 68% and 63%, respectively.

Because grass and open habitats are relatively more abundant than pines at Sunset Crater, it is most common to find *I. arizonica* growing in these associations. Roughly 80% of the plants are evenly distributed between grass associations and open habitats and 20% are found growing near pines. Assuming that 40% of the total population is growing with grasses and that 50% of these plants are grazed, we estimated that 20% of the plants in the entire population would undercompensate for herbivory in any year and that 80% would compensate equally.

Positive Effects of Herbivory—Experimental Extension of the Response

Nutrient supplementation extended the range in the compensatory responses of *I. arizonica* to include overcompensation. In 1985 and 1987, for triplets growing

without competition and with supplemented nutrients, naturally grazed plants set from 33% to 120% more fruit than ungrazed controls (table 5). In 1987, clipped plants produced 27% more fruit than controls. Because the number of seeds per fruit produced by grazed or clipped plants in comparison with ungrazed plants did not differ significantly, the increased fruit set represents a real increase in relative fitness (similar to that reported in Paige and Whitham 1987a for *I. aggregata*). In a separate study conducted in 1985, 40 grazed *I. arizonica* plants growing in the open and supplemented with fertilizer overcompensated for herbivory, producing up to 53% more fruit than 40 ungrazed controls (Maschinski and Paige, unpubl. data). Although overcompensation in *I. arizonica* required nutrient supplements in the nutrient-poor soils of Sunset Crater, overcompensation can occur naturally, as was described for *I. aggregata* (Paige and Whitham 1987a). This suggests that the compensatory response of *I. aggregata* is not limited by nutrients at the sites they studied.

Nutrient-dependent compensation has been reported in other species (Julien and Bourne 1986; Verkaar et al. 1986); however, these studies reported increased biomass rather than increased propagule production. Benner (1988) has reported greater fruit production by early-season clipped and nutrient-treated *Thlaspi arvense*; however, total seed weight per plant was less for clipped than for control plants.

Factors Influencing the Degree of Compensation

Our studies indicate that for any compensation to occur, physiological constraints on compensatory growth must be overcome and adequate abiotic and biotic conditions must exist. Conversely, limitations on the degree of compensatory response correspond to factors that limit plant growth in general.

Of the three external factors we investigated, timing of herbivory appears to most strongly influence the degree to which *I. arizonica* compensates for herbivory. We found that plants grazed early in the season produced, on the average, equal (but not greater) numbers of fruits compared with ungrazed plants. Plants clipped later in the season (after May 30) produced significantly fewer fruits than did ungrazed plants. Thus, *I. arizonica* was able to compensate equally for herbivory so long as grazing occurred early in the season. Physiological changes within the plant over the course of the growing season, as well as the length of time remaining in the growing season, can regulate the degree to which a plant compensates for herbivory (Crawley 1983). Once a plant is established beyond the seedling stage, young tissue is more readily replaced than mature tissue.

Nutrient availability interacts with the timing of herbivory to influence the degree of compensation. At the beginning of the growing season, nutrient flushes, which most plants experience, can facilitate maximum nutrient uptake and allow recovery from herbivory (Chapin 1980), whereas plants grazed later in the season are likely to suffer from lower nutrient availability, delayed phenological status, and shorter growing season. If nutrients are supplemented to *I. arizonica* plants clipped late in the season (July), plants can compensate to the same degree as plants clipped earlier in the season. Thus, nutrient supplementation can overcome the negative effects of late-season herbivory.

Competition with neighbors also affects the degree of compensation in *I. arizonica*. In general, association with grasses and pines diminished fruit set; however, only association with grasses significantly reduced the ability to compensate for vertebrate herbivory (fig. 3). Undercompensation occurred most often in plants that were clipped late in the season and were growing under low-nutrient conditions in association with grasses. As has been shown by other workers, competition with other plants can increase the degree of damage done by herbivores (Harper 1977; Bentley and Whittaker 1979; Fowler and Rausher 1985). For example, competition decreased biomass replacement and flower production in *Festuca idahoensis* and *Agropyron spicatum* (Mueggler 1970, 1972).

Although our studies suggest that nutrient availability and potential nutrient competition more strongly influence compensatory response than does competition for light, the relative importance of nutrient availability and plant association on compensatory growth requires further investigation, since the potential interactive effects of the two make it difficult to establish their individual impact on the degree of compensation.

A final requirement for compensation in *I. arizonica* is that the herbivore must consume meristematic tissue in order to remove apical dominance and induce lateral-stem growth. Here we show that *I. arizonica* can compensate from meristem feeding by vertebrates. *I. aggregata* plants grazed by vertebrates have been shown to respond by developing several lateral shoots, each of which produced flowers (Paige and Whitham 1987a). Plants can also compensate for loss of tissues other than meristems; however, replacement of these tissues again depends upon disruption of apical dominance, which allows bud development (Crawley 1983; Mariko and Hogetsu 1987). Because all compensatory growth in *I. arizonica* is constrained by apical dominance, the ungrazed growth form persists. Studies in progress suggest that the upright ungrazed growth form may survive better than the grazed bushy growth form under stressed conditions.

The Compensatory Continuum: Is Compensation Predictable?

The intraspecific gradient of compensatory responses we present is determined by the presence or absence of neighbors, the availability of nutrients, and the length of time a plant has to recover from a grazing event. Using data from 3 yr of observation, we have modeled the probability of compensating from early- and late-season herbivory for plants growing under varying nutrient and competitive regimes (fig. 4). Our model illustrates that the degree to which a plant can compensate for herbivory decreases as competition increases, as nutrient availability decreases, and as the timing of the herbivory comes later in the growing season. For our model, we have assumed a single bout of herbivory on tissue that disrupts apical dominance. In agreement with Belsky's (1986, 1987) suggestion, we would predict that under conditions of high nutrient availability, low competition, and early-season herbivory, a plant would overcompensate for herbivory. Plants grazed early in the season have the greatest probability of equal compensation, but under low-nutrient and highly competitive regimes, undercompensation is most probable.

Alternatively, late-season herbivory most often results in undercompensation,

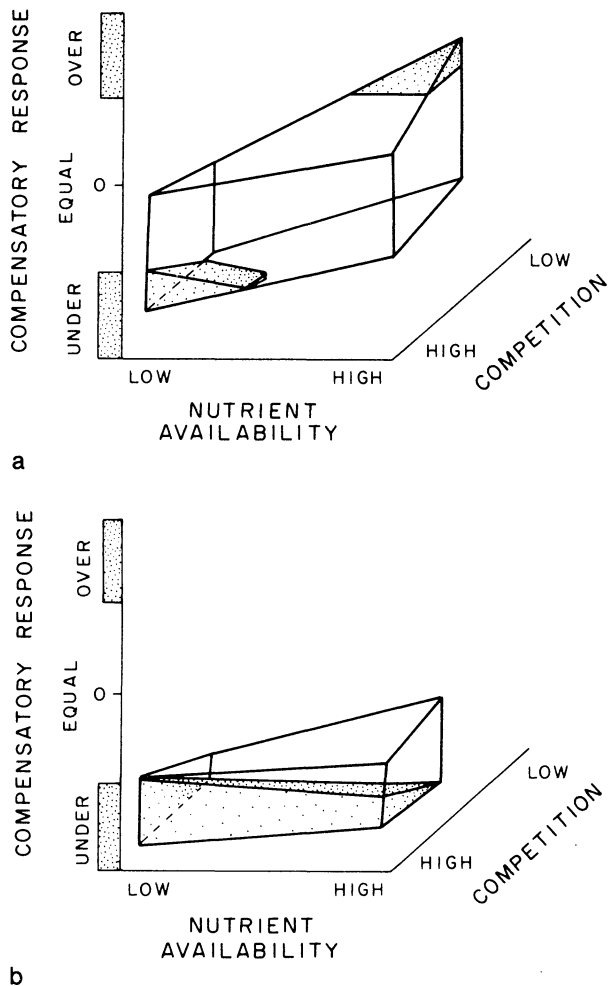


FIG. 4.—Graphic model of probable compensatory response when nutrient availability and competition are taken into account: *a*, with early-season herbivory; *b*, with late-season herbivory. *Stippling*, Overcompensation or undercompensation. Model surface is derived from 3 yr of data summarized in figure 3.

especially for plants growing in nutrient-poor soils with competitors (fig. 4*b*). The probability of equal compensation for plants grazed late in the growing season increases as nutrient and competitive conditions become more favorable (fig. 4*b*).

The degree of compensatory response depends on the strength of the external factors, either singly or in combination. For example, if nutrients are severely limited, it is likely that a plant will undercompensate regardless of the presence of competitors. Within the range of the *I. arizonica* distribution at Sunset Crater, nutrients such as potassium, nitrogen, and phosphorus can vary as much as four-fold (Maschinski, unpubl. data). Plants growing close to the cinder crater, where cinder particles larger than 2 mm in diameter constitute 95% of the soil, would not

be expected to compensate equally because of nutrient and water limitations. Similarly, if competition is severe, plants will probably undercompensate, regardless of nutrient abundance. Because any combination of these factors can occur in a single population, as we have described here, a continuum of compensation is possible and probable.

Although our model is derived from our observations of a single species, it may also be applicable across species. For example, on a population average, *I. aggregata* growing under favorable nutrient and moisture regimes overcompensates for vertebrate herbivory (Paige and Whitham 1987a), whereas *I. arizonica*, growing under more-severe conditions, compensates equally. Soil nutrients between sites where these two species grow can vary 10-fold (Maschinski, unpubl. data). We are investigating whether the differences in the average responses of these two species directly relate to their respective nutrient regimes or their genomes.

Interspecific compensatory responses are also affected by differences in growth form (Archer and Tieszen 1980), life-history strategy (Hendrix 1979; Marshall et al. 1985), carbon-allocation patterns (Ryle and Powell 1975; Coughenour et al. 1985), photosynthetic rate (Archer and Tieszen 1980; Caldwell et al. 1981; Heichel and Turner 1983; Parsons et al. 1983; Wallace et al. 1984; Richards and Caldwell 1985), growth rate (Caldwell et al. 1981), plant integration, and meristem limitations (Richards and Caldwell 1985; Whitham et al., in press). Biennial species, such as *I. aggregata* and *I. arizonica*, which grow quickly and have carbohydrate reserves, may be particularly adept at compensating for herbivory, whereas long-lived slow-growing conifers may be incapable of much, if any, compensation within a single growing season (see, e.g., Whitham and Mopper 1985). Application of our model to an interspecific continuum of compensation must take into account these morphological and physiological factors and is beyond the scope of this paper.

CONCLUSIONS

Our studies demonstrate that the degree to which a plant compensates for herbivory will vary according to local conditions. Most previous work on compensation has described compensation as a constant species-specific response without regard to the conditions influencing a plant's physiological status. Our work shows that plants have variable compensatory responses within a single population and locality; therefore, future studies on compensation should consider microsite factors that influence overall plant status and subsequent compensatory ability. Overlooking microsite differences may mask a variation in population responses to herbivory.

The probability of compensating for herbivory to any degree is governed by external factors. We have documented that a gradient of intraspecific compensatory responses results from the presence or absence of neighbors, availability of nutrients, and length of time a plant has to recover from a grazing event. In our view, the probability that a plant will compensate for herbivory decreases as competition with neighbors increases, as nutrient availability decreases, and as

the timing of the herbivory comes later in the growing season. The interaction of these three factors with weather can govern the impact an herbivore has on a plant.

SUMMARY

In a single population of *Ipomopsis arizonica* (Polemoniaceae), we show a continuum of compensatory responses to vertebrate herbivory. We demonstrate experimentally that the degree of herbivore impact depends on plant association, nutrient availability, and timing of grazing. From 1985 to 1987, the most common response to vertebrate herbivory was equal compensation, whereby grazed plants set numbers of fruits and seeds equal to controls within the same growing season. However, we also observed cases of significant overcompensation and undercompensation. In 1985 and 1987, overcompensation occurred in vertebrate-grazed plants that were supplemented with nutrients and growing free of competition. These plants produced 33% to 120% more fruit than control, ungrazed plants. Cases of undercompensation occurred in groups where *I. arizonica* grew in association with grasses or where nutrients were not supplemented. Grazed and clipped plants in these groups produced from 28% to 82% as many fruits as did ungrazed controls.

Our studies indicate that the compensatory response of plants to grazing is probabilistic when three external factors are considered. The probability of compensation for herbivory decreases as competition with other plants increases, as nutrient levels decrease, and as the timing of herbivory comes later in the growing season.

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