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DETERMINING THE EFFECTS OF HERBIVORY USING NATURALLY DAMAGED PLANTS¹

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Much recent work has addressed the possibility that herbivory may be beneficial to plants (Wallace et al. 1985, Belsky 1986, McNaughton 1986, Paige and Whitham 1987). The true effects of herbivory can be difficult to assess, however, especially when plants damaged naturally are used to quantify these effects (Neuvonen and Haukioja 1985). In some studies, effects of herbivory are estimated only with simulated herbivory treatments; no naturally damaged plants are used in statistical comparisons (Edwards 1985, Paige and Whitham 1987). Implicit in this approach may be the authors' recognition that herbivores discriminate intraspecifically among host plants (Inouye 1982, Fox and Bryant 1984, Kinsman and Platt 1984, Edwards 1985, Danell et al. 1985a). In this note, I discuss methods used to measure the effects of browsing herbivores, because randomly assigned natural herbivory is difficult to obtain in these systems.

When treatments are compared through statistical analysis, plant individuals within treatments are assumed to be a random sample of a single population. For example, if growth and reproduction are compared between browsed and unbrowsed plants, and if the resulting difference, or lack thereof, is ascribed to the effects of browsing, then the underlying assumption is that herbivores browse randomly. However, since herbivores discriminate among plants, herbivore selectivity is confounded with effects of damage. This confounding can obscure the interpretation of results when naturally damaged plants are compared to controls without data on plants prior to damage (Krefling et al. 1966, Jacobs 1969, Wolff 1978, Boscher 1979, Inouye 1982). The same situation exists more subtly in experiments using large exclosures. A random sample of undamaged plants in exclosures cannot be compared to a random sample of damaged plants outside the exclosure unless all plants outside are damaged. (This assumes plants inside and out do not differ in the traits measured prior to damage.)

One way to circumvent the bias of selective herbivory is to assign herbivory randomly (1) by simulating herbivory (but see Capinera and Roltsch 1980, Havlickova 1982, Howe et al. 1982), (2) by coercing a tame animal to eat randomly selected plants, or (3) by caging

smaller herbivores on randomly selected plants. Comparisons between simulated damage and natural damage are valid only when plant size or other traits are the same in both groups prior to damage (e.g., Danell et al. 1985b). If plants treated with simulated herbivory are chosen from the pool of plants remaining undamaged by herbivores, these plants can be correctly compared only to controls randomly selected from the same population of undamaged plants (as in Paige and Whitham 1987). Measurement of plant attributes prior to browsing can indicate when naturally damaged plants represent an unbiased sample for comparison with those left intact.

I examined browsing patterns of deer, *Odocoileus virginianus*, on smooth sumac, *Rhus glabra*, to determine at what level deer discriminate among plants. I measured ramet growth prior to winter browsing and then compared plants selected by herbivores to those not selected. To determine whether herbivores choose plants nonrandomly with respect to these traits, I recorded shoot width(s) at the base of each shoot after the growing season in 1986. In the early spring of 1987, after winter browsing, I recorded which shoots and which ramets had been browsed. At the end of the summer growing season in 1987, I measured shoot width again, as well as seed production. I did not measure belowground biomass because plants could not be destructively sampled. In comparing growth of browsed and unbrowsed ramets after browsing, I assume either negligible nutrient transfer between ramets, or equal transfer among browsed and intact ramets. Using these data, I ask the following questions: (1) Do deer browse a random sample (based on size) of ramets available? (2) Do deer discriminate *within* ramets with respect to the shoots eaten? (3) Is browsing clumped on individual ramets? (4) Do browsed ramets and shoots within ramets grow/reproduce more than intact ramets in the season after browsing?

I compared mean pre-browse shoot widths of ramets that were subsequently browsed or left unbrowsed. In this comparison, I used only ramets in which all shoots were either browsed ($n = 25$) or intact ($n = 9$) (Table 1a). Mean shoot width before browsing was significantly greater in browsed than intact ramets.

To address whether deer chose larger shoots within ramets, I examined ramets where some, but not all, shoots were browsed. Within each ramet, I compared pre-browse median shoot widths of browsed and unbrowsed shoots and scored which width was greater. In 19 of 22 cases, browsed shoots were larger than unbrowsed ones ($P < .003$, Sign Test; Table 1b).

Finally, to determine if deer respond to ramet qualities other than shoot size or, more specifically, if browsed shoots were clumped on ramets, I sorted all 51 ramets into classes based on number of shoots and

randomly assigned browsing to shoots. I next calculated the overall variance in the percentage of shoots browsed (within ramets) for these 51 randomly browsed ramets. The simulation was run 500 times to generate a distribution of variances to which I could compare the observed variance in percentage of shoots browsed within ramets. If deer tended to browse shoots within ramets as a result of some inherent ramet property (e.g., tissue nitrogen or secondary chemistry), then the observed overall variance should exceed expected (more ramets would have 100% or 0% of their shoots browsed than expected by chance alone). The observed variance in percent shoots browsed fell near the upper end of the generated distribution at the $P = .07$ tail (one-tailed test). Although there is a trend for browsed shoots to be clumped on individual ramets, shoot size influences probability of being browsed more than ramet identity does.

Measurements of browsed and unbrowsed ramets the following growing season revealed that browsed plants, which were initially larger, produced individual shoots that were, on average, significantly larger than those on unbrowsed plants (Table 2). In addition, total shoot width produced was significantly greater for browsed ramets than for unbrowsed ones. This difference was not due to increased numbers of shoots, because browsed and unbrowsed plants had the same number of shoots. Within ramets browsed shoots grew more than unbrowsed shoots, although this trend was only marginally significant ($P = .07$; one-tailed Sign Test). The proportion of plants producing seed was greater in browsed plants (32%) than in unbrowsed plants (11%, or one of nine); however, owing to small sample size, this effect cannot be reliably tested.

If the effect of winter browsing (which occurs during a physiologically quiescent time for plants) is small, then differences in growth between browsed and unbrowsed ramets may reflect initial size and not the effects of browse. In the absence of browse, total growth

TABLE 1. Plant sizes before browsing in late summer 1986.

a. Shoot width/ramet in centimetres (before browsing)		
	Browsed in winter 1986-1987 (n = 25 ramets)	Intact 1986-1987 (n = 9 ramets)
Mean	0.85	0.64
Median	0.84	0.69
Wilcoxon Rank Sum test: $H' = 518, P = .002$		
b. Median ranks of browsed and unbrowsed shoots within ramets (n = 22 ramets*) (1 is rank of largest shoot; all sizes before browsing)		
	Browsed	Unbrowsed
Ramets with two shoots	1 1 1 1 1 1 1 1 2	2 2 2 2 2 2 2 1
Ramets with three shoots	1 1 1.5 1.5 1.5 1.5 3	2.5 2.5 2.25 3 3 3 1.5
Ramets with four shoots	2 2 2 4	4 4 3 2
Ramets with five shoots	1.5 1.5	4 4
Ramet with six shoots	2.5	4.5

* Five ramets browsed in 1984-1985 were included in the within-ramet comparison of browsed vs. unbrowsed shoots.

of protected plants was significantly correlated between years ($n = 25, r = 0.761, df = 23; P < .01$).

Deer selectivity and beneficial effects of browse could function simultaneously. For example, Paige and

TABLE 2. Growth and reproduction of ramets in the season after browsing.

	Median total shoot growth* (cm)	Median shoot width (cm)	Median no. shoots	Median total seed mass (g)	Median seed mass† (g)	Median no. seeds‡
Browsed ramets (sample size)	1.94 (25)	0.80 (25)	2 (25)	2.870 (8)	0.00951 (8)	264.5 (8)
Intact ramets (sample size)	1.26 (9)	0.65 (9)	2 (9)	2.637 (1)	0.01003 (1)	263 (1)
Wilcoxon Rank Sum test for total plant growth: $H' = 488, P = .051$						
Wilcoxon Rank Sum test for mean shoot width: $H' = 517.5, P = .002$						
Wilcoxon Rank Sum test for number of shoots produced: $H' = 467, P = .258$						

* Total shoot growth = sum of widths of all shoots produced by each ramet.

† Seed mass = mean seed mass in grams based on 30 seeds/ramet.

‡ Total number of seeds = estimate from total seed mass/mean seed mass.

Whitham (1987) selected plants for the simulated herbivory and control treatments from the pool of unbrowsed plants. The fitness of plants with simulated browse exceeded that of control plants, a result arguing for positive effects of browse. Deer selectivity effects may have occurred as well: in 8 of 9 (probably non-independent) plant traits, simulated treatment means were lower, and one was significantly lower, than those of naturally browsed plants. Paige and Whitham report a 2.4-fold increase in relative fitness as a result of being eaten; this number reflects the mean difference between simulated-herbivory and control plants. Naturally browsed plants had a 3.1-fold increase in fitness compared to unbrowsed controls. The discrepancy between these relative fitnesses may reveal an herbivore selectivity effect.

The value of using simulated herbivory is great, since it often approximates the effects of natural herbivory and can be assigned at random to individual plants. Naturally damaged plants can also be incorporated into experiments. For size-based selectivity, plant size prior to browsing can be used as a covariate in evaluating performance of browsed and unbrowsed plants; alternatively, one can select simulated-herbivory and control plants equal in size to naturally damaged plants. Whether one is comparing growth, chemical, or nutritional attributes of naturally damaged plants to other plants, selectivity must be reckoned with before the true effects of damage can be assessed.

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