

THE EFFECTS OF GRAZING: CONFOUNDING OF ECOSYSTEM, COMMUNITY, AND ORGANISM SCALES

The negative effect of herbivory on plant growth and fitness approaches a paradigm in ecology. Removal of leaves, stems, sap, inflorescences, or roots reduces photosynthetic surfaces or their extension, nutrient and carbohydrate supplies, seed production, or surfaces for absorption of water and nutrients. Because plants are integrated organisms, reductions in area or biomass of one organ often lead to reductions of others. And since plant size (i.e., canopy height and width, root length and lateral extension) influences the ability of the individual to capture solar energy, nutrients, and water, reduction in size usually reduces the plant's competitive success. For these reasons, herbivory is usually assumed to be harmful to the grazed individual.

Over the last few years, several authors (Chew 1974; Harris 1974; Dyer 1975, 1980; Dyer and Bokhari 1976; Owen and Wiegert 1976, 1981, 1982*a,b*, 1984; McNaughton 1979*a,b*, 1983*a,b,c*, 1985; Owen 1980; Dyer et al. 1982) have suggested that herbivory may, or actually does, increase the total productivity, reproductive output, or fitness of some plant species. Since these hypotheses contradict "simple models of plant growth" (Mooney and Chiariello 1984, p. 310), as well as most studies on plant-herbivore interactions, the proponents need strong, replicable, and incontrovertible experimental evidence to support their assertions. Such evidence is available about the negative effects of herbivores on plants (for references, see Crawley 1983; Belsky 1986). Evidence is also available showing that low to moderate herbivory sometimes has no measurable effect. McNaughton's latest paper (1986) notwithstanding, strong experimental evidence for increased plant productivity, reproductive output, or fitness has not been produced.

Earlier (Belsky 1986), I reviewed all published papers cited in support of the hypothesis that the removal of plant tissue by herbivores benefits these plants and found the evidence lacking. Although I do not intend to repeat this exercise with the many papers McNaughton (1986) has recently added to the list, I want to caution those who might be impressed by the large number of confirmations to read the papers carefully. These newer studies also do not provide the strong evidence required. McNaughton reported, for example, that "Binnie and Clifford (1980) enhanced the seed yield of *Phaseolus vulgaris* up to threefold by defoliation" (p. 767). In fact, Binnie and Clifford reported that partial defoliation had no effect on seed production but that decapitation increased seed production in this species two- to threefold *at the node immediately below the point of decapitation*. They did not report seed yield on lower nodes or on the rest of the undecapitated

control plants. Seed production at upper nodes of the intact controls may have been considerable.

A paper by Sterner (1986), also cited by McNaughton, reported the increased net growth rate of an algal community when grazed by *Daphnia pulex*. However, in note 9 in the "References and Notes" section, Sterner reported that this increased net growth rate was found in only one of seven trials and that the nutrients necessary for the increased growth probably came from the remains of bacterial and colloidal material in the media. The two papers with which McNaughton could find no fault, Prins et al. (1980) and Cargill and Jefferies (1984), discussed the effects of grazing by geese on arctic species. They found increased plant productivity, but only aboveground (as McNaughton admitted). (For data and references showing reduced productivity as a result of grazing by geese, see Bédard et al. 1986.) Prins et al. measured growth of clipped *Plantago maritima* plants for only 2 wk, which is not strong evidence for increased net annual productivity. Furthermore, they could find no proof that grazing by geese, as opposed to mechanical clipping, stimulated growth in the field.

The paper by Cargill and Jefferies (1984) presented strong evidence for increased aboveground biomass production resulting from herbivory and is an exemplary paper about the effects of grazing on plant productivity in a natural community. They measured the productivity of grazed subarctic meadows by using temporary exclosures, and by counting goose droppings to estimate the amount of foliage consumed. This direct approach to the measurement of productivity of grazed plants is an excellent experimental model for future research. Cargill and Jefferies (1984) found that grazing by the lesser snow goose significantly increased aboveground production in the salt-marsh species *Carex subspathacea* and *Puccinellia phryganodes*. However, they could find no significant effect of grazing on belowground biomass, which in these species constitutes more than 90% of the standing biomass. Cargill (pers. comm.) doubts that the increased production of the relatively small amount of aboveground tissue would have significantly elevated total production if aboveground and belowground productions were combined.

McNaughton's hypothesis that the removal of transpiring leaf surfaces increases plant productivity by conserving soil water (McNaughton 1979a,b, 1983a,b, 1985, 1986) represents another undocumented benefit of grazing. Although I never measured water use by plants in the Serengeti National Park, Tanzania, I observed that plants growing within exclosures in sites throughout the park remained green 4–6 wk longer than nearby grazed plants. This was also true of grasses protected by fallen trees or other obstructions to grazing. I attributed this longer growing season to the ability of ungrazed plants to produce deeper and more-extensive root systems than grazed plants (for references, see Youngner 1969, 1972), making deeper groundwater available to them. In a review of the influence of grazing on American rangelands, Ellison concluded that "the effect of grazing is to encourage evaporational loss [from soils] and to create a lighter, warmer, and drier microclimate" (1960, p. 54). Observations in the Serengeti and studies reviewed by Youngner and Ellison oppose McNaughton's hypothesis that grazing improves plant water status.

Finally, I could find no evidence that McNaughton recalibrated his spectorefectance-to-biomass regression for different communities and different seasons and no mention of the "periodic checks from clipped plots" (McNaughton 1985, p. 262) in the papers cited as reporting these checks (McNaughton 1976, 1979*b*). It would be unusual if one regression ($\text{green g/m}^2 = 109.8 R - 83.8$; McNaughton 1975, 1976, 1979*a,b*, 1984, 1985) could adequately characterize the relationship of aboveground biomass to spectorefectance in communities as diverse as those found in the Serengeti. This is especially true since spectorefectance is known to vary with species composition, biomass, plant hydration, leaf-area index, plant-growth stages, and background reflectance (Myers 1971; Colwell 1974; Tucker 1977*a,b*, 1980).

WHY THE RAPID ACCEPTANCE OF THE BENEFITS OF HERBIVORY?

I would like to speculate about why these theories about the benefits of herbivory, which appear to deviate from the "paradigm" of plant-herbivore interactions, have been so readily accepted. Owen and Wiegert's theories and McNaughton's and Dyer's research are presented without critical discussion in many recent reviews of grass-grazer systems. A few typical comments are "herbivore activity stimulates primary productivity in grasslands" (French 1979, p. 182); "consumers can increase productivity of plants by pruning or by stimulating plant growth through . . . saliva" (Scott et al. 1979, p. 89); "grass production can be increased by regular cutting" (Lamotte 1983, p. 54); and "a moderate grazing of grasslands . . . stimulates the vegetative growth of the grasses to such an extent that the entire annual production . . . increases" (Walter 1985, p. 11).

At least three factors have contributed to this widespread acceptance. First, evidence supporting the hypotheses appears to be overwhelming. As found earlier (Belsky 1986), over 40 papers have been cited as showing or presenting evidence that grazing increases net productivity, seed production, fitness, etc. Few of these studies produced such evidence (some actually found the opposite), and those that did (only 4 or 5) were conducted in controlled-environment chambers or in cultivated fields where plants were fertilized and watered and their competitors (weeds) controlled. Without reading the original 40 papers, it would be hard to reject this mountain of evidence. It was also obvious that many authors had not critically read the papers they had cited, since the same references and interpretations appeared repeatedly in the literature.

Second, many plant ecologists are convinced that mowing stimulates the growth of their lawns (personal survey). Therefore, they may be predisposed to accept speculations and studies showing that grazing increases the net productivity of grasslands; that is, they may be judging the validity of research by their biases instead of by methodology and data. In general, however, turfgrass scientists have found that mowing and clipping reduce the growth and vigor of turfgrass species (Keen 1969; Youngner 1969, 1972; Madison 1971; Beard 1973; Emmons 1984). In a book on turfgrass science, Beard wrote that "any cutting or defoliation is detrimental to the turf" (1973, p. 383), a statement he backed up with over 50 references. Keen agreed that "with the possible exception of buffalo grass . . .

most grasses are not benefitted from mowing” (1969, p. 533). The only other exception to Beard’s generalization that I found in the general literature on turfgrass science was the mention by Madison that “ ‘coastal’ bermudagrass optimum yields are reached when mowed every two to six weeks” (1971, p. 102).

CONFOUNDING OF HIERARCHICAL SCALES

Many ecologists may have accepted these theories because of a confusion in the literature between arguments made on community and ecosystem levels and those made on the organismal level. The theory that grazing benefits grazed plants has developed in two directions. The first, developed by Owen and Wiegert (1976, 1981, 1982*a,b*, 1984; Owen 1980), is partly on the organismal level and partly on the ecosystem level. They speculated that by removing excess plant carbohydrates or tissues, herbivores alter local nutrient cycling and increase the supply of limiting resources. Much of their reasoning is based on the finding that photosynthesis is often limited by the availability of carbohydrate sinks within the plant. They hypothesized, for example, that aphids could act as sinks, stimulating sugar production. This excess sugar would fall to the ground as honeydew, stimulating the growth of soil microbes, which might fix nitrogen. Another example they give is that leaves dropped by leaf-cutting insects add organic matter and nutrients to the soil throughout the year, not just during the season of leaf abscission. This results in a continuous supply of nutrients to the soil beneath the tree. In both cases, the increased availability of nutrients might enhance the growth and fitness of the grazed plants. Owen and Wiegert concluded, therefore, that palatability would be an asset to these plants. Since these hypotheses have already been debated elsewhere (for references, see Belsky 1986), no further comment will be made. However, in the six papers Owen and Wiegert published as part of the debate, they presented no evidence confirming their hypotheses.

The second approach has been presented most forcibly by Dyer (1975, 1980; Dyer and Bokhari 1976; Dyer et al. 1982), who reported that herbivore saliva stimulates plant growth, and by McNaughton (1979*a,b*, 1983*a,b,c*, 1985), who reported that grazing increases productivity in grasslands in the Serengeti National Park. Their approaches are essentially physiological. Dyer reported that salivary hormones and growth factors secreted by grazers and deposited on grazed plants increase plant growth; and McNaughton attributed increased grass productivity to increased photosynthetic rates, changes in carbon allocation, increased cytokinin levels, increased tillering rates, and other mechanisms that sometimes occur when aboveground or older tissues are removed (McNaughton 1979*a,b*, 1983*a*). They hypothesized that such increases in growth would benefit the plant (Dyer and Bokhari 1976) or increase plant fitness (McNaughton 1983*a*).

What gained these theories publicity in the scientific and popular press was the radical idea that herbivory might increase, not decrease, the growth and fitness of grazed plants. Woven throughout these arguments, however, were well-documented studies showing that herbivores benefit some species by reducing the size of their competitors, altering successional trends, removing litter, and fertilizing the soil. These community- and ecosystem-level arguments were also used by

McNaughton (1986). Saying that herbivores benefit grass species by fertilizing them with dung and urine or by removing competitors are ecological truisms; but grazing does not necessarily benefit the grazed plants, which might have grown larger and produced more offspring without the loss of their tissues. Asserting that plants have evolved adaptations to increase their own consumption or to produce more biomass or seeds when grazed than when not grazed (i.e., overcompensation) are organismal and physiological arguments, implying that plants benefit directly from the removal of their tissues. They differ from the ecosystem-nutrient-cycling or community-alteration arguments, which do not require the loss of tissues by the species under consideration. The theory that herbivores benefit grazed plants has gained some acceptance, primarily because the effects of herbivores on communities and ecosystems have been confused with the effects of herbivores on individuals.

CONCLUSION

If overcompensation in total productivity is ever found in natural communities, it will most probably be found in moderately grazed wetlands such as those described by Prins et al. (1980) and Cargill and Jefferies (1984). As in cultivated fields and in controlled-environment chambers, species in these systems have plentiful water supplies, grow in monocultures where unpalatable species cannot gain a competitive advantage, receive even fertilization (by goose droppings), are grazed evenly such that individuals do not overtop one another, and grow in soils that are not compacted by large mammals. Additionally, in the Arctic, nutrients may otherwise be bound up in dead biomass for long periods, plants have protected ground-level meristems, and most of the plant biomass is belowground, where it cannot be damaged by occasional overcropping.

For ten years, several authors have speculated, suggested, and hypothesized that herbivory can increase the growth and fitness of grazed species. Until now, the evidence has been indirect, extrapolative, unconfirmed by further studies, or obtained from studies of inadequate design (Belsky 1986). The experiments necessary to accept or reject these theories are technologically simple and methodologically straightforward. It is time for the proponents of these theories to present more-convincing evidence.

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