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HOW CAN NET PRIMARY PRODUCTIVITY BE MEASURED IN GRAZING ECOSYSTEMS?

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Milchunas and Lauenroth (1993) assembled a 236-site data set from the scientific literature to examine the effects of large grazers on plants and soils over a vast range of geography and physical environment. Two sentences in the paper deserve further attention, because they suggest that there are two major problems with the manner in which grazing studies are conducted and aboveground net primary production (ANPP) is measured. First (p. 329), "In the majority of cases ANPP was estimated as peak standing crop in ungrazed treatment and in temporary caged grazed treatment; compensatory growth due to current-year defoliation is not accounted for." Second (p. 344), "More than half of grazing/plant community studies gave only qualitative estimates of grazing intensities." Fewer than one fifth of the grazing studies surveyed by Milchunas and Lauenroth met selection criteria. As with ANPP, the majority of quantitative estimates of grazing intensities that were performed used one-season or one-year, temporarily caged locations compared to uncaged, grazed locations.

Two separate, yet interrelated, problems are raised in the above quotes. First, the controversy about the effects of herbivores on plant productivity in grazing ecosystems, and about compensatory plant growth, may in part reside in the fact that our methods do not accurately assess either. Commonly used methods of estimating plant production in grazing systems do not allow the herbivore to remove biomass during the period of estimation, thereby not allowing for the positive or negative effects of removal to be manifest. Second, studies of the effects of grazing are often not accompanied by estimates of grazing intensity. The interrelated components in the two problems are consumption and the plant response to defoliation. The important issue is that both are continuous in time, but our measurements are not. How can we determine the effects of herbivores on plant productivity, or determine consumption, when those herbivores are more or less continually removing the product of that productivity and when the plants are continually responding to the removal by the herbivores?

Our objectives in this note are to examine potential alternatives to the season-long or year-long temporary caged compared to uncaged, grazed plots for measuring primary production and consumption in grazing ecosystems. There are inherent biases and weightings, and advantages and disadvantages in most, if not all, ecological methods of measurement. Surveys of, and controversies in, the grazing literature suggest that there is a need to make explicit what our methods actually measure.

When we clip grazed and season-long caged, ungrazed plots at the end of the growing season, and use the ungrazed plots as a measure of productivity and the ungrazed minus grazed plots as an estimate of consumption, we underestimate both productivity and consumption by the amount of compensatory regrowth that would have occurred had the ungrazed plots been continually grazed through that season. Similarly, when we subtract the production estimate for grazed sites that were temporarily ungrazed for one year from an estimate of production for a long-term ungrazed site, we underestimate the difference by an amount equal to the potential for compensatory regrowth on the season-long caged, normally grazed, plots. Although long-term effects of grazing can be negative or positive, stating that the above are "underestimations" is based upon the assumption that compensatory regrowth in response to current-year defoliation is never negative. Alternative methods should not, however, be based upon this assumption, but should be capable of detecting negative compensatory regrowth (e.g., injury or uprooting by pulling action during prehension) as well as positive. Our basis for there being a need to assess alternative methods is that not grazing a site that represents the grazing treatment is bound to introduce bias.

Alternative Estimation Methods

There are four alternative methods that we can think of for estimating productivity and consumption in grazing ecosystems: (1) If we know herbivore density and body size, and the range over which they feed, we can calculate how much they *should* have consumed, given a reasonable (not basal) activity budget. (2) We can employ moveable exclosures with a movement frequency timed to reflect both the intensity of herbivory and plant regrowth rate (McNaughton 1976, 1979*a, b,* 1985), measuring plant biomass and moving exclosures accordingly. (3) We can clip inside cages to simulate what is happening outside cages, clip end-of-season standing crop inside the cages, and assess cumulative removal and cumulative yield (Tomlinson 1986, Mil-

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chunas et al. 1995, Varnamkhasti et al. 1995). And, (4) the herbivores can be moved upon a scientist-determined schedule, with consumption measured over some (short) time of occupancy and regrowth measured afterward (Hik and Jefferies 1990).

The first alternative method above obviously will provide only a rough approximation of consumption at a particular sampling site. Animals do not graze uniformly across a landscape (Senft et al. 1987). Determining the density of animals and the time they spend in a particular location through a grazing season involves an intensive effort in monitoring grazing behavior.

The second method, moveable exclosures, has a clear advantage over most methods of measuring the effect of herbivory on plant growth that bias against detecting compensatory growth, since moveable exclosures account for the amount eaten and the amount that regrows between feeding bouts. In studies of the Serengeti and Yellowstone ecosystems, the use of moveable fences provided evidence for compensatory regrowth of grazed swards, resulting in greater productivity under grazing than when ungrazed (McNaughton 1976, 1979*a, b,* 1985, Frank and McNaughton 1993). Cargill and Jefferies (1990) also used moveable exclosures and, likewise, measured significantly greater production when the vegetation was grazed. However, other studies indicate that consumption may be overestimated by the moveable cage method (Sharrow and Motazadian 1983), which would result in overestimates of production.

The moveable-cage method has several advantages over the season-long-cage method: species groups that reach peak biomass early in the season, leaf turnover, and compensatory regrowth are accounted for. All have the potential to increase estimates of production. However, when production occurs as a single strong pulse, a single measurement at peak standing crop may represent a reasonable estimate of ANPP. Under other conditions, when comparing grazed vs. long-term ungrazed production, the question of whether to sequentially sample the ungrazed treatment to coincide with the timing of sampling of moveable cages in the grazed treatment would need to be addressed. If sequential sampling were not performed in the ungrazed treatment, then peaks in early season species and leaf turnover would not be accounted for in the long-term ungrazed treatment, but they would be accounted for in the grazed treatment. This would introduce error toward greater production of the grazed treatment. If sequential sampling were performed, then there is the potential bias caused by peak–trough calculations. Summation of increments in biomass from field data has the potential bias of overestimating production because random errors can generate artificial, false peaks and troughs (Singh et al. 1984, Lauenroth et al. 1986, Sala et al. 1988, Biondini et al. 1991). How this may differentially affect estimates for grazed vs. ungrazed treatments has not been specifically addressed. However, in a modeling exercise, Sala et al. (1988) found that the magnitude of overestimating production increased as real production decreased. This would have the effect of narrowing measured differences between grazed and ungrazed production in the field. If sampling frequencies are not the same for both treatments, bias is introduced because the magnitude of the overestimation error increases with increasing frequency of harvest (Sala et al. 1988).

Independent of the potential error due to statistical causes, positive or negative errors in the estimate of ANPP can be introduced purely as a function of calculating the difference between caged and uncaged vegetation when growth rates are not the same in the two. Errors will be negative when growth rates in cages are less than in uncaged plots (i.e., compensatory regrowth is occurring) and will be positive when growth rates are greater in caged than in uncaged plots (i.e., defoliation reduces the capacity of plants to grow). Thus, the frequency of moving the cages is an important factor affecting reliability of the moveable cage method. However, moving cages to match relative growth rates of vegetation in caged and uncaged plots would nullify the purpose of the method: to measure potentially different growth rates in defoliated and undefoliated vegetation. The method may still be superior to season-long cages because, if there is a defoliation effect on growth, it is most likely to be dependent on the intensity (height) and frequency of defoliation.

The two sources of error in the moveable cage method (statistical; differential growth) will not be additive, but will depend on the method of calculating ANPP. First, one could subtract uncaged from caged biomass at the end of each time period to obtain an estimate of consumption, then add the estimates of consumption for all time periods to the final harvest of residual vegetation in the grazed area. Second, one could subtract biomass outside the cage at the beginning of each time period from the biomass in the cage at the end of each period, adding all positive estimates of growth to the final harvest of residual biomass in the grazed area. With the first approach, differences in growth rates inside vs. outside the cages would be a source of potential error, but statistical sources of error described by Singh et al. (1984), Lauenroth et al. (1986), Sala et al. (1988), and Biondini et al. (1991) would not be a factor as long as "negative" values of consumption were included. The factor causing the positive bias reported in those papers is the truncation of distributions due to accepting the positive increments (peaks) in biomass and eliminating the negatives (troughs). Apparently negative values of consumption could result from compensatory growth of uncaged compared to caged vegetation being greater than actual consumption or from random chance of vegetation outside being greater than inside by an amount greater than consumption. The possibility for either of these to occur increases with decreasing grazer consumption. The potential for the latter also increases with increasing spatial heterogeneity of both grazing and the plant community. Finally, for the second method of calculation, statistical sources of error would be a factor but differential growth rates would not, because growth increments inside the cages are the object of measurement and negative increments in growth are generally not included. Estimates of consumption are not obtained from the second method of calculation, but it would be necessary to use the second method if ANPP of an ungrazed treatment was also being estimated.

Applying the third technique, Tomlinson (1986) clipped grass inside fences at three heights and three frequencies. Clipped swards were substantially more productive than grass in unclipped plots. Cumulative productivity was 2.3 times higher at a dry site, and 1.6 times higher at a wet site. Varnamkhasti et al. (1995) used reference plots in grazed shortgrass steppe to visually estimate the quantity and pattern of removal by cattle in lightly and heavily stocked pastures. Grazing in each reference plot was then simulated in an adjacent caged plot by clipping to the same height and pattern. Defoliation resulted in significantly greater production in long-term lightly grazed compared to heavily grazed treatment in a year of normal precipitation, but had no effect on comparisons between long-term grazing treatments in plots supplied with supplemental water to simulate a wet year.

Problems with the clip/simulated-grazing method center around the fact that visual estimations must be made, species pattern and composition in the reference plot may not be exactly like that in the plot to be clipped, leaf turnover is only partially accounted for, and nutrient recycling is not accounted for. Leaf turnover is only partially accounted for because some individual plants in a plot can remain ungrazed/unclipped through the season, and how many depends upon the intensity and patchiness of herbivory. Grazing animals partially return nutrients to plants in a form that is readily available to flora and soil fauna. This nutrient recycling can have large effects on plant productivity (McNaughton 1985, Hik and Jefferies 1990), and is precluded by the use of cages. On an annual basis, loss of nutrient input to caged areas would be more important at sites of high compared to low productivity with the same utilization (percentage consumption of ANPP) because higher animal densities would be required to achieve the same intensity of grazing. Because the same plots are sampled through the season, an advantage of this method is that bias associated with false peaks and troughs generated by random error when plots are moved is not a factor. Further, error is not additive as in the moveable cage method. This method is also less labor intensive. Partially defoliating a plot does not take as much time as complete harvest. If there is only one grazed treatment to sample, there are two blocks to sample when using the moveable-cage method (caged and grazed) compared to only caged when using the clip/simulated-grazing method.

The fourth method, moving the animals, will not be practical in situations involving large herbivores, but can be used successfully with small herbivores. Constraining large herbivores to particular areas is extremely difficult, and probably would not represent natural grazing behavior. For small herbivores, Hik and Jefferies (1990) allowed goslings to graze for different periods of time (up to 150 min) at nine different dates in the grazing season, in two different years, and controlled for herbivore biomass by adjusting gosling numbers as the animals grew. They found that regrowth rate was highest early in the season, at intermediate levels of grazing duration, and that recovery ability was absolutely dependent upon nutrient recycling through goose feces. Biases generated in sampling using this method would be similar to those of the moveable cage method. Williamson et al. (1989) used a nondestructive method to estimate biomass within cages, stocked cages with grasshoppers at eight different densities, nondestructively estimated biomass after a period of grazing, allowed a period for regrowth without the grazers, and destructively estimated biomass. Grazing increased ANPP in two of five of the grasshopper experiments with no effect in the others. This version of the moving-the-animals method is restricted to short-term, one-time grazing bouts.

Conclusions

To conclude: almost all studies of the effect of herbivores on primary productivity are biased against detecting any increases in production because they fail to allow plants to be consumed and, therefore, do not account for potential regrowth between grazing bouts. Both positive and negative effects of current-year defoliation can mediate differences in production estimates between long-term grazing treatments. Estimates of amounts consumed can be similarly biased. The moveable-cage method, simulation of grazing patterns and intensities by clipping inside temporary cages, and moving animals are alternatives that provide better measures of consumption and are more sensitive to detecting compensatory growth; however, they also have inherent biases that can potentially lead to over- or underestimations of productivity. Whether or not any of these methods provide better estimates of production than the season-long or year-long caged method depends on the relationship between how much compensation occurs and if or how much production is over- or underestimated. The body of literature that indicates that compensatory regrowth or current-year defoliation are important determinants of productivity suggests that further work is warranted on the magnitude and direction of the biases of these alternative methods under different environments and grazing situations.

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