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GRAZING AS AN OPTIMIZATION PROCESS: GRASS-UNGULATE RELATIONSHIPS IN THE SERENGETI

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Until recently (Vickery 1972; Harris 1974; Dyer 1975; Mattson and Addy 1975; Dyer and Bokhari 1976; McNaughton 1976), ecologists have tended to view plants as relatively passive participants in short-term interactions at the plant-herbivore interface, suffering tissue reduction from herbivory, and responding in evolutionary time through the evolution of novel antiherbivore chemicals and structures (Fraenkel 1959; Ehrlich and Raven 1964; Levin 1971, 1973; Caswell et al. 1973; Freeland and Janzen 1974). Agronomists, botanists, foresters, and range managers, however, have frequently emphasized the direct plant responses to herbivory of compensatory growth and assimilate reallocation (Parker and Sampson 1931; Robertson 1933; Canfield 1939; Labyak and Schumacher 1954; Stein 1955; Brougham 1961; Leonard 1962; Jameson 1963; Pearson 1965; Neales and Incoll 1968; Hutchinson 1971; Ryle and Powell 1975). This literature in applied ecology documents the frequent occurance of compensatory plant growth following tissue reduction by herbivores or management practices.

However, no straightforward generalizations are possible regarding the immediate effects of herbivores on plant growth and resource allocation. Consequences of tissue damage are under the complex control of plant genetics (Parker and Sampson 1931; Weaver and Houghen 1939; Newell and Keim 1947; Branson 1953; Robocker and Miller 1955; Baker and Hunt 1961; Hart et al. 1971), intensity and frequency of herbivore effects (Graber 1931; Canfield 1939; Jacques and Edmond 1952; Lodge 1960; Marshall and Sager 1965; Forde 1966; Gifford and Marshall 1973), plant developmental stage at the time of herbivore impact (Blaisdell and Pechanec 1949; Leopold 1949; Cook and Stoddart 1953; Jameson and Huss 1959; Hussey and Parr 1963; Tanisky 1969), plant tissues that are affected (Murneek 1925, 1926; Eaton 1931; Humphries 1958; Dunn and Engel 1971), and the modifying effects of such other environmental factors as light, nutrients, temperature, and water (Wilson and McGuire 1961; Madison 1962; Bean 1964; Griffith and Teel 1965; McKee et al. 1967; Wardlaw 1968; Sosebee and Wiebe 1971). Of course, growth may be inhibited by excessive defoliation (Milthorpe and Davidson 1965; Davidson and Milthorpe 1966a, 1966b), and an optimum defoliation level is anticipated (Noy-Meir 1975; Caughley 1976). Thus, simple statements about the effect of herbivores or other tissue damaging agents on plant growth, development, and resource allocation are fraught with error. Rather, the plant responds to a whole complex of environmental factors,

of which herbivore impact is only one. Further, the nature of the response will be conditioned by the genetic and developmental background of the plant.

Over a hundred years ago, Boussingault (1868) proposed that photosynthesis often may be limited by the accumulation of photosynthetic products. The rate at which assimilates accumulate in an actively photosynthesizing leaf depends upon the balance among photosynthesis, respiration, and outward translocation to assimilate consumption centers, commonly called sinks, elsewhere in the plant (Mason and Maskell 1928; Canny and Askham 1967; Neales and Incoll 1968). The plant is characterized as a source-sink system in which active photosynthetic tissue produces compounds which either are utilized for its own maintenance and growth, stored in situ, or translocated outward to other sites of utilization and storage (Burt 1964; Maggs 1964; Hartt 1963; Neales and Incoll 1968; King et al. 1967; Chatterton et al. 1972; Thorne and Koller 1974). Increasing the drain on leaf substrates by promoting translocation to sinks commonly results in increased photosynthetic rates in source leaves. This photosynthesis enhancement is accompanied by increased protein content, decreased mesophyll resistance, reduced starch levels, and increased sucrose translocation. Partial defoliation, by increasing assimilate demand in meristems of remaining shoots, usually stimulates photosynthetic rate per unit of remaining leaf area (Wareing et al. 1968; Gifford and Marshall 1973). In addition to the direct stimulatory effect of defoliation upon photosynthetic capacity of the remaining canopy, defoliation may allow more efficient light use by reducing mutual leaf shading (Donald and Black 1958; Jameson 1963; Hughes 1969; Heslehurst and Wilson 1971; Robson 1973). In particular, since large ungulates graze upon grasses from above, and growth is primarily from basal intercalary meristems, the older and less efficient tissues (Ludlow and Wilson 1971) are preferentially removed (Langer 1972), leading to greater light intensity on younger, previously shaded tissues (Jameson 1963).

Defoliation has a substantial effect upon assimilate allocation within the plant. There is pronounced diversion of carbohydrates from roots following defoliation (Kinsinger and Shaulis 1961; Gifford and Marshall 1973; Ryle and Powell 1975), and defoliation frequently reduces root growth (Crider 1955; Oswalt et al. 1959). Sosebee and Wiebe (1971) found that defoliation and soil moisture interact to determine patterns of assimilate translocation. Reduced water supply increased translocation to roots and crowns, while partial defoliation increased translocation to younger leaves. Therefore, the balance between root and crown storage and utilization of substrates by leaf meristems will be influenced by the balance between defoliation intensity and soil water potential. Although more severe defoliation is accompanied by greater diversion of assimilates from roots and a greater reduction in root growth, Dunn and Engel (1971) observed that more severe foliage clipping could result in a greater stimulation of subsequent root growth after a lag period of 3–4 wk.

The balance between vegetative and reproductive tissues also is influenced by herbivory. Dyer (1975) has shown that seed filling in maize may be enhanced by moderate herbivore damage to ears during certain developmental stages, and fruit and seed yield compensation following herbivory has been reported for many other plants (Taylor and Bardner 1968; Harris 1974). The converse of these effects is the inhibition of flowering and fruit set that commonly accompanies defoliation (Arch-

bold 1942; Sprague 1954; Laude et al. 1957; Roberts 1958; Jameson 1963; Stoy 1965). The balance between reproductive and vegetative structures, like the other effects of herbivory, is regulated by plant phenological stage, which tissue is damaged, environmental parameters, and plant genetics.

Herbivory modifies hormonal balance within the plant substantially (Avery and Briggs 1968; Avery and Lacey 1968), particularly the parity between growth promoting and retarding hormones produced in the root and translocated to the shoot (Weiss and Vaadia 1965; Meidner 1967; Pallas and Box 1970; Torrey 1976). A greater flow of growth promoting hormones to residual meristems following defoliation promotes cell division and enlargement and activity in quiescent meristems, additional mechanisms of compensatory growth accompanying herbivory. A longer-term effect of modifications of hormonal equilibria following defoliation is a reduction in the rate of photosynthesis decline with leaf aging, thus maintaining assimilatory capacity of residual leaf tissue at higher levels over a longer time period (Richmond and Lang 1957; Woolhouse 1967; Neales et al. 1971; Gifford and Marshall 1973).

Two additional longer-term effects of defoliation may account for productivity increases caused by leaf-eating herbivores. First, soil water may be conserved due to reduction of the transpiration surface (Daubenmire and Colwell 1942; Baker and Hunt 1961) and because photosynthetic rate increases are associated primarily with reductions in mesophyll resistance rather than stomatal resistance (Gifford and Marshall 1973; Thorne and Koller 1974). The latter effect suggests that water-use efficiency may be increased by partial defoliation. Second, plant growth may be stimulated by nutrients recycled from dung and urine. This is so well known as to warrant little comment (Peterson et al. 1956; Lotero et al. 1966; Weeda 1967).

Finally, one potential direct stimulatory effect of grazing ruminants upon grass productivity may rise out of plant growth promoting agents in ruminant saliva (Vittoria and Rendina 1960; Reardon et al. 1972, 1974). Direct growth stimulations up to 50% above control levels have been recorded following addition of ungulate saliva to surfaces of manually clipped leaves.

In summary, productivity of herbivore affected plant tissues may be compensated or stimulated by:

1. Increased photosynthetic rates in residual tissue;
2. Reallocation of substrates from elsewhere in the plant;
3. Mechanical removal of older tissues functioning at less than a maximum photosynthetic level;
4. Consequent increased light intensities upon potentially more active underlying tissues;
5. Reduction of the rate of leaf senescence, thus prolonging the active photosynthetic period of residual tissue;
6. Hormonal redistributions promoting cell division and elongation and activation of remaining meristems, thus resulting in more rapid leaf growth and promotion of tillering;
7. Enhanced conservation of soil moisture by reduction of the transpiration surface and reduction of mesophyll resistance relative to stomatal resistance;
8. Nutrient recycling from dung and urine;

9. Direct effects from growth promoting substrates in ruminant saliva.

It is clear from reviewing the literature of herbivore damage, whether real or simulated, that an optimum tissue reduction level should occur, beyond which plant growth will be reduced (Vickery 1972; Dyer 1975; Noy-Meir 1975; Caughley 1976). This paper reports field and laboratory experiments designed to quantify the optimization curve in an ecosystem where herbivore load is intense (Stewart and Talbot 1962; Talbot and Stewart 1964; Watson and Kerfoot 1964; Hendrichs 1970; McNaughton 1976, 1979), the fauna is one of substantial antiquity (Leakey 1965; Cooke 1968; Gentry 1968), and I therefore assume that coevolution of plants and their herbivores has had an important influence on present properties of the ecosystem.

STUDY AREA AND METHODS

As Talbot and Stewart (1964, p. 815) observed, "The last known great concentrations of mixed species of plains wildlife in Africa, or in the world, are found in the Serengeti-Mara region of (Tanzania) and Kenya." The Serengeti ecosystem is defined operationally by the annual movements of large herds of migratory wildebeest (*Connochaetes taurinus Albojubatus* Thomas) between wet season occupance areas on the open Serengeti Plains and dry season occupance areas on savanna grasslands to the west near Lake Victoria and to the north in the Mara River drainage basin (Talbot and Talbot 1963; Pennycuick 1975). Movements of zebra (*Equus burchelli* Gray) are similar in scope. Those of the other major migratory species, Thomson's gazelle (*Gazella thomsonii* Gunther), are less extensive. Together, these three species constitute over 60% of the grazing mammal biomass (Stewart and Talbot 1962; Talbot and Stewart 1964; Hendrichs 1970). The experiment reported here was done in a grassland dominated by *Andropogon greenwayi* Napper (Anderson and Talbot 1965; Schmidt 1975) from January to May, 1975, while major concentrations of the three principal ungulates were present. Although the wet season is nominally from November through May (Norton-Griffiths et al. 1975), the first substantial rain on the Serengeti Plains during the 1974–1975 wet season was on January 3, 1975. As in most equatorial regions (Livingstone 1975), rainfall in the Serengeti is largely from convective storms arising from local synoptic processes superimposed on the intertropical convergence zone and is characteristically erratic (Pennycuick and Norton-Griffiths 1976). Data are presented here from 102 grazing days, defined by presence of one of the three major animal species, during the 146-day period between January 3 and May 29 when all three species had left the study site for their dry season ranges.

A permanent exclosure was built at the beginning of the period, and adjacent temporary exclosures were used to measure short-term grass regrowth subsequent to protection from grazing. Plant biomass (g/m^2) was measured as described previously (Tucker et al. 1973; Pearson et al. 1976; McNaughton 1976, 1979). Above-ground net productivity $(g/m^2 \cdot day)$ was calculated from positive biomass increments. Grazing intensity (G) was calculated as $1 - g/ng$, where g was biomass in grazed areas unprotected by fencing and ng was biomass in the permanent exclosure. This index will be zero when grazing does not reduce plant biomass below control levels, and will approach one as grazing increases. Temporary exclosures were moved according

to the grazing rotation patterns of the three ungulate species: Whenever an influx of grazers reduced plant biomass below control levels, they were moved. Thus, short-term protection was employed to measure actual grass growth under a grazing regimen defined by the grazers movements. The temporary exclosure approach was designed because I felt traditional approaches, such as simulating grazing by clipping, were unlikely to reproduce the manifold effects of grazing animals documented in the introduction. Actual productivity was the sum of the positive biomass increments inside temporary exclosures, control productivity was the sum of positive biomass increments inside the permanent exclosure, and grazing stimulation was actual minus control productivity. Soil water potentials (S) in -bars were back-calculated from control green biomasses after I had established that the two parameters were closely related ($r^2 = .839$ for $P < .001$ with df $= 15$). The study site was routinely assayed at 6 day intervals and as frequently as daily when warranted by high rates of grass growth or consumption.

To determine whether grazing effects on net above-ground productivity could be partially simulated in the laboratory, clones of *Kyllina nervosa* Steud. were collected and returned to Syracuse University's Biological Research Laboratories. This species is a dryland sedge dominant in that part of the Serengeti ecosystem where annual rainfall is less than about 500 mm (Anderson and Talbot 1965; McNaughton, in prep.). It is abundant in one of the most intensely grazed regions of the Serengeti: The migratory animals go there whenever there is enough rain to promote plant growth (Talbot and Talbot 1963; Watson and Kerfoot 1964; Pennycuick 1975; Kreulen 1975). Although I used temporary exclosures because I felt clipping would not reproduce the effects of grazing animals, clipping seems the only feasible approach to simulating grazing under laboratory conditions. Cloned individuals were grown in Sherer CEL 37-14 growth chambers and were clipped at 2, 4, and 6 cm heights, at frequencies of $\frac{1}{2}$, 1, 3, 5, 6, and 19 days. Growth increments were oven dried and weighed, and biomass increments were converted to grams per square meters times days.

<center>RESULTS AND DISCUSSION</center>

Stimulation of net above-ground primary productivity by grazing was a complex function of grazing intensity (fig. 1), as regulated by soil water potential. There was a sharp stimulation peak when defoliation was moderate, and a long tail when grazing reduced plant biomass to less than half of control levels. Productivity stimulation was described ($R^2 = .777$, $P < .001$ with df $= 13$) by

$$\Delta P = e \exp \{.76 - 3.5(\ln G) - 1.24(\ln G)^2 - .64(\ln S)\}$$

where ΔP was experimental minus control productivity and G and S were as defined previously. Grazing explained 68.7% of the variance in productivity stimulation (X, $F_{1,13} = 10.96$, $P < .01$; X^2, $F_{1,13} = 14.14$, $P < .01$) and soil water potential contributed 9% ($F_{1,13} = 5.24$, $P < .05$). Mean control productivity was 15.1 ± 4.9 (.95 interval) g/m^2 · day, so productivity was doubled under moderate grazing if soil moisture tension was low.

Wildebeest was the only species for which sufficient data were obtained to provide
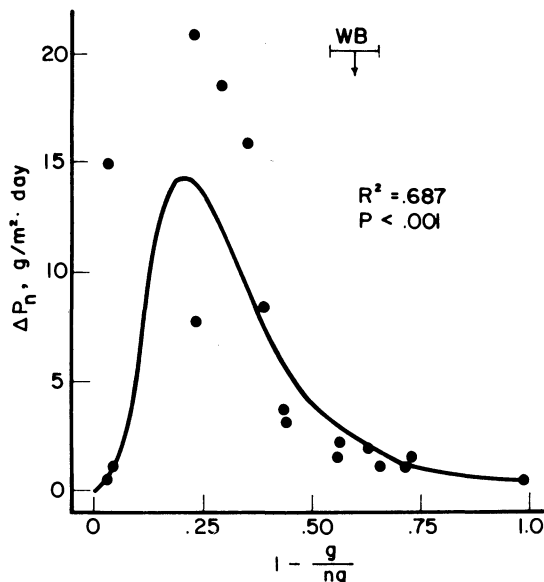
FIG. 1.—Relationship between stimulation of above-ground grassland productivity (ΔP_n) and grazing intensity $(1 - g/ng)$; the line plotted was fitted without incorporating soil moisture, which reduced the unexplained variance in stimulation by 9%. The WB indicates the mean and .95 confidence range of wildebeest grazing intensity in these grasslands throughout the wet season.

a reasonable confidence limit on G for a grazing species. On average this species overcropped the grassland significantly compared to the level that would maximize forage yield (fig. 1). Biomass yield of forage to the wildebeest population would be higher at a grazing level about half of the average they maintained.

Apparent overcropping, however, may maximize total nutrient yield to the wildebeest. Forage quality during the dry season falls below maintenance requirements of the animals with a resulting depletion of body reserves; these reserves are replenished during the wet season (Sinclair and Duncan 1972; Sinclair 1974a, 1974b). It is well known that forage quality diminishes with plant tissue age (Glover et al. 1960; Armstrong et al. 1964; Miller et al. 1965; Braun 1973) and that higher quality forage not only gives a higher nutritional yield, but can be consumed in larger quantities by ruminants (Hungate 1975). Thus, apparent overcropping by wildebeest probably maintains higher nutritional yield than would less intense grazing, allowing more rapid replenishment of body reserves than would consumption of larger quantities of lower quality forage (Baile and Forbes 1974; Hungate 1975). Most efficient exploitation of these grasslands by wildebeest, in terms of total yield, would be accomplished at lower consumption levels. Like butterfly larval grazing (Slansky and Feeny 1977), wildebeest grazing may be an optimum power system (Odum and Pinkerton 1955). The wildebeest-grass interface, however, is more interactive than the caterpillar-crucifer one (Slansky and Feeny 1977), since yield to the wildebeest is a direct consequence of their grazing and the resultant compensatory physiological responses of the dominant grasses.
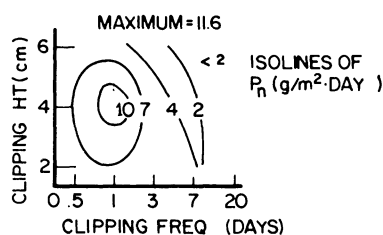
FIG. 2.—Isolines of net above-ground productivity (g/m² · day) of *Kyllinga nervosa* clipped at various heights and frequencies under controlled environment conditions. Maximum productivity of 11.6 g/m² · day occurred when plants were clipped daily at a height of 4 cm.

Two points about the form of the relationship between stimulation of above-ground productivity and grazing intensity warrant comment. First, optimization of grass growth by grazing was a complex process, reaching a peak at moderate levels of defoliation. Second, the long tail on the curve at high grazing intensities indicates that these grasslands are remarkably resistant to overgrazing; productivity was maintained at control levels even when defoliation was severe.

Although, as documented in the introduction, growth of above-ground tissues may be at the expense of substrates stored in roots and crowns, most of the species common in these grasslands cannot suffer fatal reserve depletion under the prevailing grazing regime. Many, in fact, are obligate grazophils whose occurrence depends upon the grazers. When reexamining exclosures in 1975 that were built in the early 1960's (Watson 1966), I found that most of the presently abundant grasses had substantially reduced abundances in the protected areas (McNaughton 1979). *Andropogon greenwayi*, for instance, made up 56% of the plant biomass outside, but was completely absent inside; so, in addition to having a remarkable ability to withstand heavy grazing, *A. greenwayi* is maintained in these grasslands by sustained grazing. It is one of the few sod-forming species in the flora, most species being bunchgrasses, and its prostrate growth form must allow it to sustain sufficient leaf area under most grazing intensities to prevent substantial root reserve depletion.

Net above-ground primary productivity of *Kyllina nervosa* was a complex function of clipping frequency and height (fig. 2), as revealed by a significant interaction term in the analysis of variance ($F_{8,135} = 13.9$, $P < .001$). Maximum net above-ground productivity was 11.6 g/m² · day, recorded at a 4 cm height when clipping was at daily intervals. I know of no other plant which has been reported to be able to sustain shoot growth when subjected to such intense clipping, much less have an optimum at this intensity. The productivity values reported here, however, are substantially below field data in grasslands where *K. nervosa* is abundant (McNaughton 1975). This experiment demonstrated a remarkable ability by *K. nervosa* to sustain growth under intense levels of foliage removal, undoubtedly a consequence of natural selection for compensatory growth responses during a long period of intense herbivore load.

Grasses and large grazing ungulates have a long and intimate coevolutionary history, but the Serengeti ecosystem is one of the few areas where the products of that history remain relatively undisturbed. Although the concept of optimum stocking density is well established in range management (Klipple and Costello 1960; Bement

1969; Hutchinson 1971) I would not expect the relationships between domestic forages and ungulates to necessarily resemble those documented here for a natural grazing system. *Andropogon greenwayi* and *K. nervosa* dominate grasslands subjected to intensive herbivory for a considerable period, given the antiquity of the region's fauna. A major problem in development of optimum stocking criteria for managed rangelands is the need to preserve forage for use during periods when grass growth is limited by low moisture or, in temperate grasslands, low temperature. In this system of native migratory herbivores, in contrast, a pasture rotation pattern has evolved naturally in relation to seasonal rainfall patterns.

The disappearance of *A. greenwayi* and most of the other dominant grasses from plots protected from grazing for several years indicates that they have comparatively higher fitnesses under intense grazing than other species, which became dominant when grazing was curtailed. This does not imply that the absolute fitnesses of the present dominants is enhanced by grazing. For instance, there was little seed production in grazed areas, while flowering culm density commonly exceeded $200/m^2$ in exclosures. To the extent that sexual reproduction contributes to fitness of these grasses, grazing reduced fitness of many species tangibly. However, the ability of these grasses to maintain high levels of productivity under very intense grazing is a clear adaptation to high herbivore load. Traditional standards of overgrazing, clearly applicable to domestic ungulates and forages, may have slight application to an ungulate fauna and its forages which are products of a long coevolutionary history.

Although these experiments indicate that compensatory growth responses of the plants are a significant factor in this ecosystem's energy flow, this does not imply that the relationship between the plants and herbivores is symbiotic by any conventional definition of that term (Mattson and Addy 1975). The grasses clearly pay a cost in reproductive potential as a consequence of the intense defoliation regime, and even those species whose abundance is tied to the grazers probably periodically suffer significant levels of reserve depletion. Thus, while competitive fitness is enhanced by grazing, absolute fitness may be impaired in comparison to the ungrazed condition.

SUMMARY

A substantial literature is reviewed which indicates that compensatory growth upon tissue damage by herbivory is a major component of plant adaptation to herbivores. Experiments in Tanzania's Serengeti National Park showed that net above-ground primary productivity of grasslands was strongly regulated by grazing intensity in wet-season concentration areas of the large ungulate fauna. Moderate grazing stimulated productivity up to twice the levels in ungrazed control plots, depending upon soil moisture availability. Productivity was maintained at control values even under very intense grazing, suggesting that conventional definitions of overgrazing may be inapplicable to these native plant-herbivore systems. A laboratory clipping experiment with a sedge abundant in one of the most intensely utilized regions resulted in a maximum net above-ground productivity of 11.6 $g/m^2 \cdot$ day when clipped daily at a height of 4 cm. Few plant species have been reported with the ability to maintain a significant level of productivity under such intense clipping. This suggests that the high grazing load of the Serengeti ecosystem has constituted strong selection on the plants for compensatory growth upon defoliation.

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