

# Physiological Responses of Individual Plants to Grazing: Current Status and Ecological Significance

D. D. Briske and J. H. Richards

## Abstract

Individual plant responses to herbivory were initially investigated to establish prudent guidelines for livestock grazing on pastures and rangelands. A great deal has been learned concerning the effects of defoliation on the morphology, physiology and productivity of important forage and browse species. However, our perception and understanding of individual plant responses to herbivory have been substantially altered by research findings developed during the past 15 years. Information within this contemporary research perspective can be generalized into three broad categories. First, several traditional assumptions regarding plant responses to defoliation have proven to be over simplifications. For example, questions have arisen concerning the value of carbohydrate reserves as an indicator of plant growth following defoliation and the assumption that tillering is exclusively regulated by auxin produced in the apical meristem. Second, several novel hypotheses have been proposed to explain the potentially beneficial effects of herbivory. Increased photosynthetic rates of residual foliage, accelerated growth rates, modified allocation patterns and enhanced nutrient absorption have been observed in various plant species following defoliation. Third, the ability of biotic interactions and abiotic constraints to accentuate herbivore-mediated plant responses has only recently been fully appreciated. For example, herbivore-induced modifications of competitive interactions may potentially constrain plant growth to a greater extent than the direct effects of biomass removal. Evidence from both the traditional and contemporary literature has been surveyed to assess the current status of our knowledge and evaluate the ecological significance of individual plant responses to grazing by large herbivores.

## Introduction

Domestic herbivores were initially introduced into North America in the early 1500's and their density and distribution increased steadily with colonization by the Spanish in the south and southwest, the English on the eastern seaboard, and the French in the midwest and Louisiana (Sampson 1952). Domestic herbivore popu-

lations increased to a maximum during the inflationary period following the Civil War with approximately 26 million cattle and 20 million sheep in the 17 western states in 1890 (Young, this volume). Escalating animal numbers and intensive grazing of western rangelands during the late 1800's contributed to a growing public concern for conservation of lands in the public domain. Investigations of plant responses to defoliation were soon initiated to establish a scientific basis for the conservation and management of rangeland vegetation in the western United States.

A great deal has been learned concerning the effects of grazing on the morphology, physiology, and productivity of important forage and browse plants during the 20th century. Ellison (1960) and Jameson (1963) provide excellent summaries of research addressing individual plant and community responses to grazing during the first half of the century. Examples of some of the prominent concepts developed during this period include: 1) identification of critical frequencies and intensities of defoliation to ensure plant survival and maintain productivity, 2) documentation of a proportional relationship between root growth and the severity of shoot defoliation, 3) appreciation of the significance of shoot morphology for grazing resistance, 4) development of the concept of carbohydrate reserves to explain plant survival and growth following defoliation, and 5) recognition of the interactive effects of apical dominance and defoliation on tiller initiation. However, not all of the traditional concepts have proven to be compatible with subsequent research findings.

The objective of this chapter is to provide both a synopsis of the current status of our knowledge and a discussion of the ecological significance of the physiological and morphological responses of individual plants to grazing. We have approached this objective by comparing the traditional literature with the more contemporary literature developed since 1975. Although all major growth forms have been referenced, grasses have been given the greatest emphasis. A brief overview of the hierarchical organization of grassland vegetation is presented to emphasize the significance of individual plant responses to community ecology and rangeland management.

### Ecological Scales

Grassland communities can be viewed at various scales reflecting their hierarchical organization. Individual grass plants consist of an assemblage of tillers, grass populations are comprised of individual plants with varying tiller numbers per plant, and grassland communities are further composed of an aggregation of species populations variously arranged in space and time (Briske 1991). Each of the scales is associated with overlapping temporal responses and spatial dimensions. For example, the physiological and developmental processes of individual plants react in much shorter time frames and at smaller spatial dimensions than do population or community dynamics.

Recognition of the linkage between processes at various ecological scales determines that insight into mechanisms occurring at higher scales (e.g., population and community) requires that processes at lower scales (e.g., plant and tiller) be investigated (Brown and Allen 1989, Allen and Hoekstra 1990). Although proportionate responses may occur among ecological scales to affect ecosystem struc-

ture and function, additional complexity is frequently encountered by the occurrence of disproportionate responses between or among scales. Consequently, it is essential that several ecological scales be considered simultaneously when evaluating vegetation responses to herbivory to avoid incomplete or erroneous conclusions (Brown and Allen 1989).

## Plant Responses To Herbivory

### Carbohydrate reserves

The major premise for monitoring carbohydrate reserves was to provide an index of potential regrowth based upon the assumption that these carbohydrates provided the major source of carbon for leaf regrowth. The depletion of carbohydrate reserves in response to defoliation, environmental stresses, or as a result of normal phenological processes, was thought to be the major cause of subsequent growth reductions. In extreme cases, plant mortality could also result from a substantial reduction in carbohydrate reserves (Weinmann 1948). Carbohydrate reserves, referred to as total nonstructural carbohydrates (TNC) or total available carbohydrates (TAC), are a product of photosynthesis in excess of requirements for growth and maintenance (White 1973). These labile carbon compounds are utilized for plant growth and maintenance when photosynthetic capacity is limited as evidenced by the reduction in carbohydrate reserves following defoliation, shading or other manipulations that limit photosynthesis, in a large number of grass species (Deregibus et al. 1982) (Fig. 1). The traditional interpretation assumed that carbohydrates stored in roots were remobilized to support shoot growth following defoliation.

However, a substantial amount of information has been compiled during the last three decades indicating that the contribution of carbohydrate reserves to leaf regrowth of perennial grasses may be much smaller than previously assumed (May 1960, Davidson and Milthorpe 1965, Ryle and Powell 1975, Atkinson and Farrar 1983, Richards and Caldwell 1985, Richards 1986). Carbohydrate pools (tissue mass  $\times$  TNC concentration) within root systems are primarily used for root growth and respiration and are not usually remobilized for subsequent use in shoots following defoliation. TNC pools in root systems are dispersed among the numerous fine roots and are insufficient to maintain pre-defoliation rates of root growth and function following defoliation (Richards 1984). Therefore, a decrease in TNC pools in root systems following defoliation results from the combined effects of a reduction of current photosynthates allocated to the root system and continued TNC utilization in root respiration, rather than remobilization and allocation to the shoot system (Fig. 1). This interpretation is supported by a decrease in both TNC pools and TNC concentrations of grasses even in the absence of shoot regrowth following defoliation (Richards and Caldwell 1985).

A consistent, positive relationship between the size of carbohydrate pools and plant regrowth has not been definitively established (Busso et al. 1990). In seasonal comparisons, an inverse relationship is frequently observed with carbohydrate pools increasing during periods of minimal growth and then decreasing during rapid growth (Davidson and Milthorpe 1966, Caldwell 1984). The potential

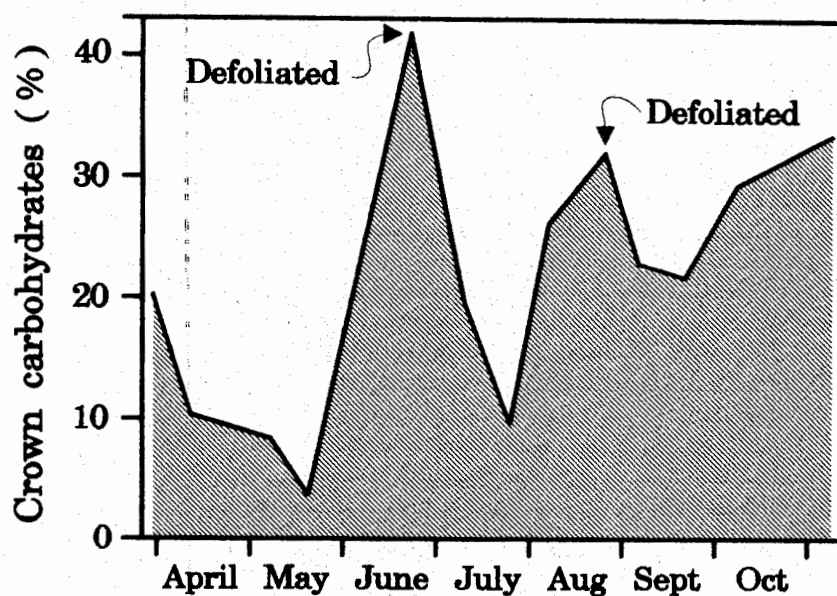


Figure 1. Carbohydrate concentrations in the crown of timothy (*Phleum pratense* L.) in response to defoliation in June and August during a single season. Rapid reductions in crown and root carbohydrate concentrations are traditionally interpreted as the remobilization of carbohydrates to support shoot growth following defoliation. The contemporary interpretation indicates that carbohydrate concentrations in the crown and roots decline in response to the combined effects of reduced carbon allocation from the shoot and continued carbohydrate utilization in root respiration following defoliation (from Smith 1972).

for plant regrowth increased only when TNC concentrations in roots and crowns of crested wheatgrass [*Agropyron desertorum* (Fisch. ex Link) Schult.] and bluebunch wheatgrass [*Pseudoroegneria spicata* (Pursh) A. Löve ssp. *spicata*; syn: *A. spicatum* (Pursh) Scribn. and Smith] increased to exceptionally high levels in response to an experimentally imposed drought (Fig. 2). Under all other conditions in a 2-year field study, crown and root TNC concentrations or pools were poor indicators of regrowth potential in early spring when these two grasses exhibit their greatest growth potential (Busso et al. 1990). In addition, neither carbohydrate concentrations nor pools account for the wide variation in grazing tolerance between crested wheatgrass and bluebunch wheatgrass (Richards and Caldwell 1985). Carbohydrate pools within the crowns, including sheath bases, of the two wheatgrass species were equivalent to carbohydrates produced in only 3 days of photosynthesis (Fig. 3). Consequently, plant growth was more dependent upon current photosynthesis than stored carbohydrates within 3 days following severe defoliation. Similarly, leaf elongation or tillering were not proportionately related to carbohydrate concentrations in leaves, crowns or roots of tall fescue (*Festuca arundinacea* Schreb.), orchardgrass (*Dactylis glomerata* L.) or reed canarygrass (*Phalaris arundinacea* L.) (Sambo 1983, Zarroug et al. 1984, Volenec and Nelson 1984). These findings support the view of May (1960), who indicated that use of the term carbohydrate "reserve" evokes a false conception of their contribution to growth following defoliation (Deregibus et al. 1982).

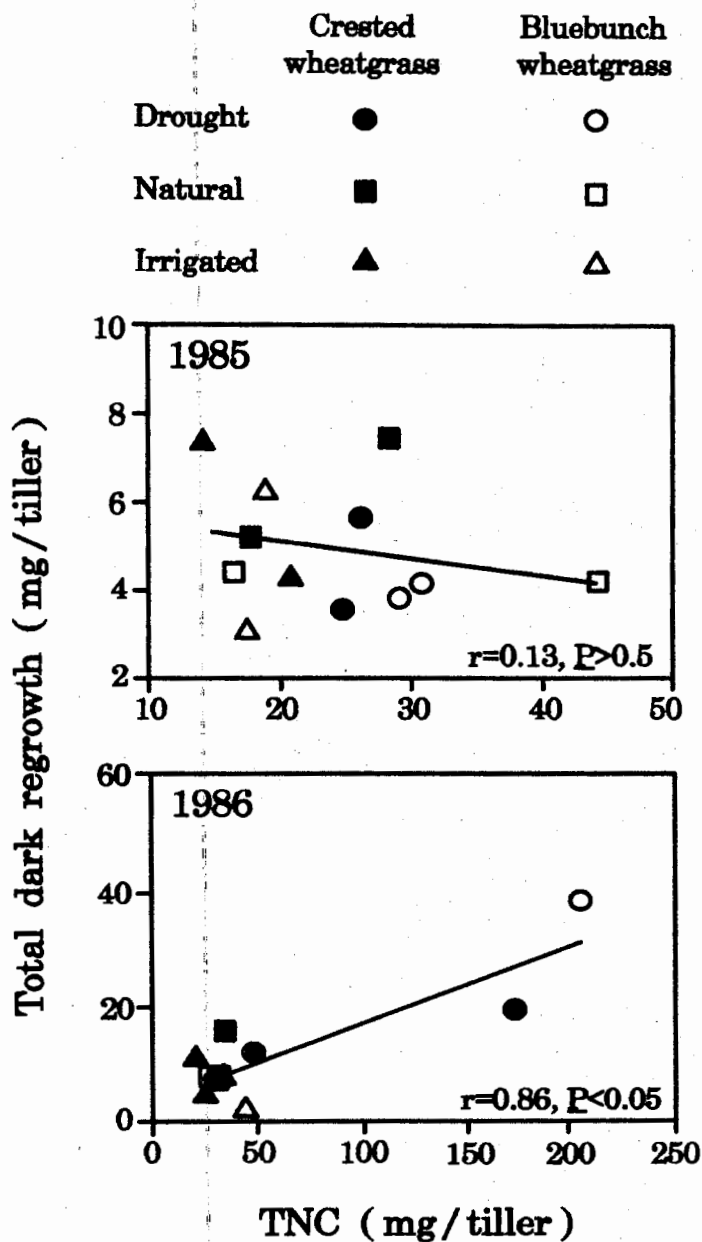


Figure 2. Relationship between root and crown TNC (total nonstructural carbohydrates) pools and regrowth of crested and bluebunch wheatgrasses produced in the dark under irrigated, natural rainfed, and drought conditions. Regrowth produced in the dark quantifies the contribution of carbohydrate reserves to regrowth in the absence of current photosynthesis. A significant, positive relationship between TNC pools and regrowth was only observed in 1986 when severely water stressed plants had unusually large TNC pools and produced large amounts of regrowth. Under all other growth conditions in both years the relationship was not significant (from Busso et al. 1990).

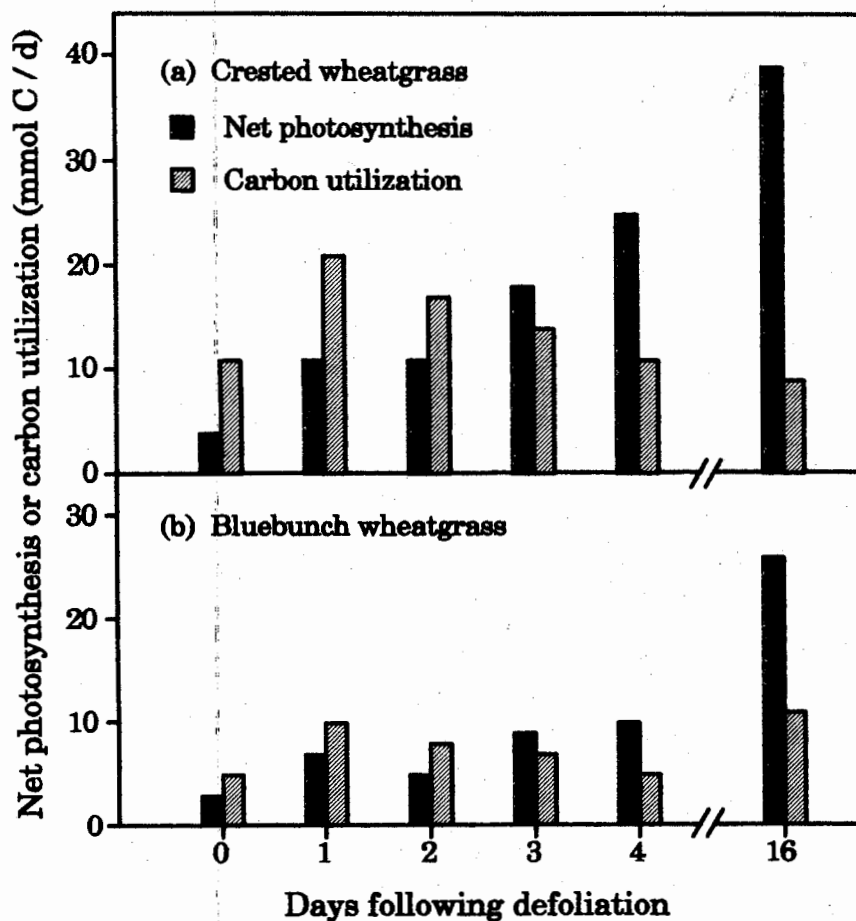


Figure 3. Daily net photosynthetic carbon uptake and carbon utilization by shoots and crowns of (a) crested wheatgrass and (b) bluebunch wheatgrass plants on the day of defoliation (day zero) and 1, 2, 3, 4, and 16 days following an early spring defoliation. The contribution of current photosynthesis exceeds the requirement of shoot regrowth and shoot and crown respiration within 3 days of severe defoliation in both species (from Richards and Caldwell 1985).

Several other considerations further limit the utility of carbohydrate pools as indicators of regrowth potential. First, TNC mass does not always account for the total reductions in crown weight or the amount of regrowth produced in the dark following defoliation indicating that compounds other than nonstructural carbohydrates (e.g., proteins, hemicellulose and organic acids), which are not commonly evaluated, may also function as carbon or energy sources during regrowth (Davidson and Milthorpe 1965, 1966, Richards and Caldwell 1985). Second, the carbohydrate concentration or pool-size necessary to ensure plant survival and maintain maximum leaf replacement potential has not been established for individual species or species groups. Carbohydrate concentrations of 1-6% have been suggested as minimal concentrations in grasses, but these estimates are far from conclusive (Caldwell 1984). Considering the dynamics of carbohydrate allocation, accumulation, and utilization

it is unlikely such a simple estimate would have much predictive value. Third, total carbohydrate pools must be quantified by determining both carbohydrate concentrations and weight of the associated plant organ(s) (Richards and Caldwell 1985). TNC concentration may decrease while total TNC pool size increases during intervals of rapid plant growth (Caldwell et al. 1981). Fourth, inconsistencies associated with analytical techniques for carbohydrate extraction have also curtailed research progress. TNC estimates derived by acid extraction may be two to three times greater than for boiling water extraction because a greater amount of structural carbohydrates are digested (Smith 1972, 1981, Richards and Caldwell 1985).

Carbohydrate pools play an important role in initiating plant growth when photosynthetic capacity is severely limited. However, the limited amount of carbohydrates stored in tiller bases (crowns and sheaths), the inaccessibility of root carbohydrates to support shoot growth, and the poor correlation between shoot growth and carbohydrate concentrations or pools limits their use as an effective index of shoot regrowth in perennial grasses and potentially other growth forms as well. The traditional interpretation of carbohydrate reserves appears to have been founded on an over-simplified, static conceptualization of the carbon economy of plants. The amount of residual photosynthetic area or the availability of active meristems following defoliation may be of equal or greater consequence in determining potential leaf regrowth of grasses.

### Apical dominance

Apical dominance in grasses was initially described by Leopold (1949) as the production of auxin within the apical meristem which suppressed the growth of axillary buds. This interpretation was based on the earlier work of Thimann and Skoog (1933) who had established that auxin controlled lateral bud growth in bean (*Vicia Faba* L.). Leopold (1949) destroyed apical meristems in twenty plants of each of two annual grasses, teosinte (*Euchlaena mexicana* Schrad.) and barley (*Hordeum vulgare* L.), and observed tillering to increase while a synthetic auxin (naphthalene acetic acid) applied to the location of the excised apical meristems reversed this effect. This single investigation has largely shaped our perception of how the tillering process is regulated in grasses, but has been criticized as being less than definitive from an experimental perspective (Bunting and Drennan 1966, Williams and Langer 1975).

This theory of apical dominance, referred to as the direct theory of auxin inhibition, encountered several technical difficulties and was soon abandoned for a theory proposing a more indirect effect of auxin. Major inconsistencies associated with the direct inhibition theory included: 1) experimental auxin concentrations several times greater than endogenous concentrations were required to inhibit bud growth, 2) auxin concentrations frequently increased rather than decreased in lateral buds shortly following plant decapitation, and 3) unidirectional auxin transport from the apical meristem toward the stem base limited the potential for entry into lateral buds (Gregory and Veale 1957, Martin 1987). The alternative indirect theory proposed that auxin inhibited lateral bud growth by either the production of a secondary inhibitor or by the regulation of resource allocation to regions other

than lateral buds. Unfortunately, the direct inhibition theory continues as the prevailing view of apical dominance in rangeland ecology and management even though insight into the physiological process has advanced substantially.

Continued adherence to the direct inhibition theory of apical dominance poses numerous inconsistencies of particular relevance to rangeland ecology and management (Murphy and Briske 1992). For example, tiller recruitment has been observed to occur in response to grazing even though apical meristems of little bluestem (*Schizachyrium scoparium* var. *frequens* Hubb.) tillers were insufficiently elevated to be removed by livestock (Butler and Briske 1988). Conversely, removal of apical meristems from tillers of crested wheatgrass and bluebunch wheatgrass did not always accelerate tiller recruitment (Olson and Richards 1988a, Richards et al. 1988). In contrast to the responses of temperate species, axillary bud growth was stimulated by both apical meristem and leaf removal in three tropical grasses. These conflicting observations attest to the complexity of apical dominance in perennial grasses and the limited interpretative ability of the direct inhibition theory.

Rigid adherence to the direct inhibition theory of apical dominance may have biased our interpretation of tillering following plant defoliation. Both Ellison (1960) and Jameson (1963), following a thorough evaluation of the early literature, concluded that defoliation does not consistently increase tillering in perennial grasses. Furthermore, much of the recent literature substantiates their conclusions (Murphy and Briske 1992). For example, four consecutive years of biweekly defoliation to stubble heights of 5, 10, and 15 cm decreased tiller densities proportionately in pinegrass (*Calamagrostis rebescens* Buckl.) (Stout et al. 1981) (Fig. 4). Two seasons of livestock grazing did not increase, and in the case of intensive grazing, decreased the total number of tillers recruited from crested wheatgrass (Olson and Richards 1988b) and little bluestem (Butler and Briske 1988) in comparison with ungrazed plants. The complexity of the physiological mechanisms regulating axillary bud growth (e.g., apical dominance, resource availability, and phytochrome reactions) and the large number of potentially intervening factors (e.g., environmental variables, species-specific responses, stage of phenological development, frequency and intensity of defoliation) also minimizes the likelihood of consistent tillering responses to defoliation.

Defoliation may more appropriately be viewed as a means of altering the timing or seasonality of tiller recruitment rather than increasing total tiller recruitment over the long-term in many range grasses (Murphy and Briske 1992). Tillers are frequently initiated within 2-3 weeks of defoliation (Olson and Richards 1988a, Richards et al. 1988), and are much more obvious following partial removal of the canopy. However, this short-term "flush" of tiller initiation following defoliation may reduce maximum tiller recruitment in defoliated plants relative to periods of maximum recruitment in undefoliated plants (Butler and Briske 1988). In addition, increased tiller recruitment following spring grazing of crested wheatgrass did not contribute to tiller replacement the following season because of greater tiller mortality in grazed plants than in ungrazed plants during the winter (Olson and Richards 1988b). Therefore, in spite of a brief period of increased recruitment immediately following defoliation, defoliated plants may not produce a greater number of tillers than undefoliated plants when evaluated over one or more growing seasons.



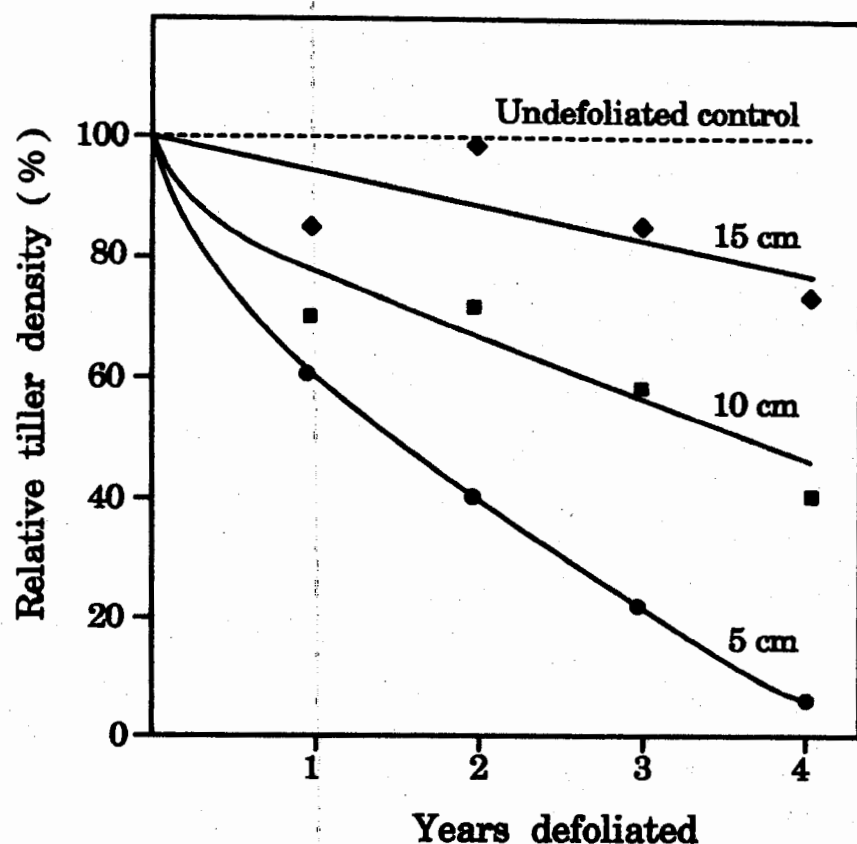


Figure 4. Relative density of pinegrass tillers in response to biweekly clipping to stubble heights of 5, 10, and 15 cm for four successive years in comparison with tiller densities of undefoliated plants. These data demonstrate that tillering was not promoted by defoliation at any time in this species population grown in the field (from Stout et al. 1981).

The current theory of apical dominance proposes that auxin produced in the apical meristem or young leaf primordia provides the principle correlative signal for bud inhibition and that a second hormone, cytokinin, is also involved (Phillips 1975, Hillman 1984, Cline 1991). Auxin appears to catabolize or prevent cytokinin transport from the root system thereby preventing bud growth. Two additional hormones, abscisic acid (Nojima et al. 1989) and ethylene (Harrison and Kaufman 1982), both of which are plant growth inhibitors, have also been associated with apical dominance in grasses, but their specific functions have not yet been established. Additional insight into the physiological mechanism(s) of apical dominance and inconsistent tillering responses following defoliation indicate that a more comprehensive model is required to interpret and explain the timing and magnitude of tiller initiation in grasses.

Radiation quality has been implicated as an environmental signal regulating tiller initiation in grasses (Kasperbauer and Karlen 1986, Casal et al. 1987, Simon and Lemaire 1987). Red radiation is attenuated more rapidly than far-red radiation as it

passes through a plant canopy. A reduction in the red:far-red ratio associated with increasing canopy development may signal the diminishing availability of resources and suppress additional tiller initiation (Deregibus et al. 1985, Casal et. al. 1987). Alternatively, partial canopy removal by grazing may increase the red:far-red ratio and promote tillering in the absence of disturbance to the apical meristem. The role of radiation quality as an environmental signal requires documentation in a greater number of species under field conditions prior to its acceptance as a process common to grasses. A cause-effect relationship has not been established between the red:far-red ratio and the physiological mechanisms of apical dominance.

### **Compensatory processes**

Range plant responses to defoliation were initially investigated to minimize the detrimental consequences of livestock grazing. This perspective on plant response to grazing is inherent in much of the early scientific literature. However, an alternative perspective indicating that an optimal level of grazing may increase plant growth (i.e., overcompensation) above that of ungrazed plants was proposed by several ecologists in the mid-1970's (Dyer 1975, McNaughton 1976, 1979). This perspective stimulated a great deal of research exploring the beneficial aspects of grazing on plant growth and function. Several novel research hypotheses were proposed and evaluated. The status of the most significant of these hypotheses is summarized below.

#### *Photosynthesis*

Grazing has long been known to dramatically affect the photosynthetic capacity of plants by reducing total photosynthetic area. However, it has more recently been appreciated that the relative proportion of foliage elements (i.e., blade, sheath, culm), age of individual foliage elements and photosynthetic rate of foliage elements are also important determinants of photosynthetic capacity following defoliation. Removal of young foliage elements, which attain maximum photosynthetic capacity at about the time of complete expansion, reduces canopy photosynthesis to a much greater extent than equivalent removal of older foliage (e.g. Ludlow and Charles-Edwards 1980, Gold and Caldwell 1989, 1990). Photosynthetic rates among foliage elements of comparable age often vary with blades frequently possessing greater rates than sheaths or culms (Caldwell et al. 1981, Nowak and Caldwell 1984, Ludlow and Mott 1988). Therefore, the photosynthetic capacity of defoliated plants may differ from that of nondefoliated plants because of a modification in the proportion and age structure of foliage elements, in addition to a reduction in total photosynthetic area and altered microenvironmental variables within the canopy.

Greater photosynthetic rates of leaves on defoliated plants than for comparably aged leaves on undefoliated plants is referred to as compensatory photosynthesis (Detling et al. 1979b, Nowak and Caldwell 1984) (Fig. 5). This response occurs over a several day period in both mature and expanding leaves remaining on the defoliated plant as well as leaves initiated following defoliation. Compensatory photosynthesis has been observed in many species. A few examples among grasses include crested wheatgrass and bluebunch wheatgrass (Nowak and Caldwell 1984),



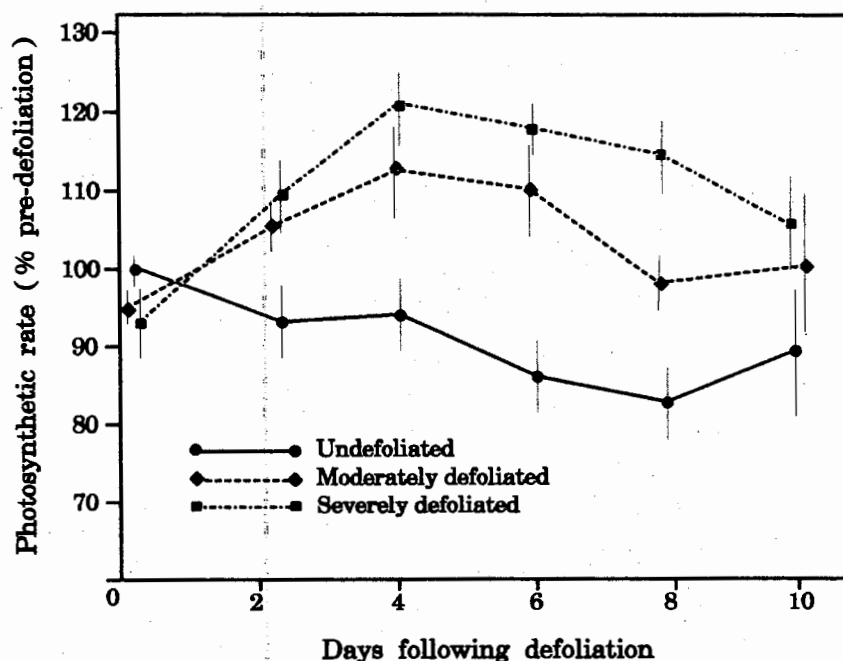


Figure 5. Photosynthetic rates (expressed as a percentage of the pre-defoliation rate) of expanded leaves on undeveloped tillers of western wheatgrass plants from which 50 (moderately defoliated) or 75% (severely defoliated) of all tillers had been defoliated at ground level. Photosynthetic rates decreased slightly immediately following defoliation, but increased to a maximum 4 days following defoliation while photosynthetic rates of leaves on undeveloped plants declined with age during the 10 day period (from Painter and Detling 1981).

western wheatgrass [*Pascopyrum smithii* (Rydb.) A. Löve, syn: *Agropyron smithii* (Rydb.) (Painter and Detling 1981), sheep fescue (*Festuca ovina* L.) (Atkinson 1986), Italian ryegrass (*Lolium multiflorum* Lam.) (Gifford and Marshall 1973), and (*Themeda triandra* Forsk.) (Wallace et al. 1984), as well as numerous herbaceous and woody dicotyledonous species. However, photosynthetic rates less than or equal to those on undeveloped plants have also been reported for some species following defoliation (Ryle and Powell 1975, Detling et al. 1979a, Ferree and Hall 1981, Atkinson 1986). Contrasting reports of reduced photosynthetic rates and those reporting compensatory photosynthesis have not been adequately explained in most cases. In addition, repeated severe defoliation can reduce photosynthetic rates, even in very grazing-tolerant species (Wallace et al. 1985, Hodgkinson et al. 1989).

Compensatory photosynthesis results from rejuvenation or inhibition of the normal decline in photosynthetic capacity as leaves age and senesce. Rejuvenation of net photosynthetic rate in leaves on defoliated plants may be partial, complete or, in some cases, result in photosynthetic rates that exceed those of newly developed leaves on undeveloped plants (Hodgkinson 1974, Heichel and Turner 1983). The ability of mature leaves to rejuvenate their photosynthetic capacity declines as they age and older leaves also require longer than young leaves to achieve maximum recovery (Hodgkinson 1974, Nowak and Caldwell 1984). Leaf photosynthetic rates

generally increase less than 50% of pre-defoliation rates. However, relative to the initially low rates of net photosynthesis in older leaves, proportional increases may be greater in old than in young leaves following defoliation. Leaves on defoliated plants often possess greater photosynthetic rates than comparable leaves on undefoliated plants even if they are not rejuvenated because the normal decline in photosynthetic capacity of aging leaves is inhibited (Gifford and Marshall 1973).

Compensatory photosynthesis appears to mechanistically result from a greater or more efficient enzymatic capacity to assimilate  $\text{CO}_2$ , rather than an enhancement of stomatal  $\text{CO}_2$  conductance (Gifford and Marshall 1973). Leaves displaying compensatory photosynthesis generally have increased chlorophyll, nitrogen and soluble protein contents (Satoh et al. 1977, Nowak and Caldwell 1984, Yamashita and Fujino 1986). Ribulose-1, 5-bisphosphate carboxylase/oxygenase (RuBPCO) activity or amount, capacity for RuBPCO regeneration, and electron transport capacity have also been documented to increase within several days following defoliation (Neales et al. 1971, Jenkins and Woolhouse 1971, von Caemmerer and Farquhar 1984).

The mechanisms regulating compensatory photosynthesis have not yet been definitively established. Compensatory photosynthesis can be induced by increases in irradiance on residual photosynthetic tissues, modification of physiological plant function induced by defoliation or by a combination of these processes. However, it has been well documented that compensatory photosynthesis can occur independently of changes in the light environment associated with plant defoliation (Hodgkinson et al. 1972, Hodgkinson 1974, Woledge 1977). Increased sink strength produced by the rapid growth of defoliated shoots and the increased transport of hormones or other substances to shoots from roots represent the two prominent physiological modifications. Compensatory photosynthesis is apparently induced by phytohormones (potentially cytokinins) transported from roots to leaves on defoliated plants, rather than in response to direct sink:source interactions (Wareing et al. 1968, Carmi and Koller 1979). The absence of an *immediate* increase in photosynthesis following an increase in the sink:source ratio following defoliation further supports the conclusion that compensatory photosynthesis is not the direct result of increased sink strength (Geiger 1976, von Caemmerer and Farquhar 1984).

Although the physiological process of compensatory photosynthesis does occur in a large number of plants, its significance to grazing tolerance and plant productivity must be assessed on a case-by-case basis because of interspecific variation and the influence of a large number of plant attributes and environmental variables. For example, compensatory photosynthesis occurs in both crested wheatgrass and bluebunch wheatgrass, but is most evident in the oldest leaves which comprise a small percentage of the total photosynthetic area (Nowak and Caldwell 1984). The total amount of compensatory photosynthesis resulting from this portion of the canopy is insufficient to explain the large difference in grazing tolerance between these two species and even very grazing tolerant species fail to exhibit compensatory photosynthesis under all conditions. Total photosynthetic area, the occurrence of favorable environmental conditions, and age of photosynthetic tissues may have an equal or greater effect on the total carbon gain capacity of plants than does photosynthetic rate.

### Allocation priorities

Defoliation consistently modifies allocation priorities within plants in addition to affecting total carbon gain. Increased carbon export from remaining photosynthetically active leaves and increased carbon allocation to growing shoots minimizes the reduction in the absolute amount of carbon available to shoots following defoliation (Marshall and Sagar 1965, Bassmann and Dickmann 1985). For example, a 51% reduction in whole plant photosynthesis on the day of defoliation reduced carbon allocation to shoots by only 40% in barley (Ryle and Powell 1975). The relative amount of carbon allocated to defoliated shoots continued to increase during the next 7 days. Increased carbon allocation to shoots occurred concomitantly with a comparable reduction in allocation to roots, which received much less carbon than in undefoliated plants (Ryle and Powell 1975) (Fig. 6).

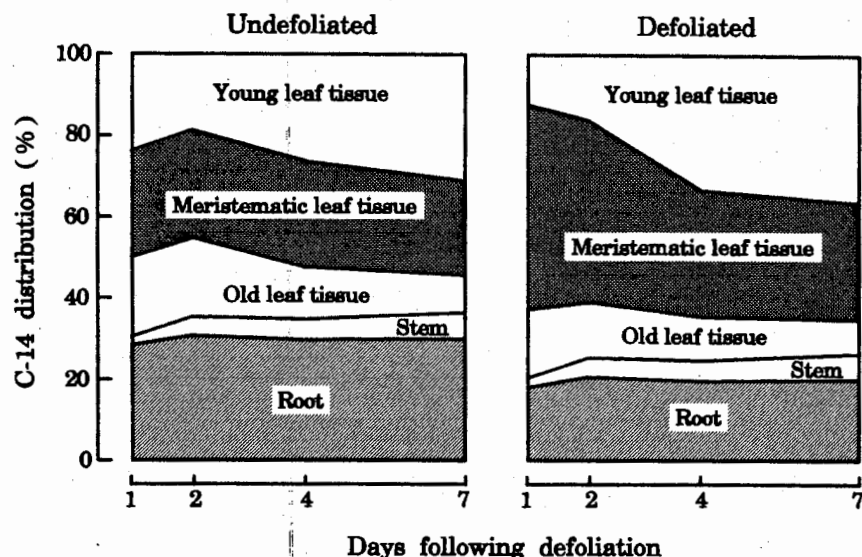


Figure 6. Relative allocation of  $^{14}\text{C}$ -labeled photosynthate to various tissues of defoliated and undefoliated barley plants. Plants were labeled for 25 minutes and harvested at 1, 2, 4, and 7 days following defoliation. Defoliated plants were cut at the ligule of the 3rd leaf at the beginning of day 1. Carbon allocation to young leaf tissue including the apical meristem, leaf primordia, and expanding leaves increased while carbon allocation to roots decreased at day 4 and 7 following defoliation (from Ryle and Powell 1975).

Defoliation may also modify allocation priorities within the shoot system. A greater proportion of available carbon is allocated to leaf blades than leaf sheaths following defoliation of blue grama [*Bouteloua gracilis* (H.B.K.) Lag. ex Steud.] (Detling et al. 1979b) and western wheatgrass (Painter et al. 1989). Increased blade:sheath ratios may function to increase the total photosynthetic capacity of plants immediately following defoliation. Leaf blades often have a greater photosynthetic capacity than leaf sheaths (Caldwell et al. 1981, Ludlow and Mott 1988). Therefore, carbon allocation to blades, rather than sheaths, would potentially provide the greatest photosynthetic gain. However, this response requires evaluation in a greater number of species, consideration of water and nitrogen-use efficien-

cies, and determination of blade and sheath longevities before it is assumed to be a widely distributed tolerance mechanism (Jaramillo and Detling 1988, Polley and Detling 1988).

Inter-tiller resource (C and N) allocation following defoliation provides a potential mechanism of herbivory tolerance by facilitating tiller survival and rapid reestablishment of photosynthetic surfaces. Rates of resource import from attached, undefoliated tillers increase rapidly following partial tiller defoliation with multiple defoliations of an individual tiller further increasing the rate of resource import (Gifford and Marshall 1973, Welker et al. 1985). However, increased rates of resource import may not necessarily represent an absolute increase in resource accumulation because defoliation reduces the total resource requirement by decreasing shoot mass and subsequently sink size (Welker et al. 1987). Resource import from attached undefoliated tillers again decreases to a low level with the reestablishment of photosynthetic surfaces within several days of a single defoliation (Gifford and Marshall 1973, Welker et al. 1985, 1987). For example, growth of tall fescue plants increased progressively following defoliation when either a greater percentage of tillers remained undefoliated or when the defoliation intensity was reduced (Matches 1966). A portion of this growth response was attributable to increased rates of  $^{14}\text{C}$  allocation from undefoliated to defoliated tillers (Watson and Ward 1970). Similar conclusions have been drawn from investigations with several rhizomatous graminoids (Mattheis et al. 1976, Archer and Tieszen 1986, Jonsdottir and Callaghan 1989).

Short-term modifications in resource allocation patterns following defoliation are controlled by the relative sink strengths of the respective tissues involved, either through source-sink feedback or hormonal signals (e.g. Bucher et al. 1987, Bassmann and Dickmann 1985, Geiger and Fondy 1985). Apical meristems and associated young leaves are sufficiently strong sinks to deprive other sinks, such as roots or young tillers, of resources until the amount of source tissue increases to exceed the demands of these sinks. If defoliation removes the predominant shoot sinks (apical and intercalary meristems), available resources are allocated to weaker sinks including roots, or storage in sheaths and stems (Bucher et al. 1987). Long-term changes in allocation patterns are mediated by hormonal signals and resulting changes in developmental morphology and sink activities (Wareing et al. 1968, Geiger 1976, Geiger and Fondy 1985).

Flexible carbon allocation patterns may be causally associated with grazing tolerance in grasses. As an example, defoliated crested wheatgrass plants reallocate carbon to reestablishment of photosynthetic tissue while temporarily reducing allocation to roots (Caldwell et al. 1981, Richards 1984). Reallocated carbon is converted into leaf area following rapid activation and growth of axillary buds (Mueller and Richards 1986). Conversely, bluebunch wheatgrass continues to allocate a large proportion of carbon to the root system following defoliation, thus reestablishing its canopy much less rapidly than crested wheatgrass. These data indicate that a short-term reduction in carbon allocation to root growth minimizes the detrimental effects of defoliation on leaf production and the long-term competitive ability of grazed plants. Short-term effects of defoliation on competitive ability are discussed below.

### Nutrient absorption

Root respiration and nutrient acquisition are rapidly reduced following shoot defoliation (Fig. 7). Root respiration begins to decline within hours after defoliation and it is substantially reduced within 24 hours (Davidson and Milthorpe 1966, Clement et al. 1978). Concomitant with a defoliation-induced reduction in root respiration, nutrient absorption is also strongly inhibited. Nitrate absorption decreased within 30 minutes following 70% shoot removal (dry weight basis) in perennial ryegrass (*Lolium perenne* L.), and decreased to less than 40% of the pre-defoliation rate within 2 hours (Clement et al. 1978). Nitrate uptake continued to decline over the next 4–12 h and remained minimal for 2 or 7 days before recovery began under high and low light conditions, respectively. Nitrate absorption did not increase until plants reestablished a positive carbon balance (Clement et al. 1978).

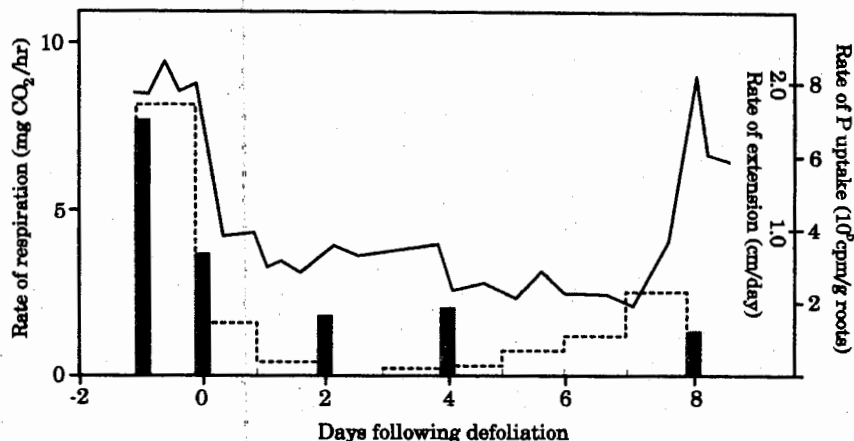


Figure 7. Rates of respiration (solid line), root length extension (broken line), and relative uptake of <sup>32</sup>P (solid bars) in orchardgrass plants prior to and for 8-days following defoliation to a height of 2.5 cm on day 0. Reductions in root growth and function result from a decrease in total carbon assimilation and a reduction in the relative proportion of carbon allocated to roots following defoliation. Plants were grown in solution culture to allow continuous physiological measurements (from Davidson and Milthorpe 1966).

Rapid reductions in root respiration and nutrient absorption following defoliation are positively related to the intensity of plant defoliation (Davidson and Milthorpe 1966, Thorpeirsson 1988). Similarly to defoliation, shading can also produce large decreases in root respiration and nutrient absorption (Massimino et al. 1981, Aslam and Huffaker 1982, Bloom and Caldwell 1988). Defoliation-induced reductions in root respiration and nutrient absorption result from a decrease in total carbon assimilation and a decrease in the relative proportion of carbon allocated to roots following defoliation.

Root function in plants from infertile habitats apparently differs from that of the more productive temperate species considered previously. Root growth, respiration and nutrient absorption are often maintained, or even increased, following defoliation (Chapin and Slack 1979). In addition to these short term responses, long-term increases in root respiration and nutrient absorption have been found in both tropical and tundra graminoids growing under nutrient-limited conditions



(Chapin and Slack 1979, Ruess et al. 1983). Energy requirements for root respiration and nutrient absorption were most likely met by carbohydrates translocated from remaining shoot tissues, or following rapid reestablishment of leaf area, because TNC concentrations in the roots were comparable to those measured in temperate perennial grasses (Davidson and Milthorpe 1966, Chapin and Slack 1979, Bloom and Caldwell 1988).

Accelerated rates of nutrient absorption have also been documented in several temperate, perennial grasses including western wheatgrass (Polley and Detling 1988) and blue grama (Jaramillo and Detling 1988) following defoliation. Mean nitrogen accumulation rate increased 200 and 122% in western wheatgrass and blue grama, respectively, even though defoliation reduced root growth in both species. A greater relative growth rate of shoots in defoliated plants may have increased shoot sinks thereby stimulating nitrogen accumulation (Polley and Detling 1988). In addition, growth may have been limited by nutrients other than carbon, in a manner comparable to that of plants in infertile habitats, thereby sustaining carbon allocation belowground to maintain root respiration and nutrient absorption.

Increased rates of root respiration and nutrient absorption in defoliated plants may function as compensatory mechanisms to offset nutrient losses to herbivores (Ruess 1984, Jaramillo and Detling 1988, Polley and Detling 1988). Increased rates of nutrient absorption may potentially restore the root:shoot equilibrium to defoliated plants and enhance growth and competitive ability. This compensatory mechanism may be especially effective in systems where grazing increases nitrogen availability by accelerating the rate of nutrient cycling (Polley and Detling 1988, Hik and Jefferies 1990). However, species-specific responses, the influence of environmental variables, and physiological mechanisms must be more clearly understood before compensatory nutrient absorption can be assumed to operate in a majority of grass species.

#### *Shoot growth*

Defoliation frequently decreases plant production because leaf removal reduces the potential for total carbon gain (e.g. Belsky 1986). However, the occurrence of compensatory physiological processes raises the possibility that growth of defoliated plants may approach or exceed that of undefoliated plants. The term "compensatory growth" has been used to describe plant growth responses ranging from a partial replacement of removed biomass to production exceeding that of ungrazed plants. Specific terms to clarify these growth responses include overcompensation which refers to instances where the cumulative total weight of defoliated plants, including biomass removed by defoliation, exceeds the cumulative total weight of undefoliated plants (Belsky 1986). Partial compensation defines instances where more growth is produced by defoliated plants than would be expected if no increase in growth rate had occurred. The grazing optimization hypothesis is based on the occurrence of compensatory growth and states that primary production increases above that of ungrazed plants with an increase in grazing intensity to an optimal level and then primary production decreases with greater grazing intensity (Dyer 1975, McNaughton 1976, 1979) (Fig. 8). Unfortunately, the general applicability of the grazing optimization hypothesis to vegetation management has not yet been resolved.

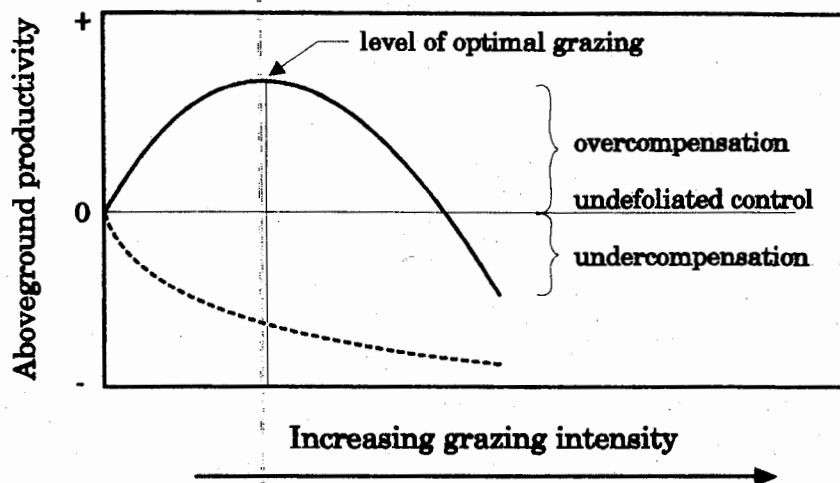


Figure 8. Illustration of the grazing optimization hypothesis proposing that aboveground primary productivity increases, above that of ungrazed plants, as grazing intensity increases to an optimal level and then decreases at greater grazing intensities (solid line). Values above those of undefoliated (control) plants indicate an increase in productivity (overcompensation) while values below those of undefoliated plants indicate a decrease in productivity (undercompensation) in response to grazing (from Belsky 1986). The alternative hypothesis proposes that grazing progressively suppresses aboveground productivity with increasing intensity (dashed line). A large number of potential production responses exist between these two extremes.

Much of the evidence in support of the grazing optimization hypothesis has been derived from containerized plant investigations conducted under highly experimental conditions (Belsky 1986). Overcompensation has been documented for *Kyllinga nervosa* Steud., an African  $C_4$  sedge (McNaughton et al. 1983, Wallace et al. 1985), *Themeda triandra* (Oosterheld and McNaughton 1988) and *Sporobolus kentrophyllus* K. Schum. (Georgiadis et al. 1989). Although these data substantiate the occurrence of overcompensation, they also demonstrate that specific growth conditions are required to induce this response. Plants with relatively low growth rates (i.e., unfavorable conditions for growth) that are provided with relatively long intervals between defoliation events possess the greatest potential for compensatory growth (Hilbert et al. 1981, Georgiadis et al. 1989).

Examples of overcompensation from field investigations are less numerous and are frequently less definitive than those from containerized plant investigations. Overcompensation by individual plants has been observed in scarlet gilia [*Ipomopsis aggregata* (Pursh) V. Grant], a herbaceous dicot from the Intermountain West (Paige and Whitham 1987), bitterbrush [*Purshia tridentata* (Pursh) DC.], a defoliation tolerant Intermountain shrub (Bilbrough and Richards, 1993), and crested wheatgrass, an Eurasian perennial grass (Olson and Richards 1988a). Examples of compensatory growth within plant communities include *Andropogon greenwayi* Napper grasslands in the Serengeti Plains of east-central Africa (McNaughton 1979), intertidal graminoid communities near Hudson Bay (Cargill and Jefferies 1984a and b), and a mixed prairie in north-central Texas (Heitschmidt et al. 1982). A greater diversity of communities require investigation to more clearly define the significance of compensatory growth to the production dynamics of grazed systems.

Numerous mechanisms have been proposed to explain the occurrence of compensatory growth. Intrinsic mechanisms, which are associated with herbivore-induced physiological processes, have received the greatest attention (McNaughton 1979, 1983) while extrinsic mechanisms, those involving herbivore-induced environmental modification, have been less thoroughly investigated, but may be of equal or greater importance. For example, accelerated rates of nutrient cycling appear to play an essential role in the occurrence of compensatory growth within plant communities (Ruess and McNaughton 1987, Hik and Jefferies 1990) thus verifying the assumption of Ellison (1960) that if vegetation benefits from herbivory it will occur as a result of ecosystem processes rather than individual plant function. Herbivory increases the rate of mineralization thereby increasing the rate at which nutrients become available for reabsorption within the system (Woodmansee et al. 1981, Floate 1981). However, intrinsic mechanisms must be the predominant explanation for compensatory growth in individual plant investigations, especially those in which defoliation is imposed by clipping.

Both intrinsic and extrinsic mechanisms presumably contribute to compensatory growth, but their relative contribution varies with species, defoliation regime, associated environmental variables and the ecological scale investigated. Compensatory growth in *Ipomopsis arizonica* (Greene) Wherry decreased in response to increasing interspecific competition, decreasing nutrient availability, and grazing during the later portion of the growing season (Maschinski and Whitham 1989). These data indicate that the potential occurrence of compensatory growth is not a constant species-specific response.

Currently, insufficient data are available to support the conclusion that overcompensation is a widely occurring phenomena in grassland ecosystems. Belsky (1986) reviewed 48 reports in the literature referencing aboveground production in response to grazing and found that 34 documented a decrease in production, 5 reported no change and 9 reported an increase in production. However, it is possible that plants increase their growth rate following defoliation, but only partially compensate for the total amount of biomass removed (Hilbert et al. 1981, Belsky 1986). Partial compensation implies that plant productivity is not suppressed in direct proportion to frequency and intensity of defoliation imposed (McNaughton 1983, 1985). Additional quantification of the magnitude, frequency and underlying mechanisms of compensatory growth is required to definitively assess its ecological significance in grazed systems.

## Biotic interactions

### *Defoliation x competition interactions*

Plants in field settings do not respond to grazing as isolated individuals, but against a background of intra- and inter-specific competition. The frequency and intensity of grazing between and among species affects these competitive interactions and directly influences growth following defoliation (Mueggler 1972, Banyikwa 1988). The rapid and substantial affect of defoliation on resource competition has clearly been illustrated in a perennial grass-shrub association. Big sagebrush [*Artemisia tridentata* ssp. *vaseyana* (Rydb.) Beetle] acquired 6 times as

much labeled phosphorus from interspaces shared with defoliated (85% canopy removal) bluebunch wheatgrass or crested wheatgrass neighbors as it did from interspaces shared with undefoliated grass plants (Caldwell et al. 1987) (Fig. 9). Significant increases in phosphorus absorption by big sagebrush occurred within 2 weeks of grass defoliation indicating that belowground competition is rapidly modified by grazing.

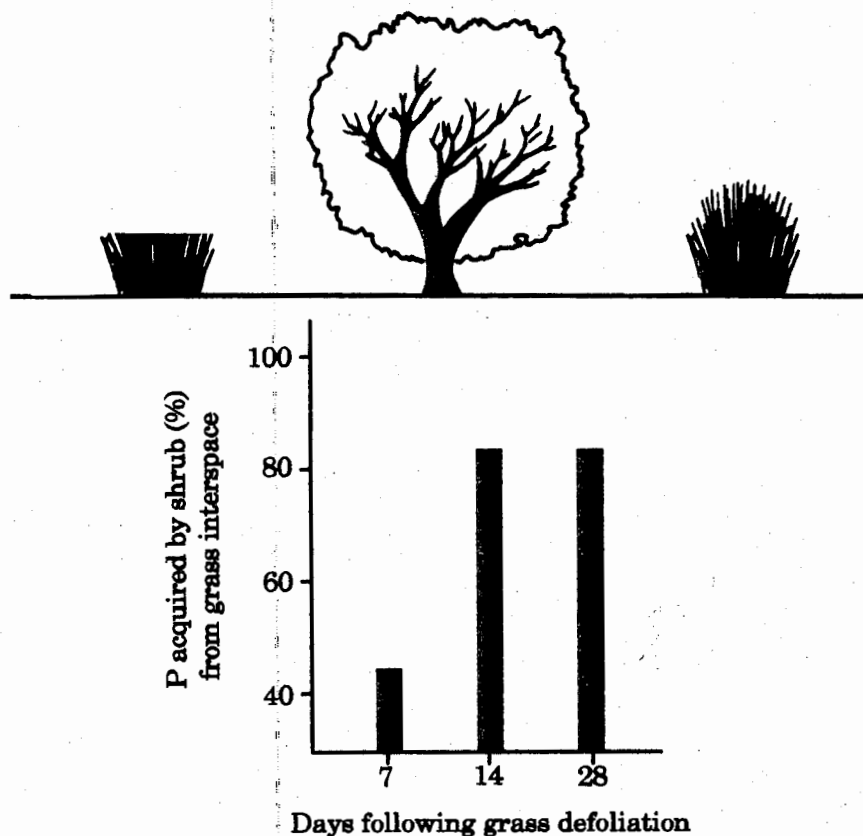


Figure 9. Percentage of labeled phosphorus acquired by big sagebrush from interspaces shared with bluebunch wheatgrass plants at 7, 14 and 28 days following removal of 85% of the grass canopy. Big sagebrush acquired as much as 6 times the amount of phosphorus from interspaces shared with defoliated bunchgrass competitors as it did from interspaces shared with undefoliated bunchgrass plants (from Caldwell et al. 1987).

The first, and most direct, mechanism by which herbivores alter competitive interactions involves selective plant utilization based on the relative display of avoidance mechanisms among species (Briske 1991). Species grazed severely are placed at a disadvantage when competing with associated species grazed less severely. Production of bluebunch wheatgrass plants subjected to 50% canopy removal just prior to culm elongation was equivalent to the production of undefoliated plants growing with full competition when competition was reduced by clipping the associated vegetation within a 90 cm radius to ground level (Mueggler

1972). When competition from associated vegetation was completely removed by tilling within a 90 cm radius, defoliated plants produced three times the biomass of undefoliated plants growing with full competition. These data clearly demonstrate that the ability of plants to respond to defoliation is not only determined by an inherent suite of morphological and physiological characteristics, but also by competition from associated species (Caldwell 1984). The inherent competitive ability of a species within the community is an important determinant of its persistence in a grazed system.

The second mechanism by which grazing may alter competitive interactions among plant species involves the differential ability of species to regrow following a similar intensity of defoliation based upon the possession of various tolerance mechanisms (Briske 1991). Species rapidly replacing photosynthetic surfaces gain a competitive advantage over associated species that grow more slowly following defoliation. Crested wheatgrass exhibits a 2-3 fold greater rate of leaf replacement than does bluebunch wheatgrass following an equivalent intensity of defoliation (Caldwell et al. 1981, Richards 1984, Richards and Caldwell 1985). This response is partially a function of the ability of crested wheatgrass to rapidly initiate a greater number of tillers and to allocate carbon to reestablish photosynthetic surfaces while temporarily decreasing allocation to the root system. Inequitable responses to defoliation between these two species can be attributed to the differential expression of tolerance mechanisms and inherent competitive ability because the similarity in plant chemistry and architecture minimizes the influence of avoidance mechanisms (Caldwell 1984).

Species grazed less severely (i.e., avoidance mechanisms), capable of regrowing more rapidly following defoliation (i.e., tolerance mechanisms), or possessing a combination of these two resistance components realize a competitive advantage within the community. These species, through the possession of a greater canopy area, are able to intercept greater amounts of solar energy, and assimilate greater amounts of carbon, further enhancing their competitive ability. Consequently, grazing resistant species are able to preempt resources that may have been utilized by associated grazing sensitive species prior to grazing (Mueggler 1972, Caldwell et al. 1987, Banyikwa 1988).

Caldwell (1984) has cautioned that many growth responses attributed to grazing resistance may actually be a consequence of the competition experienced by plants following defoliation. Although, inherent physiological and morphological mechanisms regulate plant growth following defoliation, differential resource acquisition among species may be of equal or greater significance (Mueggler 1972, Banyikwa 1988). Grazing resistance and competitive ability need to be more clearly distinguished to accurately evaluate the mechanisms of individual plant response to defoliation and to extrapolate these data to the population and community levels of grassland organization.

#### *Grazing morphs*

Long-term herbivory of several perennial grass populations is known to have selected against genotypes possessing an erect canopy architecture. Genotypic selection has been induced by several species of herbivores in approximately equal

proportion to the severity and duration of herbivory (Scott and Whalley 1984). The plant genotypes remaining in the population were characterized by a large number of small tillers with reduced leaf numbers and blade areas (Alexander and Thompson 1982, Detling and Painter 1983, Jaramillo and Detling 1988) (Fig. 10). Although the concept of biotic selection by herbivores was introduced early in the 20th century (Gregor and Sansome 1926, Kemp 1937), its potential ecological significance has only recently been appreciated.



**Figure 10.** Individual western wheatgrass plants collected from a grazing exclosure (left) and a prairie dog colony (right) at Wind Cave National Park, South Dakota. Both plants were propagated from rhizome segments collected three years earlier and maintained in a greenhouse without defoliation. Both plants were defoliated to a height of 2 cm 9 weeks prior to the time the photo was taken (from Detling and Painter 1983).

These decumbent genotypes or "grazing morphs" possess greater grazing avoidance because a greater amount of meristematic and photosynthetic tissue is protected from removal by grazing animals to facilitate growth following defoliation (Carman and Briske 1985, Briske and Anderson 1992) (Fig. 10). It is generally assumed that grazing-induced selection primarily affects architectural attributes of

plants, rather than physiological processes, including photosynthetic rate, transpiration rate and water-use efficiency (Detling and Painter 1983, Jaramillo and Detling 1988). However, root systems of grazing morphs in western wheatgrass populations had a 3-fold greater rate of nitrogen accumulation (Polley and Detling 1988) and grazing morphs of both western wheatgrass and blue grama were more productive and had less tiller mortality following defoliation than did populations with no history of grazing (Painter et al. 1989). Consequently, it must be assumed that both components of grazing resistance, avoidance and tolerance, can be affected by grazing-induced selection.

Grazing morphs are frequently less competitive than the more erect genotypes in a species population in the absence of herbivory (Eagles 1983, Painter et al. 1989). Contrastingly, genotypes characterized by fewer, larger tillers with greater leaf area are more competitive in environments with dense canopies (Grime 1977, Alexander and Thompson 1982). Correspondingly, intra-specific competition is greatest within populations composed of erect genotypes (Painter et al. 1989), but grazing is much more detrimental to the competitive ability of erect genotypes in comparison with grazing morphs because a greater portion of the canopy is removed.

The process by which grazing-induced selection occurs within species populations has not been definitively established. Although phenotypic changes occur in grazed plants, changes in plant stature and associated morphological characteristics are very likely genetically based (McNeilly 1984, Scott and Whalley 1984, Carman and Briske 1985, Painter et al. 1989). The observation that grazing morphs of western wheatgrass retained their decumbent stature in a controlled environment without defoliation for a period comparable to three growing seasons supports this viewpoint (Polley and Detling 1988). However, the involvement of developmental plasticity in the occurrence of grazing morphs can not be entirely ruled out. Several investigators have observed a loss or reduction in architectural variation between plants with contrasting grazing histories following the cessation of herbivory (Peterson 1962, Quinn and Miller 1967, Painter et al. 1989).

Although grazing-induced genotypic selection increases grazing avoidance, it also has the potential to simultaneously decrease productivity (Coppock et al. 1983, Detling 1988). Therefore, grasslands consisting of high proportions of grazing morphs within various species populations should be less productive than ungrazed or leniently grazed grasslands dominated by more erect morphs. However, grazing morphs may possess tolerance mechanisms which partially compensate for their diminished architectural stature and biomass. For example, grazing morphs have been documented to possess greater leaf N concentrations (Detling and Painter 1983), increased rates of nutrient absorption per unit root mass (Ruess et al. 1983, Polley and Detling 1988), and more rapid rates of tiller recruitment (Carman and Briske 1985, Briske and Anderson 1992). These compensatory mechanisms may potentially increase plant productivity and partially compensate for the reduced aboveground biomass associated with grazing morphs (Coppock et al. 1983, Detling 1988). However, our understanding of the extent to which species populations have been influenced by genotypic selection from domestic herbivores on a regional scale and the associated ecological consequences of this selection process is extremely limited.

## Summary And Conclusions

An evaluation of both the traditional and contemporary literature addressing individual plant responses to defoliation indicates that the widely held concepts of carbohydrate reserves and apical dominance are in need of revision. Physiological concepts were applied to rangeland ecology and management early in the century to interpret and anticipate the responses of individual plants to grazing, even though a thorough understanding of whole plant function had not yet been achieved. Consequently, concept reevaluation and refinement are a natural and necessary consequence associated with the progressive development and application of scientific information to vegetation management.

The concept of reserve carbohydrates is valid from a physiologically perspective, but was over extended as a managerial criteria. Research information developed during the past two decades indicates that carbohydrate concentrations or pools are not effective indicators of plant survival and growth following defoliation because they are much more limited than previously assumed and the total pool size of TNC has not been directly correlated with plant growth. Similarly, the direct inhibition hypothesis of apical dominance has been adopted as the sole mechanism explaining tiller development in grasses. However, physiological insight into apical dominance has advanced substantially and the traditional interpretation does not adequately explain many documented tillering responses of direct relevance to rangeland ecology and management. Even though the contemporary concept of apical dominance is not sufficiently understood to determine the specific environmental variables and physiological processes regulating tillering, the concept should no longer be viewed as the direct inhibition of lateral buds by a single growth hormone produced in the apical meristem. These observations substantiate the need to periodically reevaluate the physiological basis for vegetation management within the context of contemporary physiological information and documented plant responses.

The perspective advocating that grazing may potentially benefit plant growth and function has substantially altered our approach to plant-animal interactions research. Several physiological and morphological mechanisms potentially capable of increasing plant growth following defoliation have been identified. Compensatory photosynthesis, resource allocation, nutrient absorption and shoot growth have all been documented in a variety of species by independent investigators. However, the occurrence, magnitude and significance of these compensatory processes to individual plant and community productivity is much less clearly understood. These compensatory mechanisms may frequently prevent plant growth from being suppressed in direct proportion to the frequency and intensity of defoliation, but only infrequently increase total growth beyond that of undefoliated plants. Our understanding of the mechanisms and magnitude of compensatory growth is incomplete suggesting that the application of this concept to vegetation management is currently unwarranted.

The biotic processes of competition and grazing induced genotypic selection have long been recognized as components of grazed systems. However, the ecological significance of these processes to plant growth has only recently been fully



appreciated. Competitive ability may constrain growth to an equal or greater extent than the direct effects of defoliation. However, the relative contribution of these two processes are largely unknown, undoubtedly vary in response to plant and environmental variables, and require additional investigation. Similarly, it is well documented that both native and domestic herbivores can induce genotypic selection within species populations within a relatively short period, but the cumulative influence that grazing has had on the genotypic composition and potential productivity of rangeland plants remains largely unexplored.

The contemporary perspective on individual plant responses to grazing indicate that individual plant research is in itself insufficient to develop a complete information base for vegetation management. Individual plant research is an integral component of any investigation designed to evaluate vegetation responses to grazing, because a mechanistic understanding of community and landscape responses requires that plant and population responses must also be at least partially understood (Brown and Allen 1989, Allen and Hoekstra 1990). However, individual plant research must eventually be conducted and interpreted within the context of associated abiotic and biotic environmental variables because of the ability of these variables to constrain or modify individual plant responses. Individual plant research designed to incorporate the effects of biotic and abiotic variables provides an opportunity to determine the relative contribution of these variables on plant growth following defoliation. Individual plant data acquired in this manner will be much more appropriate for extrapolation to the plant community where vegetation management is most frequently conducted.

### Literature Cited

- Alexander, K.I. and K. Thompson. 1982. The effect of clipping frequency on the competitive interaction between two perennial grasses. *Oecologia* 53:251-254.
- Allen, T.F.H. and T.W. Hoekstra. 1990. The confusion between scale-defined levels and conventional levels of organization in ecology. *J. Veg. Sci.* 1:5-12.
- Archer, S.R. and L.L. Tieszen. 1986. Plant response to defoliation: hierarchical considerations. p. 45-59. *In*: O. Gudmundsson (ed.) *Grazing research at northern latitudes*. Plenum Publ. Corp.
- Aslam, M. and R.C. Huffaker. 1982. In Vivo nitrate reduction in roots and shoots of barley (*Hordeum vulgare* L.) seedlings in light and darkness. *Plant Physiol.* 70:1009-1013.
- Atkinson, C.J. 1986. The effect of clipping on net photosynthesis and dark respiration rates of plants from an upland grassland, with reference to carbon partitioning in *Festuca ovina*. *Ann. Bot.* 58:61-72.
- Atkinson, C.J. and J.F. Farrar. 1983. Allocation of photosynthetically-fixed carbon in *Festuca ovina* L. and *Nardus stricta* L. *New Phytol.* 95:519-531.
- Banyikwa, F.F. 1988. The growth response of two East African perennial grasses to defoliation, nitrogen fertilizer and competition. *Oikos* 51:25-30.
- Bassman, J.H. and D.I. Dickmann. 1985. Effects of defoliation in the developing leaf zone on young populus x-euramericana plants. II. Distribution of <sup>14</sup>C-photosynthate after defoliation. *For. Sci.* 31:358-366.
- Belsky, A.J. 1986. Does herbivory benefit plants? A review of the evidence. *Am. Nat.* 127:870-892.

- Bilbrough, C.J. and J.H. Richards. 1993. Growth of sagebrush and bitterbrush following simulated winter browsing: mechanisms of tolerance. *Ecology* 74:481-492.
- Bloom, A.J. and R.M. Caldwell. 1988. Root excision decreases nutrient absorption and gas fluxes. *Plant Physiol.* 87:794-796.
- Briske, D.D. and V.J. Anderson. 1992. Competitive ability of the bunchgrass *Schizachyrium scoparium* as affected by grazing history and defoliation. *Vegetatio* 103:41-49.
- Briske, D.D. 1991. Developmental morphology and physiology of grasses. p. 85-108. In: R.K. Heitschmidt and J.W. Stuth (eds.) *Grazing management: an ecological perspective*. Timber Press, Portland, Oregon.
- Brown, B.J. and T.F.H. Allen. 1989. The importance of scale in evaluating herbivory impacts. *Oikos* 54:189-194.
- Bucher, H.P., F. Machler, and J. Noesberger. 1987. Sink control of assimilate partitioning in meadow fescue (*Festuca pratensis* Huds.). *J. Plant Physiol.* 129:469-477.
- Bunting, A.H. and D.S.H. Drennan. 1966. Some aspects of the morphology and physiology of cereals in the vegetative phase. In: F.L. Milthorpe and I.D. Ivins (eds.) *The growth of cereals and grasses*. Butterworths Sci. Publs., London.
- Busso, C.A., J.H. Richards and N.J. Chatterton. 1990. Nonstructural carbohydrates and spring regrowth of two cool-season grasses: Interaction of drought and clipping. *J. Range Manage.* 43:336-343.
- Butler, J.L., and D.D. Briske. 1988. Population structure and tiller demography of the bunchgrass *Schizachyrium scoparium* in response to herbivory. *Oikos* 51:306-312.
- Caldwell, M.M. 1984. Plant requirements for prudent grazing. p. 117-152. In: *Developing strategies for rangeland management*. Westview Press, Boulder, Colorado.
- Caldwell, M.M., J.H. Richards, D.A. Johnson, R.S. Nowak, and R.S. Dzurec. 1981. Coping with herbivory: photosynthetic capacity and resource allocation in two semiarid *Agropyron* bunchgrasses. *Oecologia* 50:14-24.
- Caldwell, M.M., J.H. Richards, J.H. Manwaring, and D.M. Eissenstat. 1987. Rapid shifts in phosphate acquisition show direct competition between neighbouring plants. *Nature*. 327:615-616.
- Cargill, S.M. and R.L. Jefferies. 1984a. Nutrient limitation of primary production in a sub-arctic salt marsh. *J. Appl. Ecol.* 21:657-668.
- Cargill, S.M. and R.L. Jefferies. 1984b. The effects of grazing by lesser snow geese on the vegetation of a sub-arctic salt marsh. *J. Appl. Ecol.* 21:669-686.
- Carman, J.G. and D.D. Briske. 1985. Morphologic and allozymic variation between long-term grazed and non-grazed populations of the bunchgrass *Schizachyrium scoparium* var. *frequens*. *Oecologia* 66:332-337.
- Carmi, A. and D. Koller. 1979. Regulation of photosynthetic activity in the primary leaves of bean (*Phaseolus vulgaris* L.) by materials moving in the water-conducting system. *Plant Physiol.* 64:285-288.
- Casal, J.J., R.A. Sanchez, and V.A. Deregibus. 1987. Tillering responses of *Lolium multiflorum* plants to changes of red/far-red ratio typical of sparse canopies. *J. Exp. Bot.* 38:1432-1439.
- Chapin III, S.F. and M. Slack. 1979. Effect of defoliation upon root growth, phosphate absorption and respiration in nutrient-limited tundra graminoids. *Oecologia* 42:67-79.
- Clement, C.R., M.J. Hopper, L.H.P. Jones, and E.L. Leafe. 1978. The uptake of nitrate by *Lolium perenne* from flowing nutrient solution. II. Effects of light, defoliation, and relationship to CO<sub>2</sub> flux. *J. Exp. Bot.* 29:1173-1183.
- Cline, M.G. 1991. Apical dominance. *Bot. Rev.* 57:318-358.

- Coppock, D.L., J.K. Detling, J.E. Ellis, and M.I. Dyer. 1983. Plant-herbivore interactions in a North American mixed-grass prairie. I. Effects of black-tailed prairie dogs on intraseasonal aboveground plant biomass and nutrient dynamics and plant species diversity. *Oecologia* 56:1-9.
- Davidson, J.L. and F.L. Milthorpe. 1966. Leaf growth in *Dactylis glomerata* following defoliation. *Ann. Bot.* 30:173-184.
- Davidson J.L. and F.L. Milthorpe. 1965. Carbohydrate reserves in the regrowth of cocksfoot (*Dactylis glomerata* L.) *J. Br. Grassld. Soc.* 20:15-18.
- Deregibus, V.A., M.J. Trlica, and D.A. Jameson. 1982. Organic reserves in herbage plants: Their relationship to grassland management. p. 315-344. *In*: M.J. Recheigl (ed.), *Handbook of agricultural productivity*. Vol. I. Plant productivity. CRC Press, Inc.
- Deregibus, V.A., R.A. Sanchez, J.J. Casal, and M.J. Trlica. 1985. Tillering responses to enrichment of red light beneath the canopy in a humid natural grassland. *J. Appl. Ecol.* 22:199-206.
- Detling, J.K. 1988. Grasslands and savannas: Regulation of energy flow and nutrient cycling by herbivores. *In*: L.R. Pomeroy and J.J. Alberts (eds.) *Concepts of ecosystem ecology—A comparative view*. Springer-Verlag New York, Inc.
- Detling, J.K. and E.L. Painter. 1983. Defoliation responses of western wheatgrass populations with diverse histories of prairie dog grazing. *Oecologia* 57:65-71.
- Detling, J.K., M.I. Dyer, and D.T. Winn. 1979a. Effect of simulated grasshopper grazing on CO<sub>2</sub> exchange rates of western wheatgrass leaves. *J. Econ. Ent.* 72:403-406.
- Detling, J.K., M.I. Dyer, and D.T. Winn. 1979b. Net photosynthesis, root respiration, and regrowth of *Bouteloua gracilis* following simulated grazing. *Oecologia* 41:127-134.
- Dyer, M.I. 1975. The effects of red winged blackbirds (*Agelaius phoeniceus* L.) on biomass production of corn grains (*Zea mays* L.) *J. Appl. Ecol.* 12:719-726.
- Eagles, C.F. 1983. Relationship between competitive ability and yielding ability in mixtures and monocultures of populations of *Dactylis glomerata* L. *Grass For. Sci.* 38:21-24.
- Ellison, L. 1960. Influence of grazing on plant succession of rangelands. *Bot. Rev.* 26:1-78.
- Ferree, D.C. and F.R. Hall. 1981. Influence of physical stress on photosynthesis and transpiration of apple leaves. *J. Amer. Soc. Hort. Sci.* 106:348-351.
- Floate, M.J.S. 1981. Effects of grazing by large herbivores on nitrogen cycling in agricultural ecosystems. *In*: F.E. Clark and T. Rosswall (eds.) *Terrestrial nitrogen cycles*. *Ecol. Bull. (Stockholm)* 33:585-601.
- Geiger, D.R. 1976. Effects of translocation and assimilate demand on photosynthesis. *Can. J. Bot.* 54:2337-2345.
- Gieger, D.R. and B.R. Fondy. 1985. Responses of export and partitioning to internal and external factors. p. 177-194. *In*: B. Jeffcoat, A.F. Hawkins and A.D. Stead (eds.) *Regulation of sources and sinks in crop plants*. British Plant Growth Regulator Group Monograph 12, Bristol, UK.
- Georgiadis, N.J., R.W. Ruess, S.J. McNaughton, and D. Western. 1989. Ecological conditions that determine when grazing stimulates grass production. *Oecologia* 81:316-322.
- Gifford, R.M. and C. Marshall. 1973. Photosynthesis and assimilate distribution in *Lolium multiflorum* Lam. following differential tiller defoliation. *Aust. J. Biol. Sci.* 26:517-526.
- Gold, W.G. and M.M. Caldwell. 1989. The effects of the spatial pattern of defoliation on regrowth of a tussock grass. II. Canopy gas exchange. *Oecologia* 81:437-442.
- Gold, W.G. and M.M. Caldwell. 1990. The effects of the spatial pattern of defoliation on regrowth of a tussock grass. III. Photosynthesis, canopy structure and light interception. *Oecologia* 82:12-17.

- Gregor, J.W. and F.W. Sansome. 1926. Experiments on the genetics of wild populations. I. Grasses. *J. Genet.* 17:349-364.
- Gregory, F.G. and J.A. Veale. 1957. A reassessment of the problem of apical dominance. *Symp. Soc. Expt. Biol.* 11:1-20.
- Grime, P.J. 1977. Plant strategies and vegetation processes. John Wiley and Sons, Inc., New York.
- Harrison, M.A. and P.B. Kaufman. 1982. Does ethylene play a role in the release of lateral buds (tillers) from apical dominance in oats? *Plant Physiol.* 70:811-814.
- Heichel, G.H. and N.C. Turner. 1983. CO<sub>2</sub> assimilation of primary and regrowth foliage of red maple (*Acer rubrum* L.) and red oak (*Quercus rubra* L.): response to defoliation. *Oecologia* 57:14-19.
- Heitschmidt, R.K., D.L. Price, R.A. Gordon, and J.R. Frasure. 1982. Short duration grazing at the Texas Experimental Ranch: effects on above ground primary production and seasonal growth dynamics. *J. Range Manage.* 35:367-372.
- Hik D.S. and R.L. Jefferies. 1990. Increases in the net above-ground primary production of a salt-marsh forage grass: a test of the predictions of the herbivore-optimization model. *J. Ecol.* 78:180-195.
- Hilbert, D.W., D.M. Swift, J.K. Detling, and M.I. Dyer. 1981. Relative growth rates and the grazing optimization hypothesis. *Oecologia* 51:14-18.
- Hillman, J.R. 1984. Apical dominance. p. 127-148. *In*: M.B. Wilkins (ed.) *Advanced plant physiology*. Pitman Publ. London.
- Hodgkinson, K.C. 1974. Influence of partial defoliation on photosynthesis, photorespiration and transpiration by lucerne leaves of different ages. *Aust. J. Plant Physiol.* 1:561-578.
- Hodgkinson, K.C., M.M. Ludlow, J.J. Mott, and Z. Baruch. 1989. Comparative responses of the savanna grasses *Cenchrus ciliaris* and *Themeda triandra* to defoliation. *Oecologia* 79:45-52.
- Hodgkinson, K.C., N.G. Smith, and G.E. Miles. 1972. The photosynthetic capacity of stubble leaves and their contribution to growth of the lucerne plant after high level cutting. *Aust. J. Agri. Res.* 23:225-238.
- Jameson, D.A. 1963. Responses of individual plants to harvesting. *Bot. Rev.* 29:532-594.
- Jaramillo, V.J. and J.K. Detling. 1988. Grazing history, defoliation, and competition: effects on shortgrass production and nitrogen accumulation. *Ecology* 69:1599-1608.
- Jenkins, G.I. and H.W. Woolhouse. 1971. Photosynthetic electron transport during senescence of the primary leaves of *Phaseolus vulgaris* L. I. Non-cyclic electron transport. *J. Exp. Bot.* 32:467-478.
- Jonsdottir, I.S. and T.V. Callaghan. 1989. Localized defoliation stress and the movement of <sup>14</sup>C-photoassimilates between tillers of *Carex bigelowii*. *Oikos* 54:211-219.
- Kasperbauer, M.J. and D.L. Karlen. 1986. Light-mediated bioregulation of tillering and photosynthate partitioning in wheat. *Physiol. Plant.* 66:159-163.
- Kemp, W.B. 1937. Natural selection within plant species as exemplified in a permanent pasture. *J. Hered.* 28:329-333.
- Leopold, A.C. 1949. The control of tillering in grasses by auxin. *Amer. J. Bot.* 36:437-440.
- Ludlow, M.M. and D.A. Charles-Edwards. 1980. Analysis of regrowth of a tropical grass/legume sward subjected to different frequencies and intensities of defoliation. *Aust. J. Agric. Res.* 31:673-692.
- Ludlow, M.M. and J.J. Mott. 1988. Photosynthetic capacities of lamina and sheaths. pp. 47 *In*: CSIRO Division of tropical crops and pastures annual report 1987-88, CSIRO, Brisbane, Australia.

- Marshall, C. and G.R. Sagar. 1965. The influence of defoliation on the distribution of assimilates in *Lolium multiflorum* Lam. Ann. Bot. 29:365-370.
- Martin, G.C. 1987. Apical dominance. HortScience 22:824-833.
- Maschinski, J. and T. G. Whitham. 1989. The continuum of plant responses to herbivory: The influence of plant association, nutrient availability, and timing. Am. Nat. 134:1-19.
- Massimino, D., M. Andre, C. Richaud, J. Massimino and J. Vivoli. 1981. The effect of a day at low irradiance of a maize crop. I. Root respiration and uptake of N, P and K. Physiol. Plant. 51:150-155.
- Matches, A.G. 1966. Influence of intact tillers and height of stubble on growth responses of tall fescue (*Festuca arundinacea* Schreb.). Crop Sci. 6:484-487.
- Mattheis P.J., L.L. Tieszen, and M.C. Lewis. 1976. Responses of *Dupontia fischeri* to simulated lemming grazing in an Alaskan arctic tundra. Ann. Bot. 40:179-197.
- May, L.H. 1960. The utilization of carbohydrate reserves in pasture plants after defoliation. Herb. Abst. 30:239-245.
- McNaughton, S.J. 1985. Ecology of grazing ecosystem: the Serengeti. Ecol. Monogr. 55:259-294.
- McNaughton, S.J., L.L. Wallace, and M.B. Coughenour. 1983. Plant adaptation in an ecosystem context: effects of defoliation, nitrogen, and water on growth of an African C<sub>4</sub> sedge. Ecology 64:307-318.
- McNaughton, S.J. 1983. Compensatory plant growth as a response to herbivory. Oikos 40:329-336.
- McNaughton, S.J. 1979. Grazing as an optimization process: grass-ungulate relationships in the Serengeti. Am. Nat. 113:691-703.
- McNaughton, S.J. 1976. Serengeti migratory wildebeest: facilitation of energy flow by grazing. Science 191:92-94.
- McNeilly, T. 1984. Ecotypic differentiation in *Poa annua*: within population variation in response to competition and cutting. New Phytol. 96:307-316.
- Mueggler, W.F. 1972. Influence of competition on the response of bluebunch wheatgrass to clipping. J. Range Manage. 25:88-92.
- Mueller, R.J. and J.H. Richards. 1986. Morphological analysis of tillering in *Agropyron spicatum* and *Agropyron desertorum*. Ann. Bot. 58:911-921.
- Murphy, J.S. and D.D. Briske. 1992. Regulation of tillering by apical dominance: Chronology, interpretive value, and current perspectives. J. Range Manage. 45: 419-430.
- Neales, T.F., K.J. Treharne, and P.F. Wareing. 1971. A relationship between net photosynthesis, diffusive resistance, and carboxylating enzyme activity in bean leaves. p. 89-97. In: M.D. Hatch, C.B. Osmond, and R.O. Slatyer (eds.) Photosynthesis and photorespiration. New York:Wiley-Interscience.
- Nojima, H., S. Fuketa, A. Isoda, and Y. Takasaki. 1989. Levels of abscisic acid in lateral buds during regrowth of *Sorghum bicolor* M. p. 505-506. In: Proc. XVI Int. Grassld. Cong., Nice, France.
- Nowak, R.S. and M.M. Caldwell. 1984. A test of compensatory photosynthesis in the field: implications for herbivory tolerance. Oecologia 61:311-318.
- Oosterheld M. and S.J. McNaughton. 1988. Intraspecific variation in the response of *Themeda triandra* to defoliation: the effect of time of recovery and growth rates on compensatory growth. Oecologia 77:181-186.
- Olson, B.E. and J.H. Richards. 1988a. Tussock regrowth after grazing: intercalary meristem and axillary bud activity of *Agropyron desertorum*. Oikos 51:374-382.
- Olson, B.E. and J.H. Richards. 1988b. Annual replacement of the tillers of *Agropyron desertorum* following grazing. Oecologia 76:1-6.

- Paige, K.N. and T.G. Whitham. 1987. Overcompensation in response to mammalian herbivory: the advantage of being eaten. *Am. Nat.* 129:407-416.
- Painter, E.L. and J.K. Detling. 1981. Effects of defoliation on net photosynthesis and regrowth of western wheatgrass. *J. Range Manage.* 34:68-71.
- Painter, E.L., J.K. Detling, and D.A. Steingraeber. 1989. Grazing history, defoliation, and frequency-dependent competition: effects on two North American grasses. *Amer. J. Bot.* 76:1368-1379.
- Peterson, R.A. 1962. Factors affecting resistance to heavy grazing in needle-and-thread grass. *J. Range Manage.* 15:183-189.
- Phillips, I.D.J. 1975. Apical dominance. *Ann. Rev. Plant Physiol.* 26:341-367.
- Polley, H.W. and J.K. Detling. 1988. Herbivory tolerance of *Agropyron smithii* populations with different grazing histories. *Oecologia* 77:261-267.
- Quinn, J.A. and R.V. Miller. 1967. A biotic selection study utilizing *Muhlenbergia montana*. *Bull. Torrey Bot. Club.* 94:423-432.
- Richards, J.H., R.J. Mueller, and J.J. Mott. 1988. Tillering in tussock grasses in relation to defoliation and apical bud removal. *Ann. Bot.* 62:173-179.
- Richards, J.H. 1986. Plant response to grazing: the role of photosynthetic capacity and stored carbon reserves. p. 428-430. *In*: P.J. Joss, P.W. Lynch, and O.B. Williams (eds.) *Rangelands: a resource under siege*. Cambridge Univ. Press.
- Richards, J.H. and M.M. Caldwell. 1985. Soluble carbohydrates, concurrent photosynthesis and efficiency in regrowth following defoliation: A field study with *Agropyron* species. *J. Appl. Ecol.* 22:907-920.
- Richards, J.H. 1984. Root growth response to defoliation in two *Agropyron* bunchgrasses: field observations with an improved root periscope. *Oecologia* 64:21-25.
- Ruess, R.W. 1984. Nutrient movement and grazing: experimental effects of clipping and nitrogen source on nutrient uptake in *Kyllinga nervosa*. *Oikos* 43:183-188.
- Ruess, R.W. and S.J. McNaughton. 1987. Grazing and the dynamics of nutrient and energy regulated microbial processes in the Serengeti grasslands. *Oikos* 49:101-110.
- Ruess, R.W., S.J. McNaughton, and M.B. Coughenour. 1983. The effects of clipping, nitrogen source and nitrogen concentration on the growth responses and nitrogen uptake of an east african sedge. *Oecologia* 59:253-261.
- Ryle, G.J. and C.E. Powell. 1975. Defoliation and regrowth in the graminaceous plant: the role of current assimilate. *Ann. Bot.* 39:297-310.
- Sambo, E.Y. 1983. Leaf extension rate in temperate pasture grasses in relation to assimilate pool in the extension zone. *J. Exp. Bot.* 34:1281-1290.
- Sampson, A.W. 1952. *Range management principles and practices*. John Wiley and Sons, Inc., New York.
- Satoh, M., P.E. Kriedemann, and B.R. Loveys. 1977. Changes in photosynthetic activity and related processes following decapitation in mulberry trees. *Physiol. Plant.* 41:203-210.
- Scott, A.W. and R.D.B. Whalley. 1984. The influence of intensive sheep grazing on genotypic differentiation in *Danthonia linkii*, *D. richardsonii* and *D. racemosa* on the New England Tablelands. *Aust. J. Ecol.* 9:419-429.
- Simon, J.C. and G. Lemaire. 1987. Tillering and leaf area index in grasses in the vegetative phase. *Grass Forage Sci.* 72:373-380.
- Smith, D. 1972. Carbohydrate reserves of grasses. *In*: V.B. Youngner and C.M. McKell (eds.) *The biology and utilization of grasses*. Academic Press, New York.
- Smith, D. 1981. Removing and analyzing total nonstructural carbohydrates from plant tissue. University of Wisconsin, College of Agriculture and Life Sciences Publication, R-2107. University of Wisconsin, Madison.

- Stout, D.G., J. Hall, B. Brooke, and A. McLean. 1981. Influence of successive years of simulated grazing (clipping) on pinegrass growth. *Can. J. Plant Sci.* 61:939-943.
- Thimann, K.V. and F. Skoog. 1933. Studies on the growth hormone of plants. 3. The inhibiting action of the growth substance on bud development. *Proc. Nat. Acad. Sci. USA* 19:714-716.
- Thorgeirsson, H. 1988. The modeling and measurement of respiratory carbon use and net carbon gain of two *Agropyron* bunchgrasses. Ph.D. dissertation, Utah State University, Logan, Utah.
- Volenc, J.J., and C.J. Nelson. 1984. Carbohydrate metabolism in leaf meristems of tall fescue. II. Relationship to leaf elongation rates modified by nitrogen fertilization. *Plant Physiol.* 74:595-600.
- von Caemmerer, S. and G.D. Farquhar. 1984. Effects of partial defoliation, changes in irradiance during growth, short-term water stress and growth at enhanced  $p(\text{CO}_2)$  on the photosynthetic capacity of leaves of *Phaseolus vulgaris* L. *Planta* 160:320-329.
- Wallace, L.L., S.J. McNaughton, and M.B. Coughenour. 1985. Effects of clipping and four levels of nitrogen on the gas exchange, growth, and productivity of two east African graminoids. *Amer. J. Bot.* 72:222-230.
- Wallace, L.L., S.J. McNaughton, and M.B. Coughenour. 1984. Compensatory photosynthetic responses of three African graminoids to different fertilization, watering, and clipping regimes. *Bot. Gaz.* 145:151-156.
- Wareing, P.F., M.M. Khalifa, and K.J. Treharne. 1968. Rate-limiting processes in photosynthesis at saturating light intensities. *Nature* 220:453-457.
- Watson, V.H. and C.Y. Ward. 1970. Influence of intact tillers and height of cut on regrowth and carbohydrate reserves of Dallisgrass (*Paspalum dilatatum* Poir.) *Crop Sci.* 10:474-476.
- Weinmann, H. 1948. Underground development and reserves of grasses. *J. Brit. Grassld. Soc.* 3:115-140.
- Welker, J.M., D.D. Briske, and R.W. Weaver. 1987. Nitrogen-15 partitioning within a three generation tiller sequence of the bunchgrass *Schizachyrium scoparium*: response to selective defoliation. *Oecologia* 74:330-334.
- Welker, J.M., E.J. Rykiel, Jr., D.D. Briske, and J.D. Goeschl. 1985. Carbon import among vegetative tillers within two bunchgrasses: assessment with carbon-11 labeling. *Oecologia* 67:209-212.
- White, L.M. 1973. Carbohydrate reserves of grasses: A review. *J. Range Manage.* 26:13-18.
- Williams, R.F. and R.H.M. Langer. 1975. Growth and development of the wheat tiller. II. The dynamics of tiller growth. *Aust. J. Bot.* 23:745-759.
- Wolledge, J. 1977. The effects of shading and cutting treatments on the photosynthetic rates of ryegrass leaves. *Ann. Bot.* 41:1279-1286.
- Woodmansee, R.G., I. Vallis, and J.J. Mott. 1981. Grassland nitrogen. In: F.E. Clark and T. Rosswall (eds.) *Terrestrial nitrogen cycles*. *Ecol. Bull.* 33:443-462.
- Yamashita, T. and A. Fujino. 1986. Effects of pruning of young and old shoots on ribulose biphosphate carboxylase and other constituents in leaves of the mulberry tree (*Morus alba* L.). *J. Exp. Bot.* 37:1836-1841.
- Zarrough, K.M., C.J. Nelson, and D.A. Sleper. 1984. Interrelationships between rates of leaf appearance and tillering in selected tall fescue populations. *Crop Sci.* 24:565-569.

*David D. Biske*

**Ecological Implications  
of Livestock Herbivory  
in the West**

**Editors:**

**Martin Vavra**

**William A. Laycock**

**Rex D. Pieper**

**Published by the  
Society for Range Management  
1839 York Street  
Denver, CO 80206**