PLANT RESPONSES TO DEFOLIATION:
A PHYSIOLOGICAL, MORPHOLOGICAL AND DEMOGRAPHIC EVALUATION

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INTRODUCTION

The importance of developing the fundamental principles of rangeland management from knowledge of the growth requirements and life history attributes of important plant species was recognized early in the development of the Range Science profession (Sampson 1914). Since then, a great deal has been learned concerning plant responses to a wide array of environmental variables and management practices. Plant responses to defoliation have been emphasized because of the extensive use of rangelands as a forage source for both wild and domestic herbivores. Knowledge of plant response to defoliation has been incorporated into various procedures and prescriptions to effectively manage both vegetation and herbivores to minimize the detrimental consequences of grazing and maintain plant and animal production on a sustainable basis.

Research activity in plant-herbivore interactions was stimulated to an unprecedented level with the introduction of the grazing optimization hypothesis in the mid-1970's (Dyer 1975, McNaughton 1976, 1979). This hypothesis proposes that maximum plant productivity occurred at an optimal intensity of grazing rather than in ungrazed vegetation. The grazing optimization hypothesis also implies that grazed plants must exhibit mechanisms enabling them to increase their growth rates above those of ungrazed plants if they are to replace biomass removed by herbivores. This alternative perspective of the production responses of plants to grazing has created a substantial amount of confusion and generated a great deal of controversy among ecologists and natural resource managers (e.g., McNaughton 1979, Belsky 1986, Painter and Belsky 1993, Belsky et al. 1993).

The introduction and wide acceptance of ecological hierarchy theory, at about the same time that the grazing optimization hypothesis was initially being debated, has further modified our interpretation of plant responses to grazing. Ecological hierarchy theory indicates that communities consist of a series of graded hierarchies or ecological scales that possess unique temporal and spatial characteristics (Belsky 1987, Brown and Allen 1989, Allen and Hoekstra 1990). Grasslands are very well suited to the application of the hierarchy theory. For example, individual grass plants consist of an assemblage of tillers, populations are defined by both plant density and tiller number

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per plant, and grassland communities are further composed of an aggregation of species populations (Archer and Smeins 1991, Briske 1991). The structure and function of lower hierarchical levels (i.e., tiller and plant) partially defines the higher levels of vegetation organization, while the higher hierarchical levels (i.e., communities) constrain the structure and function of lower levels in ways that are not readily predictable from an evaluation of the lower levels in isolation. This theory establishes that environmental variables and processes at the higher hierarchical levels (i.e., competition and nutrient cycling) can regulate plant growth following defoliation to an equal or greater extent than the direct effects of defoliation (McNaughton 1979, Archer and Smeins 1991).

The objective of this chapter is to present a comprehensive synthesis of the information addressing plant responses to grazing in a hierarchical context. Physiological and morphological responses of individual plants to defoliation are evaluated in chronological sequence beginning with plant function during "steady state" growth prior to defoliation, followed by the short-term effects of defoliation, and concluding with long-term processes contributing to the reestablishment of "steady-state" growth. Our knowledge of plant populations are assessed through an evaluation of tiller and plant demography in the absence of grazing followed by an assessment of the affects of grazing on these demographic processes. Grazing resistance is addressed by evaluating its component mechanisms of avoidance and tolerance and assessing the potential costs of these mechanisms. The chapter concludes with an assessment of how the effects of grazing are translated from individual plants through populations to affect productivity within plant communities.

INDIVIDUAL PLANT RESPONSES TO DEFOLIATION

Individual plant responses to defoliation encompass a large number of physiological and morphological processes spanning a broad range of temporal scales. The objective of this section is to evaluate individual plant responses in a chronological sequence beginning with plant function during "steady-state" growth prior to defoliation, followed by the short-term effects of defoliation, and conclude with long-term processes contributing to the reestablishment of "steady-state" growth.

Immediate effects of defoliation

Whole-plant photosynthesis

Whole-plant photosynthesis is instantaneously reduced in response to canopy removal by grazing or clipping. Large portions of the canopy of individual plants are frequently removed by grazing animals in a single grazing event (e.g., Jarman and Sinclair 1979, Norton and Johnson 1983, Anderson and Shumar 1986, Krueger 1986). Rapid, large-scale reductions in canopy area are less likely to occur as a result of chronic defoliation which is often associated with herbivorous insects (e.g., Coley 1983, Seastedt et al. 1983, Lowman 1984, see Evans and Seastedt this volume). These contrasting patterns of defoliation modify whole-plant photosynthesis in very different ways. Plants adjust to conditions of chronic defoliation and the associated reduction in whole-plant photosynthetic rates by altering resource allocation patterns and reducing relative growth rates. In contrast, a transient period of modified physiological function frequently accompanies plant defoliation by large herbivores followed by recovery of steady-state plant function. Relatively few studies have adequately monitored the immediate (<48 hours) effects of reduced whole-plant photosynthesis on plant function in response to defoliation. Knowledge of the immediate responses of plants to defoliation is critical for understanding the process of plant recovery following defoliation.

The reduction in whole-plant photosynthesis following defoliation is not necessarily proportional to leaf-area or biomass removal because of associated modification in canopy microclimate, the unequal photosynthetic contributions of leaves of various age and, in some cases, compensatory photosynthesis. For example, when

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mature, previously shaded leaves remain on the plant following defoliation, canopy photosynthesis is reduced to a greater extent than the proportion of leaf area removed because of the low photosynthetic capacity of the remaining leaves (Ludlow and Charles-Edwards 1980, Gold and Caldwell 1989b). A large decrease in the photosynthesis/transpiration ratio of the canopy (i.e., water-use efficiency) is also associated with this pattern of plant defoliation (Caldwell et al. 1983, Gold and Caldwell 1989b). Conversely, if a high proportion of relatively young leaves remain on the plant following defoliation, the reduction in canopy photosynthesis is more directly related to amount of leaf area removed. Consequently, canopy measurements of photosynthesis are more strongly correlated with the potential for regrowth than are measurements of single-leaf photosynthesis (Ludlow and Charles-Edwards 1980, Parsons et al. 1983a, 1983b, King et al. 1984, 1988, Nowak and Caldwell 1984, Gold and Caldwell 1989b). Estimates of canopy photosynthesis integrate the disparate photosynthetic activities of foliage elements, including leaf blades, sheaths and culms, their relative surface areas, and the influence of microclimatic variables in a way that is difficult to achieve with measurements of single-leaf photosynthesis.

Root growth, respiration, and nutrient uptake

Immediately following defoliation the effects of reduced canopy photosynthesis are rapidly propagated throughout the plant. Studies of numerous grazing-tolerant C_3 and C_4 forage grasses growing with high nutrient availability in controlled-environment or greenhouse conditions have demonstrated that root elongation essentially ceases within 24 hours after removal of approximately 50% or more of the shoot system (Fig. 1) (Crider 1955, Troughton 1957, Oswalt et al. 1959, Davidson and Milthorpe 1966a, Ryle and Powell 1975) and root mortality and decomposition may begin within 36-48 hours (Oswalt et al. 1959). Root respiration and nutrient acquisition are also reduced following defoliation, but to a lesser extent than root growth (Fig. 1) (Davidson and Milthorpe 1966a, Chapin and Slack 1979, Macduff et al. 1989). Root respiration begins to decline within hours of defoliation and it may decrease substantially within 24 hours (Davidson and Milthorpe 1966a, Clement et al. 1978, Thorgeirsson 1988).

Concomitant with the reduction in root respiration following defoliation is a rapid reduction in nutrient absorption (Fig. 1). Experiments conducted with perennial

ryegrass (<u>Lolium</u> <u>perenne</u>) growing in nutrient solution demonstrated that the rate of nitrate (NO_3^-) absorption began to decline within 30 minutes following removal of 70% of shoot biomass. NO_3^- absorption decreased to less than 40% of the pre-defoliation rate within 2 hours following defoliation (Clement et al. 1978). In these experiments, NO_3^- absorption continued to decline over the next 4-12 hours until it became negligible for 2 or 7 days before recovery began under high and low light intensities, respectively. NO_3^- absorption did not resume until a positive daily carbon balance was reestablished within the plant (Clement et al. 1978). Rapid reductions in root respiration and nutrient absorption following plant defoliation are proportional to the intensity of defoliation (Davidson and Milthorpe 1966a, Thorgeirsson 1988). Similarly, canopy shading or root severing causes large, rapid decreases in root respiration and nutrient absorption (Clarkson et al. 1974, Hansen and Jensen 1977, Massimino et al. 1981, Saglio and Pradet 1980, Aslam and Huffaker 1982, Thorgeirsson 1988, Bloom and Caldwell 1988, Macduff and Jackson 1992). These experiments clearly demonstrate the importance of current photosynthesis for the maintenance of root growth and function in rapidly growing plants.

The responses of plants adapted to infertile environments differ from those previously described for rapidly growing species adapted to fertile environments. For example, root growth was unaffected for 48 hours following a single, severe defoliation of two nutrient-limited tundra graminoids, cottongrass (<u>Eriophorum</u> <u>vaginatum</u>) and <u>Carex</u> <u>aquatilis</u> (Chapin and Slack 1979). Root growth was not reduced until the plants were subjected to two or more successive defoliations. Respiration and nutrient absorption were maintained, or even increased, following defoliation of these nutrient-limited plants (Chapin and Slack 1979). Defoliation has even been documented to increase NO_3^- absorption in perennial ryegrass within 8 hours when plants were grown with low fertility, rather than high fertility (Macduff et al. 1989). In addition to these short-term responses, long-term increases in specific root respiration rate and nutrient absorption capacity (V_{max}) have been found in both tropical and tundra graminoids growing under nutrient-limited conditions (Chapin and Slack 1979, Ruess et al. 1983, McNaughton and Chapin 1985).

Root growth and function can only be maintained by the continuous utilization of carbon within the plant (Chapin and Slack 1979). Therefore, the maintenance or

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increase in root activity following defoliation in these species was dependent upon carbohydrate translocation from remaining shoot tissues (e.g., stem bases, rhizomes) or the rapid reestablishment of canopy photosynthesis. Carbon allocation to roots may have continued following defoliation in these species because they were nutrient-limited and possessed especially strong root sinks. It is unlikely that an adequate amount of soluble carbohydrates existed in the roots to support root activity following defoliation. For example, the total nonstructural carbohydrate (TNC) concentration in roots of the tundra graminoid, cottongrass, at the time of defoliation (69 mg.g^{-1} dry wt.; Chapin and Slack 1979) was well within the range of TNC concentrations observed for roots of temperate species in which root respiration and nutrient absorption rapidly declined following defoliation or root excision [e.g., barley (Hordeum vulgare), 166 mg.g^{-1} sucrose, glucose and fructose, Bloom and Caldwell 1988; white clover (Trifolium repens), 81 mg.g^{-1}, Gordon et al. 1986; orchardgrass (Dactylis glomerata), 32 mg.g^{-1}, Davidson and Milthorpe 1966a]. Tundra graminoids do not appear to possess unusually high concentrations of carbohydrate reserves in comparison with ecologically and genetically similar temperate populations (Chapin and Shaver 1989). Whether the immediate defoliation responses of plants adapted to infertile environments are a function of nutrient availability, unique adaptations to low nutrient supply (Chapin 1980), or both, has not been determined.

Nitrogen fixation

Biological nitrogen fixation in nodulated legumes is more sensitive to the reduction in leaf area or current photosynthesis following defoliation than are root growth or respiration (Hardy and Havelka 1976, Vance et al. 1979, Ryle et al. 1985). Removal of all expanded leaves from white clover plants resulted in a decline in nitrogenase-linked nodule respiration within 10-30 minutes, depending on plant size, and nodule respiration was reduced 80-90% within 2 hours (Ryle et al. 1985). Shading and chemical inhibition of photosynthesis also led to a rapid decline in nodule respiration in these experiments, but the subsequent decline was slower than that observed following defoliation. A short time lag existed between the time of defoliation and the reduction in nodule respiration based on the time required for the utilization of carbon that was in transit between the leaf and the nodules (Ryle et al. 1985).

The dependence of nitrogenase activity, in addition to nodule respiration, on current photosynthesis has also been documented in studies with white clover. In this case, the rapid decline in nodule respiration and nitrogen fixation was not related to the carbohydrate content of the nodules immediately following defoliation (Gordon et al. 1986). However, it has been demonstrated that oxygen diffusion into nodules is reduced after defoliaton causing an oxygen, rather than a carbohydrate, limitation to nitrogenase-linked respiration (Hartwig et al. 1987, 1990). These results indicate that a reduction in current photosynthesis was not directly responsible for the decrease in nitrogen fixation after defoliation. Other effects or signals associated with leaf removal apparently regulate oxygen diffusion into nodules. Although the regulatory mechanism is undefined, the rapid reduction in nodule respiration may be important for nodule maintenance during the period of reduced carbon availability after defoliation. In additon to these very rapid effects on nodule respiration, total root and nodule respiration, and carbohydrate content decline after 24-48 hours (Gordon et al. 1986, Culvenor et al. 1989a, 1989b). Apparently both current photosynthesis and an additional signal originating in the shoot system are necessary for continued nitrogen fixation within nodules.

Carbohydrate depletion

The previous investigations demonstrate that root growth, respiration, and nutrient absorption in rapidly growing plants are all dependent upon a continuous supply of labile carbohydrates produced in the shoot system. However, root growth and function may be partially buffered for 2-48 hours after defoliation by carbohydrate translocation from remaining shoot tissues (Fig. 1). The dependence of root growth and function on a continuous supply of carbohydrates produced in the shoots is further supported by investigations in which exogenously applied carbohydrates have prevented the usual decline in root respiration and nutrient absorption following defoliation (Saglio and Pradet 1980, Aslam and Huffaker 1982, Davidian et al. 1984). Without the addition of exogenous carbohydrates, the decline in root respiration and nutrient absorption is accompanied by the depletion of soluble carbohydrate pools in both attached and excised roots (Davidson and Milthorpe 1966a, Chapin and Slack 1979, Gordon et al. 1986, Bloom and Caldwell 1988, Thorgeirsson, 1988).

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The rapid decline in soluble carbohydrates within roots commonly observed following defoliation (Jameson 1963, Deregibus et al. 1982) results from: 1) a reduction, although not necessarily a complete cessation, in the amount of photosynthetic carbon translocated from the shoot system and 2) a continuation of carbohydrate utilization by root respiration.   Quantitative carbon balance studies have shown that the root system continues to function as a net sink for carbon immediately following defoliation (Davidson and Milthorpe 1966a, Ryle and Powell 1975, Muldoon and Pearson 1979, Richards and Caldwell 1985, Danckwerts and Gordon 1987, Thorgeirsson 1988). Therefore, it is unlikely that soluble carbohydrates in the root systems are mobilized to meet the carbon demands of the shoot system during regrowth as widely assumed. Continuous carbohydrate allocation from the shoot system or the mobilization of substrates other than TNC from source tissues within the plant is required to maintain minimal root activity following defoliation (Davidson and Milthorpe 1966a).   In orchardgrass for example, the net loss of TNC from the root system following moderate or severe defoliation only accounted for a fraction of the total respiratory carbon loss from the roots.   The inability of carbohydrate reserves within roots to balance root respiratory demands resulted in the utilization of compounds other than TNC. Several other studies have also produced data suggesting that alternative substrates which are not evaluated in TNC analyses, including hemicelluloses, proteins and organic acids, may be utilized by plants following severe defoliation (Muldoon and Pearson 1979, Chung and Trlica 1980, Dewald and Sims 1981, Richards and Caldwell 1985).

Carbohydrate pools within the crowns, including sheath bases, of crested wheatgrass (Agropyron desertorum) and bluebunch wheatgrass (Pseudoroegneria spicata ssp. spicata; syn: Agropyron spicatum) were equivalent to the amount of carbohydrates produced in only 3 days of photosynthesis (Richards and Caldwell 1985).   Consequently, plant growth was more dependent upon current photosynthesis than stored carbohydrates within 3 days following severe defoliation (Fig. 2).   Similarly, leaf elongation or tillering were not proportionately related to carbohydrate concentrations in leaves, crowns or roots of tall fescue (Festuca arundinacea), orchardgrass (Dactylis glomerata) or reed canarygrass (Phalaris arundinacea) (Sambo 1983, Zarrough et al. 1984, Volenec and Nelson 1984) and carbohydrate concentrations were not correlated with tiller development in switchgrass (Panicum

<u>virgatum</u>) (Anderson et al. 1989).   These data collectively indicate that the contribution of carbohydrate reserves to plant growth following defoliation is considerably smaller than previously assumed.

A consistent, positive relationship between the size of carbohydrate pools and plant regrowth has not been definitively established (e.g., Richards and Caldwell 1985, Busso et al. 1990).   In fact, an inverse relationship is frequently observed with carbohydrate pools increasing during periods of minimal plant growth and then decreasing during rapid plant growth (Davidson and Milthorpe 1966a, 1966b, Caldwell 1984).   The potential for plant regrowth increased only when TNC concentrations in roots and crowns of crested wheatgrass and bluebunch wheatgrass increased to exceptionally high levels in response to an experimentally imposed drought (Fig. 3). 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 play an important role in initiating plant growth when photosynthetic capacity is severely limited.   However, the minimal amounts 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 and other forage species.

Resource allocation

Carbon. Carbohydrate availability within roots is reduced immediately after defoliation in response to: 1) a reduction in whole-plant photosynthesis and 2) the preferential allocation of photosynthetic carbon to active shoot sinks. For example, in sugarcane (Saccharum officinarum) the relative proportion of photosynthetically fixed ^{14}C translocated to the growing stem and leaves above a labeled, mature leaf was 2.7-fold greater in defoliated shoots within 2 hours after defoliation than it was in undefoliated shoots (Hartt et al. 1964). Two-three fold increases in the relative proportion of photosynthetic carbon allocated to rapidly growing shoots have been reported for barley within 24 hours after defoliation (Ryle and Powell 1975) (Fig. 4) and 2-10 fold increases have been documented in Populus x euramericana (Bassman and Dickmann 1985). The relative proportion of photosynthetic carbon allocated to roots decreases as the proportion of photosynthetic carbon allocated to growing shoots increases following defoliation (Hartt et al. 1964, Marshall and Sagar 1965, Ryle and Powell 1975, Bassman and Dickmann 1985).

An increased proportion of photosynthetic carbon is exported from the remaining photosynthetic surfaces following defoliation which minimizes the absolute reduction in carbon allocation to the roots. Both the increase in carbon export from source tissues and greater relative carbon allocation to rapidly growing shoots are compensatory processes that promote canopy reestablishment by maintaining carbon availability for shoot meristems. Both compensatory processes may occur within hours following defoliation. For example, defoliation reduced whole plant photosynthesis in barley by 51% on the day of defoliation, but carbon allocation to the growing shoots was only reduced by 40% (Ryle and Powell 1975). Allocation of photosynthetic carbon to shoot sinks was proportionally greater in the defoliated plants than in the undefoliated plants for the next 7 days following defoliation. The increase in carbon allocation to shoot sinks occurred largely at the expense of carbon allocation to roots, which received both a lower total and relative amount of carbon than did the roots of undefoliated plants (Ryle and Powell 1975) (Fig. 4).

Carbon allocation between connected shoots or branches within a plant is also rapidly modified when a portion of the shoot system remains undefoliated or is defoliated to a lesser extent than the remainder of the plant (Marshall and Sagar 1965,

1968, Gifford and Marshall 1973, Welker et al. 1985).   Carbon import from attached, undefoliated parental tillers increased 36-85% within 30 minutes following defoliation of a single daughter tiller of brownseed paspalum (Paspalum plicatulum) and little bluestem (Schizachyrium scoparium) (Welker et al. 1985).   Carbon allocation from undefoliated parental tillers to defoliated daughter tillers increased to a maximum 10-84 hours following defoliation and then declined as daughter tillers reestablished their own photosynthetic capacity.   Similar allocation patterns have been found in partially defoliated Italian ryegrass (Lolium multiflorum) plants (Marshall and Sagar 1968, Gifford and Marshall 1973) and in regularly mown Kentucky bluegrass (Poa pratensis) (Hull 1987).   Carbon import from undefoliated, attached parental tillers can be maintained for a longer period or increased to a greater extent when the importing tiller is repeatedly defoliated (Gifford and Marshall 1973, Welker et al. 1985).   The rapid resumption of carbon import by tillers following defoliation is dependent upon the maintenance of physiological integration among connected tillers during steady-state growth (Welker et al. 1985).

The allocation of carbon, nitrogen, and presumably other resources from undefoliated to defoliated tillers within a plant, may provide a potential mechanism of herbivory tolerance by facilitating tiller survival and growth following defoliation.   For example, growth of tall fescue tillers increased progressively when either a greater percentage of tillers remained undefoliated or when the defoliation intensity was reduced (Matches 1966, Watson and Ward 1970).   A portion of this growth response was attributable to resource allocation from nondefoliated to defoliated tillers.   Similar conclusions have been drawn from investigations with several other graminoid species including Dupontia fischeri (Mattheis et al. 1976), Carex aquatilis (Archer and Tieszen 1986) and Carex bigelowii (Jónsdóttir and Callaghan 1989). Even though intertiller resource allocation functions as a mechanism to enhance herbivory tolerance, the primary function of parental resource support is very likely to increase the probability of juvenile tiller establishment in the competitive environment created by the high tiller density within established plants (Welker et al. 1991, Williams and Briske 1991).

In contrast to carbon allocation between roots and shoots, increased carbon export to defoliated tillers does not necessarily occur at the expense of carbon allocation to the root systems of undefoliated tillers.   For example, increased carbon

allocation to defoliated tillers of Italian ryegrass was accompanied by a large increase in carbon export from the undefoliated parental tillers so that the amount of carbon allocated to the root system of the parental tiller remained unchanged (Marshall and Sagar 1968). The pattern of intertiller resource allocation is dependent upon the relative leaf areas of the undefoliated parental tiller(s) and the attached, daughter tiller(s) remaining after defoliation (Gifford and Marshall 1973).

It is important to recognize that actively growing shoot meristems remained on the plants following defoliation to produce the patterns of carbon allocation previously described. Carbon allocation patterns in plants in which most sinks have been removed by defoliation will be modified substantially. The reorganization of carbon allocation priorities following defoliation is largely sink controlled, through either direct source-sink feedback or hormonal signals (Bucher et al. 1987a, Bassman and Dickmann 1985, Geiger and Fondy 1985). When actively growing shoot sinks are absent or limited, available carbon is allocated to alternative sinks, including roots (Richards 1984) and storage sites in the sheath and stem base in grasses (Bucher et al. 1987a, 1987b).

Increased carbon export from the remaining source leaves on defoliated plants can be interpreted as a response to decreased source/sink ratios. These short-term modifications in the pattern of carbon allocation probably result from competition among sinks of various strengths and locations in relation to the availability of carbon produced by source tissues. Long-term changes in allocation patterns, however, involve less direct interactions between sources and sinks and involve adaptive modifications most likely mediated by hormonal signals (Wareing et al. 1968, Geiger 1976, Geiger and Fondy 1985).

Nitrogen. Short-term changes in nitrogen (N) allocation within and between shoots have also been documented following defoliation. Previously absorbed N was allocated to regrowing leaves of perennial ryegrass within 2 days following defoliation (Fig. 5) (Ourry et al. 1988, 1990). The majority (80%) of the N was remobilized from remaining shoot tissues while the remainder was allocated from the root system. The contribution of remobilized N exceeded that of concurrent N absorption for 6 days following defoliation, after which concurrent absorption supplied the majority of N for regrowth.

N availability in the growth medium greatly affects the relative contribution of remobilized N to regrowth in perennial ryegrass following defoliation. The contribution of remobilized N to regrowth from the residual shoot system increased proportionally with decreasing N availability within the growth medium, while the amount of N contributed by the root system decreased with decreasing N availability (Millard et al. 1990, Ourry et al. 1990). For example, 69% of the N in shoot regrowth originated from remobilized N when plants were grown with low N availability, but only 40% of the N in regrowth originated from remobilized N when plants were grown with high N availability (Ourry et al. 1990). Similarly, in excess of 50% of the N in new leaves and tillers was derived from remobilized N in nondefoliated thickspike wheatgrass (Agropyron dasystachyum) plants grown with low N availability (Li et al. 1992). However, only 11% of the N in these tissues was derived from remobilized N when the plants were grown with high N availability. These data demonstrate, that in contrast to carbohydrate pools, N pools in the roots of grasses can be mobilized to support shoot growth following defoliation (Millard et al. 1990, Ourry et al. 1990). Similar conclusions have been drawn from investigations with herbaceous dicots including alfalfa (Hendershot and Volenec 1993) and subterranean clover (Trifolium subterraneum) (Culvenor et al. 1989a).

Previously absorbed N is transported from roots to shoots in an organic form requiring simultaneous carbon transport (Ourry et al. 1989). The carbon associated with the nitrogenous compounds is included in estimates of the amount of TNC mobilized from roots to shoots in whole-plant labeling investigations. However, the reallocated organic N, and associated carbon, are primarily used for synthesis of proteins and other N-containing compounds within regrowing shoots rather than as substrate for respiration or synthesis of carbon-based compounds (e.g., celluose, hemicelluose). The biochemical identity of remobilized carbon and N in regrowing shoots must be determined to clarify the relative contributions of TNC and protein remobilization during regrowth.

N was preferentially concentrated in rapidly growing, defoliated daughter tillers which were attached to nondefoliated parental tillers that had been labelled with ^{15}N prior to defoliation (Welker et al. 1987, 1991). The absolute amounts of N imported by defoliated daughter tillers was much lower, however, than that of undefoliated tillers because of a reduction in the total N requirement created by the removal of shoot

biomass. Nitrogen was preferentially allocated to defoliated daughter tillers until they reestablished a substantial amount of the leaf area which had been removed by defoliation. The patterns of N allocation within or between shoots of defoliated plants appear to be qualitatively similar to those for carbon allocation.

Photosynthetic capacity

The rapid modifications in carbon and nitrogen allocation patterns following defoliation are not paralleled by rapid increases in net photosynthetic rates of the remaining foliage.   In fact, net photosynthetic rates are commonly reduced within hours for both partially defoliated and undefoliated leaves on plants subjected to partial canopy removal.   The duration of the temporary decline in photosynthetic rate ranges from a few hours to 2 days.   For example, net photosynthesis of undefoliated western wheatgrass (Agropyron smithii) tillers declined by 6-7% within 30 minutes following defoliation of all other attached tillers (Painter and Detling 1981) and simulated grasshopper grazing of leaf blades in this species reduced net photosynthesis by 31% after 1 hour (Detling et al. 1979a).   Undefoliated leaves on defoliated alfalfa (Medicago sativa) plants had net photosynthetic rates 4-20% lower than comparable leaves on undefoliated plants, regardless of leaf or plant age, on the day of defoliation (Hodgkinson et al. 1972, Hodgkinson 1974).   Nowak and Caldwell (1984) also documented a brief period of reduced ($\leq$ 30%) photosynthetic rates relative to comparable leaves on undefoliated crested wheatgrass plants after each of three sequential clippings.   A similar response occurred in bluebunch wheatgrass plants, but photosynthetic rates of defoliated plants were only reduced below those of undefoliated plants after the first clipping.   Net photosynthesis was reduced 30-80% in the basal portion of leaf blades in three species (Deschampsia flexuosa, Nardus stricta, Juncus squarrosus) from upland acidic, nutrient-poor soils within 10 hours following removal of the distal portion of the blades (Atkinson 1986).   Dark respiration was not significantly altered by defoliation in these species. In a fourth species from the same site, net photosynthesis of sheep fescue (Festuca ovina) was not reduced until three sequential clippings had been imposed (Atkinson 1986).   Both net photosynthesis and dark respiration increased within 20 hours of the first and second defoliation in sheep fescue.   The mechanisms contributing to the rapid reduction in photosynthetic rates following

defoliation have not been studied in detail, but may involve a direct wounding response (Macnicol 1976) or a response to physical disturbance (Ferree and Hall 1981).

A review of the immediate effects of defoliation on individual plants indicates that both the carbon and nitrogen economy are modified within 24 - 48 hours after defoliation and prior to the initiation of substantial regrowth. Soluble carbohydrate pools are depleted within several days following defoliation in response to continued respiratory demands, rather than as a result of allocation to regrowth that is produced over a period of weeks following defoliation. Carbon and nitrogen allocation priorities are rapidly modified to increase resource allocation to active meristematic sinks in the shoot. Rapid growth in the apical meristem region of existing shoots and new tillers produces sufficient sink strength to divert resources from other sinks, including root respiration and nutrient absorption, until leaf area expansion and whole-plant photosynthesis increase sufficiently to exceed the carbon demands of the actively growing shoot sinks. Consequently, root growth and function are substantially reduced within 24 - 48 hours after moderate or severe defoliation in response to a carbon limitation. An increase in photosynthesis and carbon export from remaining and regrowing leaves frequently minimizes the absolute reduction in carbon allocation to the roots. These sink-driven modifications are fundamental to plant recovery from defoliation and are well expressed in defoliation tolerant plants. When strong shoot sinks are absent or can not be rapidly activated after defoliation, recovery takes longer and defoliation tolerance is reduced. An understanding of the immediate effects of defoliation is critical because these initial processes establish the potential for subsequent plant recovery from defoliation.

Reestablishment of whole-plant photosynthetic capacity

Defoliation-induced changes in leaf photosynthetic capacity and carbon allocation that enable defoliated plants to compensate for foliage losses have been the focus of a great deal of attention. The initial manifestations of these compensatory processes, especially in allocation patterns, become apparent immediately following defoliation. However, adjustments in photosynthetic capacity occur over a period of several days following defoliation. Two commonly observed responses in defoliated

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plants that greatly affect the recovery rate of whole-plant photosynthetic capacity are: 1) increased photosynthetic capacity of remaining and regrowing foliage, and 2) increased growth rates of leaves and shoots. Increased rates of these two processes have a multiplicative effect on the rate of canopy reestablishment following defoliation. Although increased photosynthetic capacities of leaves during regrowth have been emphasized, the rates of both photosynthesis and leaf area expansion must be known to quantify the respective effects of either process for plant recovery.

Compensatory photosynthesis

Photosynthetic rates of foliage on defoliated plants are often higher than those of foliage of the same age on undefoliated plants. This response, which develops over a several-day period following defoliation, is termed compensatory photosynthesis and has been documented for both mature and expanding leaves remaining on the defoliated plant and for leaves that are produced during regrowth. Compensatory photosynthesis is a very consistent physiological response following defoliation that has been documented in a large number of species, including Acer rubrum (Heichel and Turner 1983), crested wheatgrass (Caldwell et al. 1981, Nowak and Caldwell 1984), western wheatgrass (Painter and Detling 1981, Detling and Painter 1983), sheep fescue (Atkinson 1986), fine thatching grass (Hyparrhenia filipendula) (Wallace et al. 1984), Italian ryegrass (Gifford and Marshall 1973), perennial ryegrass (Woledge 1977), alfalfa (Hodgkinson et al. 1972, Hodgkinson 1974), bean (Phaseolus vulgaris) (Wareing et al. 1968, Neales et al. 1971, Alderfer and Eagles 1976, Carmi and Koller 1979, von Caemmerer and Farquhar 1984), Monterey pine (Pinus radiata) (Sweet and Wareing 1966), bluebunch wheatgrass (Caldwell et al. 1981, Nowak and Caldwell 1984), Quercus rubra (Heichel and Turner 1983), red oatgrass (Themeda triandra) (Wallace et al. 1984), mesa dropseed (Sporobolus flexuosus) (Senock et al. 1991), and maize (Zea mays) (Wareing et al. 1968). Compensatory photosynthesis has also been documented for leaves that were produced following plant defoliation (Bassman and Dickmann 1982, Heichel and Turner 1983, Caldwell et al. 1981, Nowak and Caldwell 1984). The relative increase in photosynthetic rates in these cases was less than those observed for leaves existing on the plant prior to defoliation.

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While increased photosynthesis of foliage on defoliated plants is frequently observed, rates less than or equal to those on undefoliated plants have also been reported (Ryle and Powell 1975, Poston et al. 1976, Detling et al. 1979a, Hall and Ferree 1976, Ferree and Hall 1981, Atkinson 1986, Boucher et al. 1987). The discrepancy between these studies and those reporting compensatory photosynthesis has not been adequately explained in most cases. There appears to be a tendency for minimal compensatory photosynthesis in leaves damaged by insects or clipped so that a long cut edge (wound) remained (Hall and Ferree 1976, Poston et al. 1976, Detling et al. 1979a, Ferree and Hall 1981). However, experimental aphid infestation of pea (Pisum sativum), bean (Vicia faba) and Vigna unguiculata induced compensatory photosynthesis to an extent that just balanced the photosynthate demand of the aphids (Hawkins et al. 1987). Repeated severe defoliation may also reduce photosynthetic rates, in even very grazing-tolerant species, such as Kyllinga nervosa (Wallace 1981, Wallace et al. 1985, Hodgkinson et al. 1989).

Compensatory photosynthesis originates from a rejuvenation of leaves and/or an inhibition of the decline in photosynthetic capacity that normally occurs as leaves age and senesce (Fig. 6). The degree and duration to which net photosynthetic rates are rejuvenated following defoliation varies greatly among species and among leaves on individual plants. Rejuvenation may only partially occur indicating that photosynthetic rates do not attain values comparable to those of newly developed leaves or photosynthetic rates of rejuvenated leaves may exceed those of newly developed leaves on undefoliated plants (Hodgkinson 1974, Heichel and Turner 1983). For example, in alfalfa the ability of mature leaves to increase photosynthetic rates to values equivalent to those of recently expanded leaves declined with age; 65-day-old leaves only increased to 66% of maximum capacity while younger leaves attained maximum photosynthetic rates (Fig. 6) (Hodgkinson 1974). However, because of the low initial rates of net photosynthesis in older leaves, proportional increases were greater in older than in younger leaves. Photosynthetic capacity exceeded the predefoliation rates by 181% in 65-day-old leaves compared to 12 and 74% in 16- and 30-day-old leaves, respectively (Hodgkinson 1974). Older leaves also required longer than younger leaves to achieve maximum recovery (5 versus 12 days; Hodgkinson

1974). Similar patterns were observed in perennial bunchgrasses by Nowak and Caldwell (1984).

Leaves on defoliated plants which do not rejuvenate may still exhibit higher photosynthetic rates than comparable leaves on undefoliated plants because the normal decline in photosynthetic capacity associated with aging is inhibited (Gifford and Marshall 1973). A reduced rate of leaf senescence is also expressed as an increase in mean leaf lifespan on defoliated plants (Jones et al. 1982, Nowak and Caldwell 1984).

Regulation. Modifications in microclimate and plant function are both potentially important processes regulating compensatory photosynthesis following defoliation. Leaves remaining on defoliated plants are often exposed to greater light intensity and altered light quality (Wallace 1990, Senock et al. 1991). Light intensity and quality influence the development of photosynthetic capacity in expanding leaves and leaf senescence in the absence of defoliation. Consequently, compensatory photosynthesis may occur in response to modifications in the light environment alone. The reallocation of carbon and nitrogen resources that accompanies compensatory photosynthesis may be a plant response to more closely optimize photosynthetic carbon gain in the altered light environment (Field 1983, Gutschick and Wiegel 1988). For example, compensatory photosynthesis of developing leaves of perennial ryegrass was inhibited when they were maintained in a shaded environment (Woledge 1977). This response indicates that the occurrence of compensatory photosynthesis was at least partially light dependent, rather than being completely determined by source-sink or hormonal changes in the plant. In many other cases, however, compensatory photosynthesis occurs independent of changes in the light environment (Wareing et al. 1968, Hodgkinson et al. 1972, Gifford and Marshall 1973, Hodgkinson 1974, Woledge 1977). These data indicate that compensatory photosynthesis can be induced by both changes in the light environment, and by physiological modifications in plant function following defoliation, or by a combination of these processes.

The relative importance of two potential physiological mechanisms of compensatory photosynthesis was assessed by Carmi and Koller (1979). They considered the role of increased carbon demand per unit photosynthetic area following defoliation (i.e., direct source-sink interaction), and the increased supply of hormones or other substances transported from the root system to the defoliated shoot system (i.e.,

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increased root/shoot ratio). Compensatory photosynthesis in primary leaves of bean was not caused by direct source-sink interactions, but was dependent on substances transported in the xylem from the root system to the leaves on defoliated plants. Further support for this mechanism comes from studies demonstrating that modifications in photosynthetic capacity following defoliation are consistent with the effects of exogenously applied cytokinins (Wareing et al. 1968). Finally, the absence of immediate increases in photosynthesis following a decrease in the source/sink ratio supports the conclusion that compensatory photosynthesis is not the direct result of increased carbon demand (King et al. 1967, Geiger 1976, von Caemmerer and Farquhar 1984). Rather, indirect effects resulting from the increased root/shoot ratio, presumably mediated by cytokinins or other signals produced in the root, appear to affect leaf development and aging so that the photosynthetic apparatus is rejuvenated and/or its senescence is inhibited.

Mechanisms. Gas exchange and biochemical analyses of leaves exhibiting compensatory photosynthesis have documented a number of closely coordinated physiological and morphological modifications that result in increased photosynthetic capacity per unit leaf area. Many of the mechanistic components associated with compensatory photosynthesis have been consistently observed in numerous species, although every component has not been documented in each case.

Compensatory photosynthesis results from an increased photosynthetic capacity within the mesophyll, rather than improved stomatal conductance, with very few exceptions (e.g., Gifford and Marshall 1973). Increased leaf nitrogen content is the most frequently documented modification related to compensatory photosynthesis. Increased nitrogen content is consistent with increased mesophyll conductance and decreased internal CO_2 concentrations under ambient conditions and is associated with increased RNA, soluble protein, and chlorophyll content (e.g., Satoh et al. 1977, Nowak and Caldwell 1984, Yamashita and Fujino 1986). Dark respiration rates may also be higher in leaves exhibiting compensatory photosynthesis than in leaves on undefoliated plants which is characteristic of leaves with higher protein contents (e.g., Atkinson 1986). Direct measurements of increased RuBP carboxylase activity or amount, and electron transport capacity have also been correlated with compensatory photosynthesis as determined by gas exchange (Wareing et al. 1968, Neales et al.

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1971, Jenkins and Woolhouse 1981, Aoki 1981, von Caemmerer and Farquhar 1984, Yamashita and Fujino 1986). Yamashita and Fujino (1986) also documented increased RNA content in leaves of defoliated mulberry (Morus alba) plants. These coordinated biochemical changes provide the basis for increased photosynthetic capacity in leaves on defoliated plants. Mature leaves on defoliated plants frequently develop increased specific leaf mass (mass per unit area) within 1 - 14 days after defoliation and expanding leaves tend to grow larger on defoliated than on undefoliated plants (Alderfer and Eagles 1976, Satoh et al. 1977, Carmi and Koller 1979, Bassman and Dickmann 1982). The coordination of these physiological and morphological changes and the time required for their development is consistent with the hypothesis that root produced substances and increased nitrogen allocation are important processes regulating the occurrence of compensatory photosynthesis.

Significance. Compensatory photosynthesis enables defoliated plants to fix more carbon than if photosynthetic rates were maintained at levels comparable to undefoliated plants. Unfortunately, few analyses have been done to determine the quantitative contribution of compensatory photosynthesis to the carbon budget of defoliated plants. Heichel and Turner (1986) calculated that the carbon assimilation associated with compensatory photosynthesis of two defoliated tree species was 19-67% greater than would have been expected if no compensatory photosynthesis had occurred. Gold and Caldwell (1990), however, present evidence indicating that recovery of whole-plant photosynthesis in crested wheatgrass subjected to various defoliation treatments was more closely correlated with the rate of leaf area expansion than with the photosynthetic rate per unit foliage area, which partially reflected compensatory photosynthesis. The compounding effect of increasing leaf area on canopy photosynthetic capacity and the transient nature of compensatory photosynthesis are at least partially responsible for these conflicting interpretations. These data suggest that the contribution of compensatory photosynthesis is variable among species and is influenced by a large number of plant and environmental variables.

Compensatory photosynthesis is a relatively consistent response of defoliated plants. The physiological basis for this response is a coordinated set of changes in the biochemical composition and morphological structure of leaves that is consistent with the reversal of developmental processes that normally occur during leaf aging. Compensatory photosynthesis appears to be an important component of compensatory growth in defoliated plants, yet it occurs in many defoliation-sensitive as well as defoliation-tolerant species and it often does not persist throughout the recovery period. The quantitative contribution of compensatory photosynthesis to plant recovery following defoliation cannot be evaluated without considering the simultaneous modifications in leaf area expansion and canopy microenvironment.

Canopy reestablishment

Compensatory leaf and tiller growth. Recovery of whole-plant photosynthetic capacity is dependent on the rate at which new photosynthetic surfaces are produced to an equal or greater extent than compensatory photosynthesis. The rate of canopy reestablishment, or the leaf replacement potential (Hyder 1972), is affected by environmental, physiological and morphological considerations. Reinvestment of current photosynthetic carbon in new leaf area by allocation to shoot meristems has a compounding effect on whole-plant photosynthetic capacity, making small increases in the rate of refoliation an important component of compensatory growth. The capacity for rapid canopy reestablishment is an important characteristic of defoliation tolerant plants (Davidson and Milthorpe 1966b, Caldwell et al. 1981, Richards and Caldwell 1985, Fankhauser and Volenec 1989, Hodgkinson et al. 1989).

Rates of leaf and tiller growth on defoliated plants may occasionally exceed those of undefoliated plants and can increase the rate of canopy reestablishment. More rapid leaf expansion on defoliated plants than on undefoliated plants has been observed in a number of species, including crested wheatgrass, tall fescue, Kyllinga nervosa, and kleingrass (Panicum coloratum) (Wallace 1981, Wolf and Parrish 1982, Wallace et al. 1985, Gold and Caldwell 1989a). In crested wheatgrass, grazed tillers had higher relative growth rates than tillers of ungrazed plants when grazing occurred prior to internode elongation in the spring (Olson and Richards 1988c). Enhanced leaf and tiller growth rates usually persist for only a few weeks and are not consistently

expressed in all environmental conditions or phenological stages within the growing season (e.g., Volenec and Nelson 1983, Olson and Richards 1988c) (see Compensatory Growth section).

Developmental controls. The potential for canopy reestablishment in grasses is determined by the availability and activity of intercalary, apical and axillary meristems. The interaction among meristem type, environmental variables, and resource availability determines the rate of leaf area expansion in plants. For example, the availability of active intercalary and apical meristems following defoliation establishes high priority sinks which sequester currently produced photosynthetic carbon or reserve compounds located in stem and sheath bases (Richards and Caldwell 1985, Bucher et al. 1987a, 1987b, Schnyder and Nelson 1989, Danckwerts and Gordon 1987). Activity of these sinks induces the modified allocation patterns observed immediately following defoliation and contributes to the rapid replacement of the photosynthetic canopy. When active shoot meristems are removed, or when unfavorable environmental conditions limit growth, recovery is delayed or slowed (Muldoon and Pearson 1979, Richards and Caldwell 1985, Bucher et al. 1987a, 1987b). Recovery is most rapid in plants possessing abundant resources to support growth through a large number of active shoot meristems (Davidson and Milthorpe 1966b, Richards and Caldwell 1985, Hodgkinson et al. 1989, Busso et al. 1990).

Differences in herbivory tolerance between rhizomatous grasses and bunchgrasses, and among species within each group, is largely a function of meristem availability at the time of defoliation. Rhizomatous species frequently possess large numbers of active meristem throughout the growing season. The presence of these active shoot sinks rapidly sequesters available carbon and nitrogen within the plant increasing the relative rate of shoot growth following defoliation. For example, switchgrass plants exhibited reduced growth and reproduction when defoliated the same year they were initiated from seed, while established plants with well developed rhizomes increased growth and reproduction when subjected to a comparable defoliation intensity (Hartnett 1989). Rhizomatous species are most severely impacted by defoliation when tiller densities are at a seasonal low (Hull 1987). However, additional attributes such as intertiller resource allocation and defoliation avoidance

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characteristics (see Grazing Resistance section) also contribute to the grazing resistance of rhizomatous grasses in the field (Youngner 1972, Briske 1991).

Synchronous tiller development increases the susceptibility of bunchgrasses to a greater loss of active shoot meristems when grazed after internode elongation (Branson 1953, Westoby 1980, Olson and Richards 1988c). Synchronous tiller development also contributes to wide fluctuations in grazing tolerance with the progression of phenological plant development. For example, the grazing-sensitive, bluebunch wheatgrass, is quite tolerant of defoliation in the early spring when culmless, because active intercalary and apical meristems are located at or below ground level. However, defoliation tolerance decreases rapidly following internode elongation (Richards and Caldwell 1985, Busso et al. 1990). Seasonal variation in defoliation tolerance is much less pronounced in species with asynchronous tiller development. The most grazing tolerant bunchgrasses frequently possess asynchronous tiller development, producing a situation similar to that described for rhizomatous grasses. Examples of grazing tolerant bunchgrasses include buffelgrass (Cenchrus ciliaris), tanglehead (Heteropogon contortus), and guineagrass (Panicum maximum) (e.g., Hodgkinson et al. 1989, Mott et al. 1992).

Patterns of plant defoliation including the type, amount, and frequency of tissue removal, must be given careful consideration because the number and source of available meristems function as important determinants to plant recovery following grazing. The following sections review the developmental considerations that influence the rate of plant recovery following defoliation and the associated patterns of resource allocation among the various sinks on defoliated plants.

Intercalary meristems. Cellular division and expansion from a zone of meristematic tissue located at the base of the blade, sheath and internode collectively contribute to phytomer growth (Fig. 7) (Evans and Grover 1940, see Dahl, this volume). The initiation and maturation of intercalary meristems (i.e., meristems separated from the apical meristem by a region of nonmeristematic tissue) occurs in sequence beginning with the blade and terminating with the internode (Stubbendieck and Burzlaff 1971, Sims et al. 1971). Meristematic activity of the blade ceases at about the time the leaf tip emerges from the subtending sheaths, which is comparable to the time of ligule differentiation. Meristematic activity of the sheath ceases when the ligule emerges

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from the subtending sheaths (Sharman 1942). Leaf growth continues following the completion of cell division as recently divided cells in the blade and sheath expand. Although, intercalary meristem activity is short-lived and the total amount of biomass differentiated per individual meristem is relatively small, phytomer growth collectively determines the production potential of individual tillers.

Defoliation influences phytomer growth by primarily affecting cell expansion rather than cell division (Grant et al. 1981, Volenec and Nelson 1983). Defoliation at 2-week intervals reduced leaf elongation rate by 30% in tall fescue and was associated with a reduction in the length of mature epidermal cells in comparison with plants defoliated at 6-week intervals (Volenec and Nelson 1983). The reduction in cellular elongation suggests that growth is restricted by substrate availability from either stored carbohydrates (Grant et al. 1981) or current photosynthesis (Richards and Caldwell 1985, Gold and Caldwell 1989a, 1989b). However, in some cases defoliation may also promote leaf elongation, as discussed previously. For example, improved water status, resulting from a reduction in transpirational area following defoliation, promoted cell expansion which contributed to an increased rate of leaf elongation in tall fescue plants (Wolf and Parrish 1982).

Apical meristems. Growth from apical meristems is dependent upon the successive differentiation of leaf primordia (i.e., blades and sheaths of differentiating phytomers). These primordia provide the meristematic source for leaf replacement following defoliation (Fig. 7). Initially, the entire primordium is meristematic, but cellular division is quickly restricted to individual intercalary meristems of the blade and sheath (Dahl, this volume, Sharman 1945). The interval between the appearance of successive leaf primordia is approximately 7 days in vegetative tillers under favorable environmental conditions (Anslow 1966). However, the rate of leaf appearance is known to be species specific and influenced by a wide range of environmental conditions.

Differentiation and growth of leaf primordia are relatively insensitive to defoliation based on the limited number of species that have been evaluated (Anslow 1966, Jones et al. 1982, Chapman et al. 1983). Severe defoliation reduces leaf appearance by directly removing apical meristems or indirectly by reducing photosynthetic carbon availability. Removal of more than two entire leaves per tiller is required to decrease

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the rate of leaf appearance in perennial ryegrass (Davies 1974, Grant et al. 1983). Defoliation may also increase leaf initiation by increasing irradiance on the remaining portions of the canopy thereby potentially increasing photosynthetic efficiency and increasing carbon availability for leaf replacement (e.g., Gold and Caldwell 1989b). An increase in leaf initiation rate with increasing irradiance (Anslow 1966) and leaf area per tiller (Grant et al. 1983) is well documented.

Grazing tolerance in grasses is partially attributable to the basal location of both the apical and intercalary meristems. The apical meristem remains near the soil surface continually differentiating leaf primordia until it undergoes floral induction in grasses that do not produce culmed vegetative shoots (Branson 1953, Dahl, this volume). Culm elongation occurs from the activation of intercalary meristems at the base of the several uppermost internodes. Although apical meristems are much more vulnerable to removal by large herbivores following floral induction, the capacity to differentiate subsequent leaf primordia has already been terminated (Sharman 1947). Culm elongation does occur in vegetative tillers in a number of species elevating the apical meristem while it is still capable of differentiating leaf primordia (Branson 1953, Dahl, this volume). Apical meristem removal in these species determines that leaf replacement must occur from immature intercalary meristems or tiller growth from axillary buds. Consequently, species producing a large proportion of reproductive or culmed vegetative tillers are best suited to intermittent defoliation rather than continuous grazing (Branson 1953, Hyder 1972). Intermittent defoliation provides a sufficient period of time for tillers to express maximum vegetative production prior to the termination of growth following floral induction or apical meristem removal.

Axillary buds. Axillary buds are rudimentary apical meristems which possess the capacity to differentiate into complete tillers. A single bud is differentiated from the apical meristem of the parent tiller as a component of each phytomer (Fig. 7). However, within an individual phytomer, axillary bud growth is preceded by growth of the blade, sheath and potentially the internode. If conditions are unfavorable for growth at the time of bud maturation, or if apical dominance is imposed, the buds may be inhibited for a period of time prior to growth. Axillary bud development in response to environmental conditions and defoliation are discussed in the tiller demography section.

Relative contribution of meristematic sources. Growth is dependent on all three meristematic sources in perennial grasses, but their relative contributions differ in magnitude and chronology (Briske 1986, 1991). Although intercalary meristems form the basis for phytomer growth, their contribution is limited to the relatively brief period of growth associated with the respective intercalary meristems of individual phytomers (Table 1). Apical meristems play a central role in the meristematic potential of grasses because they are the source of phytomer production including axillary buds. Axillary buds develop into mature apical meristems, which can differentiate successive axillary buds, thereby contributing to the persistence and sustainable productivity of perennial grasses.

Canopy reestablishment proceeds most rapidly from intercalary meristems because cell division has previously occurred within leaf primordia (Cook and Stoddart 1953, Hyder 1972, Briske 1991) (Table 1). Leaf replacement from apical meristems occurs at a slower rate because of the time required for differentiation and cell expansion within individual leaf primordia. Canopy reestablishment is slowest from axillary buds because of the time required for bud activation and leaf primordia differentiation. Although growth of these three meristematic sources can be considered independently, all three grow simultaneously during canopy reestablishment. The relative contribution of these meristematic sources to plant growth varies among species and is influenced by environmental variables and stage of phenological development (Coughenour et al. 1985a, 1985b, Olson and Richards 1988c). Knowledge of the relative availability and activity of meristematic sources is necessary to accurately interpret and potentially anticipate the regrowth potential of grasses.

TILLER AND PLANT DEMOGRAPHY

Information addressing tiller and plant demography of important North American grasses is extremely limited. Demographic processes including recruitment, mortality, density, and size class distribution of tillers and plants, have important consequences for the persistence and sustainable productivity of species populations. The objectives of this section are to address the essential aspects of tiller and plant demography in ungrazed plants and populations and then evaluate the effects of grazing on these demographic processes.

Plant organization and persistence

The developmental morphology of grasses is based upon the successive differentiation of phytomers from apical meristems (Briske 1991, Dahl, this volume). However, an individual plant can also be viewed as a population of tillers because each tiller is composed of a series of phytomers differentiated from an individual apical meristem. Regardless of the growth unit recognized, the architecture and productivity of plants is partially determined by the population dynamics of growth units (i.e., phytomers or tillers). This concept is clearly demonstrated by the relatively constant leaf number maintained by tillers throughout the growing season (Anslow 1966, Vine 1983). A relatively constant number of leaves is maintained because leaf production (recruitment) and leaf mortality occur at approximately comparable rates. Similarly, the relative rates of tiller recruitment and mortality establish the number of live tillers per plant or per unit area (White 1980).

Grasses can adjust to resource availability within their environment by altering plant density, tiller density or tiller weight because of their modular construction (Kays and Harper 1974). The demographic principle stating that a plant population can potentially yield a comparable level of production over a wide range of plant densities is known as the law of constant yield (Harper 1977, p. 154). This principle indicates that a plant population possesses sufficient plasticity to adjust to a particular level of resource availability through various combinations of plant size and density. In other words, resource availability within the environment, rather than plant growth potential, ultimately imposes an upper limit on population growth.

Population persistence and productivity may be maintained through either sexual or asexual (i.e., vegetative growth) reproduction, but available information suggests that vegetative growth (i.e., tillering) is the dominant form of reproduction in both semiarid and mesic grasslands (e.g. Belsky 1992). Investigations conducted in the tallgrass (Rabinowitz 1981, Johnson and Anderson 1986), midgrass (Kinucan 1987), and shortgrass (Coffin and Lauenroth 1989) prairies of North America consistently demonstrate a lack of correspondence between the existing vegetation of late-successional grassland communities and the species composition of the seed bank. Although caryopses are frequently produced, few appear to retain their viability within the soil for greater than one year (Thompson and Grime 1979, Pyke 1990). In addition, the number of seedlings recruited within established grasslands are frequently low and occur only sporadically during years of favorable moisture and temperature conditions (Wilson and Briske 1979, Salihi and Norton 1987, Pyke 1990, Jónsdóttir 1991).

Tiller recruitment from vegetative growth is more consistent than recruitment from seed because juvenile tillers import resources from parental tillers (Tripathi and Harper 1973, Welker et al. 1991). Consequently, vegetative growth is much less dependent upon immediate resource availability than is sexual reproduction. However, sexual reproduction is necessary for the maintenance of genetic diversity in populations and for population regeneration following plant mortality associated with large scale disturbances (O'Connor 1991). Additional research is needed to assess the relative contributions of vegetative and sexual reproduction to sustainable productivity and population maintenance in grasslands.

Tiller recruitment and mortality

Tiller recruitment may occur throughout the growing season, but maximum recruitment frequently occurs in the spring and/or autumn in both cool-season (Langer 1956, Langer et al. 1964, Robson 1968) and warm-season perennial grasses (Reidenbaugh 1983, Butler and Briske 1988). For example, crested wheatgrass, bluebunch wheatgrass (Mueller and Richards 1986), Arizona cottontop (Trichachne californica) (Cable 1971), big bluestem (Andropogon gerardii) (McKendrick et al. 1975), and Nebraska sedge (Carex nebraskensis)(Ratliff and Westfall 1992) recruit a single

tiller cohort in the autumn or spring, while Indiangrass (<u>Sorghastrum</u> <u>nutans</u>) (McKendrick et al. 1975) and little bluestem (Butler and Briske 1988) recruit two tiller cohorts in the late spring, early summer or autumn.

Tillers recruited early in the growing season frequently become florally induced and terminate their life cycle during the same growing season while tillers recruited later in the season frequently over-winter and resume growth the subsequent growing season. This pattern of tiller development results in greater tiller longevity, but longevity does not generally exceed two complete growing seasons in temperate perennial grasses (Langer 1956, Robson 1968, McKendrick et al. 1975, Butler and Briske 1988, Ratliff and Westfall 1992). Culms of Arizona cottontop survived three years in some cases, but the vegetative tissue they supported was comprised of younger tissues originating from elevated axillary buds along the culm (Cable 1971).

Tiller longevity is greater for grasses and sedges growing at higher latitudes than it is for grasses at lower latitudes. For example, tillers of <u>Agrostis</u> <u>stolonifera</u>, <u>Poa</u> <u>pratensis</u> ssp. <u>irrigata</u>, and <u>Festuca</u> <u>rubra</u> survived 3, 3, and 5 years, respectively, in a Baltic seashore meadow near Stockholm, Sweden (Jónsdóttir 1991). Tillers of <u>Dupontia</u> <u>fischeri</u> survived 4 - 5 years near Barrow, Alaska (Mattheis et al. 1976) and mean longevities of <u>Carex</u> <u>bigelowii</u> tillers have been estimated at 3 - 4.6 years (Carlsson and Callaghan 1990). The mechanism(s) promoting greater tiller longevities in high latitude graminoids in comparison with temperate grasses is unknown.

Mortality of vegetative tillers is frequently associated with reproductive development of parental tillers. Young vegetative tillers succumb to shading by the taller reproductive tillers and/or the cessation of resource allocation from parental tillers because of the additional resource demand created by culm and inflorescence development (Smith and Leinweber 1973, Ong 1978). Apparently the smallest tillers within the plant, which are partially dependent upon parental tillers for resources, are unable to effectively compete for resources when the plant encounters stress and are the first to undergo mortality (Ong 1978, Parsons et al. 1984). The longevity of reproductive tillers is established by the transition of the apical meristem from a vegetative structure to a reproductive structure. The capacity for vegetative growth is lost during this transition and subsequent vegetative growth can only be initiated from axillary buds (Sharman 1945, Langer 1972).

Mechanisms of tiller population regulation

Tiller populations of numerous species, including <u>Cyperus</u> <u>esculentus</u> (Lapham and Drennan 1987), big galleta (<u>Hilaria</u> <u>rigida</u>) (Robberecht et al. 1983) and crested wheatgrass (Olson and Richards 1989), are known to be regulated by density-dependent mechanisms. Density-dependent mechanisms regulate population size by increasing recruitment and survival at low densities, while reducing recruitment and survival at high densities (Silvertown and Lovett Doust 1993, p. 136). Presumably competition influences resource availability and therefore tiller recruitment and/or mortality. Tiller populations of little bluestem in east central Texas were regulated in similar proportion by competition from associated tillers within plants and by neighboring plants (Briske and Butler 1989). Tiller recruitment increased 57 and 71% following removal of neighboring plants and approximately one-half of the existing tillers within plants, respectively. Neither tiller survival nor reproductive development were affected as dramatically as recruitment by reduced competition in comparison with undisturbed plants. However, density-dependent regulation may only be a significant mechanism of population regulation in specific communities and during certain seasons of the year (Fowler 1986, Olson and Richards 1989). In addition, density-dependent mortality, rather than recruitment, has been documented to be an important population regulation mechanism in several herb species (Lovett-Doust 1981).

Numerous environmental variables are known to influence tillering in perennial grasses. Environmental variables which promote growth, including favorable temperatures, irradiance, water and nutrient availability, generally promote tillering as well (Langer 1963, Williams 1970a). Tillering is also affected by interactions among environmental variables, plant age and genotype. Even though environmental variables, either singly or in combination, influence various aspects of plant growth, they do not appear to directly regulate tillering (Phillips 1975). Presumably, environmental variables must interact with the mechanisms of apical dominance to regulate the dynamics of tiller populations. Apical dominance defines the physiological processes by which the apical meristem exerts hormonal regulation over axillary bud growth (Murphy and Briske 1992). The theory was initially developed by Thimann and Skoog

(1933, 1934) who demonstrated the regulatory influence of auxin on lateral branching in bean.   The concept was extended to grasses when Leopold (1949) demonstrated that indoleacetic acid inhibited axillary bud growth in teosinte (Euchlaena mexicana) and barley.   This theory of apical dominance, termed the direct inhibition theory, continues as the prevailing view of apical dominance in grassland ecology and management even though insight into the physiological mechanisms has advanced substantially (Murphy and Briske 1992).   Although auxin produced in the apical meristem or young leaf primordia provides the principle correlative signal for bud inhibition, a second growth hormone, cytokinin, is also involved (Phillips 1975, Hillman 1984).   Auxin is proposed to interfere with the metabolic function of cytokinin in the bud or prevent its transport into the bud 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 several grasses. These growth inhibitors may transmit the correlative signal of auxin into the axillary buds because auxin has not been observed to directly enter the buds (Tucker 1977, 1978).   Although apical dominance is not thoroughly understood, recent advances indicate that the direct inhibition theory is no longer an appropriate interpretation of the phenomena (Murphy and Briske 1992).

Continued adherence to the direct inhibition theory of apical dominance in grassland ecology and management poses several disconcerting questions. How do plants initiate replacement tillers if the apical meristem is undisturbed?   What mechanisms regulate tiller recruitment in specific seasonal patterns?   How does tiller recruitment respond to changes in resource availability in the immediate environment? These considerations suggest that apical dominance may potentially respond or interact with environmental signals.

Radiation quality is an environmental signal documented to regulate a variety of developmental processes including seed germination, chlorophyll synthesis, leaf expansion, and internode elongation in a large number of vascular plants.   The ratio of red:far-red (660:730 nm) radiation is correlated with the abundance of biologically active and inactive forms of phytochrome which can induce a broad range of photomorphogenetic effects (Smith and Morgan 1983).   Radiation quality may also function as an environmental signal capable of regulating tiller recruitment in grasses

(Fig. 8) (Kasperbauer and Karlen 1986, Casal et al. 1986, 1987, Simon and Lemaire 1987).   Red radiation is attenuated more rapidly than far-red radiation as it passes through a plant canopy.   The decreasing red:far-red ratio may function as a signal to reduce tiller recruitment before the carrying capacity of the environment it exceeded (Deregibus et al. 1985, Casal et al. 1986, 1987).   Alternatively, prior to complete canopy development or following partial canopy removal by grazing, the red:far-red ratio may function as a signal to initiate tiller recruitment.

The hypothesis indicating that depressions in the red:far-red ratio directly suppresses tiller recruitment was tested with a single cohort of parental tillers on established little bluestem plants in the field (Murphy and Briske 1994). The red:far-red ratio was modified at the site of juvenile tiller initiation near plant bases throughout the daylight hours without increasing the amount of photosynthetically active radiation by either 1) supplementing red light beneath canopies to raise the naturally low red:far-red ratio or 2) supplementing far-red light beneath partially defoliated canopies to suppress the natural increase in the red:far-red ratio following defoliation. Neither supplemental red nor far-red radiation influenced the rate or magnitude of tiller recruitment despite the occurrence of tiller recruitment in all experimental plants (Fig. 9).

The hypothesis advocating direct regulation of tiller recruitment by the red:far-red ratio is further challenged by three categories of experimental evidence. First, reduced tiller recruitment is only one of several shade avoidance responses exhibited by tillers in response to the red:far-red signal (Murphy and Briske 1994). It is possible that a low red:far-red ratio reduces tiller recruitment indirectly by increasing carbon allocation to the blades at the expense of the axillary buds after tiller initiation has already occurred. Second, increases in the red:far-red ratio at the plant bases following partial canopy removal are relatively transient and do not override the associated constraints on tiller recruitment resulting from defoliation (Murphy and Briske 1992, 1994). Third, immature leaf blades appear to function as sites of red:far-red photoperception on individual tillers in addition to the previously recognized site at the tiller base (i.e., leaf sheaths or axillary buds) (Skinner and Simmons 1993, Murphy and Briske 1994). If blades are an important site of red:far-red photoperception, the ecological significance of the light quality signal is potentially minimized because the site of perception and a low red:far-red signal would spatially coincide only in young, juvenile tillers or seedlings

located beneath or near established plant canopies. Therefore, depressions in the red:far-red ratio are probably of greater ecological significance as a signal of impending competition for light in vegetation canopies than they are as a density-dependent signal capable of directly regulating tiller recruitment. These findings demonstrate that additional research is required before definitive ecological or managerial conclusions can be established concerning the significance of radiation quality as an environmental signal capable of regulating tiller recruitment.

Axillary bud longevity

Axillary buds accumulate on the stem bases (crowns) of individual tillers as they are successively differentiated with each phytomer (Fig. 7). This population of buds comprises a bud bank and provides the potential for subsequent tiller recruitment within the population (Harper 1977, p. 108, Noble et al. 1979). The bud bank is depleted as buds grow out to form tillers, succumb to biotic or abiotic stresses or age and senesce. Unfortunately, the extent of bud longevity is largely unexplored and two contrasting viewpoints have developed concerning their contribution to population persistence. One perspective maintains that if buds do not develop shortly following maturation they quickly become senescent (Hyder 1972, 1974) while the alternative perspective suggests that buds express a greater longevity forming a reserve of meristematic potential (e.g., Cable 1971, McKendrick et al. 1975).

Axillary bud longevity has tremendous ecological consequences for sustainable productivity and persistence of grasses. Species populations which rely on short-lived axillary buds are entirely dependent upon on the successive recruitment of tillers for their persistence. If climatic variation or biotic stresses (e.g., grazing or pathogens) eliminates recruitment of one or two tiller generations, persistence would be jeopardized because meristematic potential could potentially be depleted within the population. Contrastingly, species populations which possess axillary buds with greater longevities are less susceptible to a loss of meristematic potential following the interruption of successive tiller recruitment.

The limited amount of available data suggests that a portion of the axillary buds survive as long as the parental tiller remains alive (Briske and Butler 1989). However,

it is consistently buds which have most recently matured that grow out to form tillers even though several ontogenetically older buds may exist on the crown (Mitchell 1953, Busso et al. 1989). The longer buds remain inhibited and the further they become distanced from the apical meristem the less likely they are to form tillers (e.g., Mueller and Richards 1986). Therefore, the contribution of mature, inhibited buds to the persistence of grass populations is largely unknown.

Tiller demography in response to grazing

An incomplete understanding of the mechanisms regulating tiller recruitment and the contribution of axillary bud banks severely limits our ability to anticipate the demographic responses of grasslands to grazing. Defoliation can potentially influence tillering by affecting substrate availability for bud growth, the degree of bud inhibition (i.e., apical dominance), the number of viable buds and microclimatic conditions for growth. The end result is that the conceptual model currently used to anticipate and manage tiller population dynamics in grazed systems requires additional development.

Tiller recruitment

The widely held assumption that apical meristem removal stimulates tillering in rangeland grasses is not consistently supported by the available information (Murphy and Briske 1992). Both Ellison (1960) and Jameson (1963), following a thorough evaluation of the early literature, concluded that defoliation does not consistently increase tillering in native, perennial grasses. Many of the recent research findings substantiate their conclusions. For example, two seasons of livestock grazing did not increase, and in the case of the intensive grazing decreased, the total number of tillers recruited by crested wheatgrass (Olson and Richards 1988b and 1988c) and little bluestem (Butler and Briske 1988) in comparison with ungrazed plants. In addition, four consecutive years of biweekly defoliation to stubble heights of 5, 10, and 15 cm decreased tiller densities proportionately in pinegrass (Calamagrostis rubescens) (Stout et al. 1981). The apparent complexity of the physiological mechanisms regulating axillary bud growth (i.e., apical dominance) and the large number of potentially intervening factors including, environmental variables, species specific responses,

stage of phenological development, and the frequency and intensity of defoliation, further minimize the likelihood of a consistent tillering response to defoliation.

The time interval during which tillering is evaluated following defoliation may be the single greatest factor contributing to our misinterpretation of this response. Tillers are frequently initiated within 2 - 3 weeks of defoliation (Olson and Richards 1988c), and are much more obvious following partial removal of the canopy. However, this short-term "flush" of tiller initiation following defoliation may reduce subsequent tiller recruitment by a comparable number in comparison with maximum tiller recruitment in undefoliated plants (Fig. 10) (Butler and Briske 1988). In addition, tiller recruitment following spring grazing of crested wheatgrass did not contribute to tiller replacement the following growing season because of greater tiller mortality in grazed than in ungrazed plants during the winter (Olson and Richards 1988b). Therefore, in spite of an increased rate of tillering shortly following defoliation, defoliated grasses may not produce a greater number of tillers than undefoliated grasses when evaluated over one or more growing seasons. 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 native range grasses. However, forage grasses adapted to mesic, fertile environments (e.g., perennial ryegrass) frequently do increase net tiller production in response to grazing (Jones et al. 1982, Tallowin et al. 1989). The mechanism(s) associated with these contrasting responses is unknown.

Increased tiller densities per plant or per unit area do not necessarily translate into greater productivity in accordance with the law of constant yield previously discussed (Kays and Harper 1974). An inverse relationship is commonly observed between individual tiller weight and tiller density (Grant et al. 1981). For example, continuously-grazed populations of perennial ryegrass maintained tiller densities 2 to 5 times greater than those of infrequently mowed populations (Jones et al. 1982). However, greater weights and leaf areas of individual tillers in the mown populations compensated for the low tiller density enabling both populations to produce comparable amounts of biomass annually.

Phenological development

The interaction between the phenological stage of plant development and plant defoliation is not well understood given its potential significance to grassland production and management; consequently, the available data are inconsistent and difficult to interpret. For example, defoliation during early vegetative growth exerts a negligible (Olson and Richards 1988b and 1988c) or slight stimulatory effect on tillering (Vogel and Bjugstad 1968). However, defoliation during vegetative growth promotes tiller recruitment in Arizona cottontop to a greater extent than any other phenological stage (Cable 1971). Defoliation at the time of culm elongation, but prior to inflorescence emergence, stimulates tillering in crested wheatgrass (Olson and Richards 1988c), little bluestem (Jameson and Huss 1959), timothy (Phleum pratense) and meadow fescue Festuca pratensis (Fig. 11). However, defoliation at this phenological stage has been documented to suppresses tillering in big bluestem, little bluestem and Indiangrass (Vogel and Bjugstad 1968). Defoliation during inflorescence emergence stimulates tillering in the three tallgrasses mentioned previously (Jameson and Huss 1959, Vogel and Bjugstad 1968), but contradictory responses have been documented for big bluestem (Neiland and Curtis 1956), timothy and meadow fescue (Langer 1959).

It is tempting to speculate that a portion of the confusion associated with tiller initiation during the reproductive stage is based upon whether or not the apical meristem is removed by defoliation. However, defoliation did not consistently stimulate tillering in several wheatgrass species even when the apical meristem was removed (Branson 1956, Richards et al. 1988). Apical meristem removal was more consistently associated with increased tillering in several grasses of tropical origin. Apparently, physiological processes and/or environmental variables in addition to direct regulation by apical meristems are involved in the regulation of tillering in perennial grasses (Tainton and Booysen 1965, Richards et al. 1988, Murphy and Briske 1992).

Defoliation severity

The effects of defoliation frequency and intensity on tiller initiation are also difficult to generalize and easily confounded with phenological development and the seasonal progression of environmental variables. Tiller recruitment did not differ significantly between moderate and severe intensities of livestock grazing in crested

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wheatgrass (Olson and Richards 1988b) and little bluestem (Butler and Briske 1988). In some instances, the more severely grazed plants recruited a greater number of smaller tillers. Crested wheatgrass grazed twice during the spring (Olson and Richards 1988b) and intensively grazed perennial ryegrass display this pattern of tillering (Grant et al. 1983). However, more often, tiller recruitment decreases with increasing frequency and intensity of defoliation (Stout et al. 1981). It has been suggested that a stubble height of 2 - 3 cm is the optimal grazing intensity to maintain high tiller densities in populations of perennial ryegrass (Grant et al. 1983). More lenient grazing reduces tiller densities by decreasing tiller recruitment and increasing tiller mortality through self-shading while more severe grazing decreases tiller densities by limiting substrate availability following removal of excessive leaf area (Grant et al. 1983). This may serve as a useful generalization of the effect of defoliation intensity on tiller densities even though the optimal defoliation intensity will undoubtedly vary with species, stage of phenological development and associated environmental variables (Langer 1963).

System of grazing

The best documented examples of the effect of grazing systems on tiller dynamics are for perennial ryegrass. Continuous grazing maintains greater tiller densities than rotational grazing or infrequent mowing in contrast to native range grasses (Jones et al. 1982, Tallowin et al. 1989). Similarly, the more intensive, continuous grazing regimes produce the greatest number of tiller cohorts within the population (Parsons et al. 1984). Both responses are associated with a reduction in foliage density allowing more irradiance to penetrate into the canopy. This microenvironmental modification facilitates both tiller recruitment and daughter tiller survival (Parsons et al. 1984, Tallowin et al. 1989). Even though continuously grazed populations maintain the highest tiller densities, they also possess tillers with the lowest weights (Grant et al. 1981, Jones et al. 1982). However, perennial ryegrass has undergone substantial genetic selection, is subject to intensive management practices (e.g., fertilization and livestock movement), and is restricted to mesic, temperate climates (e.g., United Kingdom and New Zealand). Consequently, it is questionable to what extent these results are directly applicable to native grasslands in extensively managed systems with more rigorous climatic regimes.

Plant demography in response to grazing

Grazing-induced modifications in tiller recruitment, longevity and phenological development are eventually manifested in plant architecture and population structure. Population structure includes the attributes of density, size class distribution and age structure of plants and has important implications to grazing resistance, competitive ability and population persistence.

Population structure

The most pronounced modifications induced by grazing in native, bunchgrass populations are the reduction in individual plant basal area and increase in total plant density (Fig. 12). Both processes apparently result from the fragmentation of individual large plants within the population and may represent the initial and predominant process contributing to the decline of bunchgrass populations in response to grazing (Butler and Briske 1988). Grazed populations of several perennial grasses have been documented to consist of individuals with smaller basal areas in comparison with ungrazed populations including Idaho fescue (Festuca idahoensis) (Pond 1960), crested wheatgrass (Hickey 1961), tussock grasses in Kazakhstan (Vorontzova and Zaugolnova 1985), grasses in the flooding pampas of Argentina (Sala et al. 1986), and dune grasses in Wales (Gibson 1988). Grazing-induced population degradation eventually reduces tiller numbers and total basal area on a per unit area basis and potentially decreases the productivity and competitive ability of plants within the community (Fig. 13).

However, the ecological consequences of grazing-induced modifications in population structure are largely unexplored. Comparable tiller densities distributed in a low density of plants with large basal areas or a high density of plants with small basal areas did not significantly influence aboveground production of defoliated plants in comparison with undefoliated plants over a 2 year investigation (Briske and Anderson 1990). Apparently, both defoliated and undefoliated plants were equally capable of accessing and incorporating resources into production regardless of the spatial pattern of tiller distribution. However, tiller distribution did significantly affect the relative

increase in tiller density and basal area for both defoliated and undefoliated plants. Relative increases in both variables were greatest for the high density of small plants and least for the low density of large plants in the second year of the investigation. A population structure consisting of a high density of small plants confers a greater potential for tiller recruitment and basal area expansion because a majority of tiller recruitment occurs on the plant periphery rather than in the interior (Butler and Briske 1988, Olson and Richards 1988a).

Although the spatial distribution of tillers did not influence production following defoliation, it represents only one aspect of grazing-induced modifications in population structure. Grazing also modifies plant size class distribution and absolute tiller densities among the various species populations which comprise the community (Sala et al. 1986, Butler and Briske 1988). A large portion of the population growth of bunchgrasses can be ascribed to processes associated with individuals in the largest size classes (Moloney 1988). Eventually, small plants with few tillers will be placed at a competitive disadvantage in relation to their larger neighbors (Liddle et al. 1982, Fowler 1986, Olson and Richards 1989, Hartnett 1989). Similarly, populations possessing the greatest tiller densities may potentially acquire the greatest proportion of available resources within the community (Caldwell et al. 1987, Soriano et al. 1987). The population attributes of plant size class distribution and absolute tiller density appear to be of greater significance to herbivory tolerance in perennial bunchgrass populations than is the spatial distribution of tillers (Briske and Anderson 1990).

Plant longevity

Estimates of perennial grass longevity are limited and a portion of the available data document the occurrence of relatively short lifespans. Plant longevity estimates from the Santa Rita Experimental Range in Arizona (Canfield 1957), Jornada Experimental Range in New Mexico (Wright and Van Dyne 1976), and the U.S. Sheep Experimental Station in Idaho (West et al. 1979) are summarized in Table 2. Maximum longevities ranged from 4 years in curly mesquite (Hilaria belangeri) to 43 years in needle-and-thread (Stipa comata). Mean maximum plant longevities were shortest at the Santa Rita Experimental Range (8.4 years), intermediate at the Jornada

Experimental Range (13.1 years), and longest at the Sheep Experimental Station (34.4 years).

Observations of relatively short lifespans may partially originate from the architectural pattern of bunchgrass growth and the charting procedures frequently used to monitor plant survival. Basal area expansion and subsequent plant fragmentation may yield estimates of premature plant mortality even though the genotype continues to survive in the form of one or more remnants of the original plant (West et al. 1979). Chronological estimates of the architectural development of tufted hairgrass (Deschampsia caespitosa) in northern Europe suggest that 25 - 60 years is required for plants to progress from seedlings to complete fragmentation of the plant (Gatsuk et al. 1980). Comparable evaluations of tussock grasses in Kazakhstan, including Festuca, Koeleria, and Stipa spp., suggest maximum plant longevities of 30 - 80 years (Vorontzova and Zaugolnova 1985, Zhukova and Ermakova 1985). However, the remnants of fragmented plants were assumed to have a limited probability of survival requiring that population densities be maintained by sexual reproduction. Chronological estimates of architectural development throughout the life history of temperate perennial grasses are not available.

The limited amount of information addressing the effects of grazing on plant longevity indicates that both increases and decreases in longevity may occur. Longevity of Chloris acicularis, the sole representative of the late-successional vegetation in New South Wales, Australia was reduced by grazing while longevity of the mid-successional dominant, Danthonia caespitosa, was unaffected (Williams 1970b). Longevities of three perennial grasses increased in relation to that of three-tipped sagebrush (Artemisia tripartita) which decreased in response to autumn grazing (West et al. 1979). Similarly, longevities of late-successional grasses decreased in response to grazing while longevities of the mid-successional species increased (Fig. 14) (Canfield 1957). These seemingly contradictory responses suggest that the late-successional grasses may have been grazed more severely than the associated mid-successional species. Selective grazing may have placed the late-successional plants at a competitive disadvantage with the less severely grazed mid-successional species thereby reducing their longevity. However, grazing did not significantly affect

plant longevity in the investigations conducted on the Jornada Experimental Range (Wright and Van Dyne 1976) and Sheep Experimental Station (West et al. 1979).

A review of the population ecology literature for North American grasses confirms the conclusion of Crawley (1987) indicating that our understanding of herbivore-induced effects on population processes is poorly understood. Only limited data exist to substantiate that herbivory is a key regulatory process influencing the population dynamics of plants. Alternatively, the seemingly minimal impacts of herbivory on demographic processes may result from the complexity of the combined processes and associated interactions. The impacts of herbivory on population processes are difficult to discern because it may not directly induce plant mortality, but rather reduce growth, seed production (Verkaar 1987), and competitive ability (Briske 1991). These latter effects may only become evident in subsequent plant generations.

GRAZING RESISTANCE

A relative degree of grazing resistance can be assigned to numerous grasses based on the currently available information. Species characterized by decumbent canopy architectures (Arnold 1955, Hodgkinson et al. 1989, Painter et al. 1989), rapid rates of tiller recruitment (Richards et al. 1988) or high concentrations of secondary compounds (Coley et al. 1985, Georgiadis and McNaughton 1988, Briggs and Schultz 1990) are frequently more resistant than species which do not display these characteristics. Many characteristics associated with grazing resistance have been attributed to the selection pressure exerted by grazing and are frequently presented as evidence in support of the occurrence of coevolution between grasses and grazers (Georgiadis and McNaughton 1988). However, in both instances, the supporting evidence is limited and available data do not strongly confirm the role of grazers as selective agents in the evolutionary development of grass structure and function (Stenseth 1978, Herrera 1982, Simms and Rausher 1987, Belsky et al. 1993). Several environmental variables, other than herbivory, may have functioned as selective agents in the evolution of grasses (Coughenour 1985). For example, the basal location of meristems may have evolved in response to drought or fire as well as herbivory. If either of these abiotic variables were the selective agent which initially contributed to the evolution of basal meristems, then the occurrence of this trait in relation to grazing avoidance would be considered an ex-adaptation (i.e., adaptation to an environmental variable other than the one which originally contributed to its selection; syn. pre-adaptation; Coughenour 1985). These considerations indicate that even though the concept of herbivory resistance is frequently used by ecologist and resource managers, it is based on a limited amount of quantitative information.

Avoidance and tolerance components

The concept of grazing resistance defines the relative ability of plants to persist in a grazed plant community. Grazing resistance can be divided into avoidance and tolerance components based on the general mechanism(s) conferring resistance (Briske 1986, 1991). Grazing avoidance includes mechanisms that reduce the probability and severity of grazing while grazing tolerance consists of mechanisms that

facilitate growth following defoliation. Avoidance mechanisms include anatomical and architectural attributes in addition to secondary compounds which reduce tissue accessibility and palatability at several levels of grassland organization (Table 3). In Table 3, silicification refers to the occurrence of the mineral silica in epidermal cells (McNaughton et al. 1985) and interspecific association describes the protection afforded a species with a lesser expression of avoidance mechanisms when growing in close proximity to species with a greater expression of avoidance mechanisms (McNaughton 1978). Meristematic activity and compensatory physiological processes which increase growth following defoliation comprise the tolerance component (Table 4) (see Individual Plant Responses to Defoliation section).

The occurrence of varying degrees of grazing resistance among plants is well established by the predictable patterns of species selection by herbivores and species replacement in response to long-term herbivory (e.g., Dyksterhuis 1949, Heitschmidt et al. 1990). However, in most cases, it is uncertain whether herbivory induces species replacement through the selective utilization of plant species (i.e., avoidance mechanisms) or the occurrence of unequal growth capabilities among species following grazing (i.e., tolerance mechanisms). Although, both mechanisms are known to occur, the predominant mechanism, or relative combination of mechanisms, remains unknown for most species combinations and plant communities (e.g., van der Meijden et al. 1988). Selective grazing of the late-successional dominant, little bluestem, relative to mid-successional species, has been recognized as the predominant mechanism contributing to species replacement in the southern true prairie of Texas (Brown and Stuth 1993, Anderson and Briske, unpublished). Alternatively, more rapid canopy reestablishment in crested wheatgrass than bluebunch wheatgrass following comparable levels of defoliation demonstrates that these two species possess different degrees of grazing tolerance (Caldwell et al. 1981, Richards and Caldwell 1985, Caldwell et al. 1987). In this comparison, the potential contribution of avoidance mechanisms is minimized by comparable canopy architectures, phenology, and leaf nitrogen content between the two species and the imposition of equivalent defoliation intensities. The observation that plant productivity is often not reduced in direct proportion to the severity of defoliation imposed also substantiates the occurrence of

tolerance mechanisms which facilitate growth following defoliation (McNaughton 1983, Painter et al. 1989).

Recognition of herbivory avoidance or tolerance as the predominant mechanism inducing species composition shifts has important implications to grassland management. It is especially important in cases where the reduction and local extinction of late-successional dominants in severely grazed grasslands may have been misinterpreted as a consequence of inferior herbivory tolerance, rather than inferior herbivory avoidance, in relation to the associated mid-successional species. If the late-successional dominants are perceived as being relatively intolerant of herbivory, the only viable management strategy to maintain dominance of the late-successional species is to reduce the severity of grazing within the community. Alternatively, if inferior herbivory avoidance by the late-successional dominants is the predominant mechanism inducing species replacement, then managerial decisions to regulate the uniformity of grazing among species may be implemented to maintain dominance of the late-successional species. Intensive grazing of mid-successional species when the relative expression of avoidance mechanisms is lowest, including the period of maximum vegetative plant height (Arnold 1955, Belsky 1992) and prior to reproductive culm development (Willms et al. 1980, Ganskopp et al. 1992), can minimize, although not eliminate, selective herbivory among grass species (Briske and Heitschmidt 1991, Brown and Stuth 1993).

Grazing morphotypes

An indication of the relative contribution of avoidance and tolerance mechanisms to grazing resistance can be derived from the occurrence of morphotypic selection within species populations subjected to long-term grazing. Grazing or mowing selects against morphotypes possessing an erect canopy architecture in approximate proportion to the severity of defoliation (e.g., Scott and Whalley 1984). Grazing by domestic cattle has been demonstrated to function as a selection pressure capable of inducing architectural variation in perennial grass populations in an ecological time frame (ca $\leq$ 25 years; Peterson 1962, Briske and Anderson 1992). Selection has been documented to occur within much shorter time periods (2-12 years) in several perennial

grasses subjected to intensive grazing by prairie dogs (<u>Cynomys</u> <u>ludovicianus</u>) in the mixed prairie (Detling and Painter 1983, Jaramillo and Detling 1988, Painter et al. 1993). Kemp (1937) was among the first to quantify that grazing selected against erect morphotypes of Kentucky bluegrass, orchardgrass and white clover, but similar responses have been documented for several perennial grasses (Table 5). Decumbent morphotypes, in contrast to erect morphotypes, are characterized by a large number of small tillers with reduced leaf numbers and blade areas. However, physiological variables that may potentially contribute to grazing tolerance, including photosynthetic rate, transpiration rate and water-use efficiency, did not differ significantly between erect and decumbent growth forms of western wheatgrass (Detling and Painter 1983). Limited evidence does exist to suggest that morphotypes subjected to long-term grazing may possess a greater degree of grazing tolerance in addition to greater grazing avoidance. Decumbent morphotypes of western wheatgrass with a history of grazing had 3-fold greater rates of nitrogen accumulation per unit root mass than did populations with no history of grazing (Polley and Detling 1988). Plants with a history of grazing had greater rates of shoot growth following defoliation which may have generated the greater demand for nitrogen. In addition, tillers of western wheatgrass and blue grama (<u>Bouteloua</u> <u>gracilis</u>) plants with a history of grazing produced more biomass and had greater survivorship following defoliation than did populations which had not been subjected to intensive selection by herbivores (Painter et al. 1989).

The inference drawn from morphotypic selection in grazed grass populations is that avoidance mechanisms, rather than tolerance mechanisms, are the predominant component of grazing resistance (Detling and Painter 1983, Jaramillo and Detling 1988). Decumbent morphotypes are better able to avoid grazing because less biomass is removed by herbivores and a greater number of meristems remain to facilitate growth following defoliation (Carman and Briske 1985) (see Canopy Reestablishment section). In contrast, morphotypes characterized by a small number of large tillers with large leaf areas are more competitive in environments with dense canopies (but see Briske and Anderson 1992). Correspondingly, intra-specific competition is greatest within populations composed of erect morphotypes (Painter et al. 1989). However, grazing imposes a much greater detrimental impact on the

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competitive ability of erect morphotypes than of decumbent morphotypes because a greater portion of the canopy is removed.

The process by which grazing-induces variation among growth forms within species populations has not been definitively established. However, a majority of the evidence indicates that grazing-induced selection among growth forms is genetically based (McNeilly 1984, Scott and Whalley 1984, Carman and Briske 1985, Painter et al. 1989, 1993). The fact that grazing morphs of several midgrasses retained their decumbent stature for several growing seasons after being transplanted into a common garden or in a greenhouse in the absence of defoliation supports this interpretation (Polley and Detling 1988, Painter et al. 1993).

Paradoxically, there is little indication that grazing decreases genetic variability within species populations by selecting against the erect genotypes possessing limited avoidance mechanisms. A minimum of 66% of the individual plants subjected to electrophoretic analysis in both long-term grazed and ungrazed populations of little bluestem represented distinct morphotypes even though plants in the grazed population displayed characteristics of a decumbent growth form in comparison with those of the ungrazed population (Carman and Briske 1985). Comparable genetic diversity between these two populations indicates that grazing does not necessarily eliminate the larger, slower tillering genotypes from grazed populations. Alternatively, grazing may influence the expression of relative dominance among genotypes variously adapted to herbivory, competition and associated environmental variables (McNeilly 1984, McNeilly and Roose 1984). Although a portion of the erect genotypes may be eliminated from a population following frequent, intense herbivory, the majority of genotypes less adapted to herbivory may exist in a subordinate position in the community or in areas less frequented by herbivores (Carman and Briske 1985). Eventually, when herbivory is eliminated or reduced, canopy expansion and mulch accumulation increase self-shading and potentially shift relative dominance toward the larger, fewer tillered genotypes. Genetic variation may also be maintained by the development of stable associations between and among interspecific neighbors (Aarssen and Turkington 1985) and the occurrence of disturbances which characterizes most grasslands (Collins and Barber 1985, Collins 1987, Coffin and Lauenroth 1988).

Role of competition

Plants rarely respond to defoliation as isolated individuals in field settings. Defoliation affects the intensity of both intra-and interspecific competition in addition to directly influencing plant function (Caldwell 1984). For example, 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 associated vegetation within a 90 cm radius of the defoliated plants was clipped at ground level (partial competition) (Mueggler 1972)(Fig. 15). When competition from associated vegetation was removed by tilling within a 90 cm radius (no competition), defoliated plants produced three times the biomass of undefoliated plants growing with full competition. Similarly, defoliation of big bluestem to a height of 4 cm reduced biomass production 25% when plants were grown with a low density of nondefoliated neighbors, but production was reduced 90% by the same defoliation intensity when plants were grown with a high density of nondefoliated neighbors (Hartnett 1989). These data indicate that competition may influence growth following defoliation to an equal or greater extent than the direct effects of defoliation. The inherent competitive ability of a species within the community is an important determinant of its response to grazing.

Defoliation reduces the competitive ability of plants by reducing the effectiveness of resource acquisition within the environment. For example, the proportion of phosphorus isotope acquired by big sagebrush (<u>Artemisia</u> <u>tridentata</u>) from interspaces shared with bluebunch and crested wheatgrass increased by as much as 6-fold following a single defoliation removing 85% of the grass canopies (Caldwell et al. 1987). Significant increases in phosphorus absorption by big sagebrush occurred within 2 weeks of grass defoliation, indicating that resource competition is rapidly modified by grazing. Similarily, the competitive ability of big bluestem for nitrogen was reduced by a single defoliation to a height of 10 cm regardless of whether the neighbors within a 50 cm radius were defoliated or not (Wallace and Macko 1993).

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 (Fig. 15) (Mueggler 1972, Caldwell et al. 1985, Banyikwa 1988, Maschinski and Whitham 1989). The benefit a plant derives from defoliation of its neighbors coincident with its own defoliation has been termed competitive fitness (Belsky 1986). Larger statured grasses are frequently placed at a competitive disadvantage when grown with smaller statured grasses following defoliation to a comparable height because a greater proportion of biomass is removed from the larger plants (Arnold 1955, Belsky 1992).

The inherent mechanisms of grazing resistance are probably similar over the distributional range of a species, but the expression of relative resistance mechanisms will vary in relation to the grazing resistance and competitive ability of associated species. Species responses to grazing have been observed to vary depending upon the grazing intensity and topographic position within a mixed-grass prairie community (Archer and Smeins 1991). Relative abundance of western wheatgrass decreased regardless of grazing intensity or topographic position suggesting that it possessed limited grazing resistance relative to the associated species (Fig. 16). By contrast, the relative grazing resistance of buffalograss (Buchloë dactyloides) was relatively low in the swale, but relatively high on the ridge. Blue grama consistently expressed a high degree of grazing resistance except in the swale in response to severe grazing. The relative grazing resistance of buffalograss and sun sedge (Carex eleocharis) varied in response to 1) species specific patterns of livestock grazing, 2) site specific distribution of environmental variables, and 3) unique competitive interactions among the various plant species even though the inherent mechanisms of grazing resistance remained relatively constant (Archer and Smeins 1991).

Cost-benefit theory

The concept of grazing resistance is at least partially based on the assumption that the possession of grazing resistance mechanisms represent an associated cost to the plant (Simms and Rausher 1987, 1989). This assumption is most readily quantified in plants which produce secondary compounds to deter herbivory. For example, seedlings of the neotropical tree, Cecropia peltata, possessing high tannin concentrations, experienced less insect herbivory, but displayed lower growth rates in

the absence of herbivory than did seedlings which possessed lower tannin concentrations (Coley 1986). The difference in growth rate between these two groups of seedlings was attributed to the cost of producing secondary compounds and can be interpreted as the cost of herbivory resistance. Similar conclusions have been drawn from other investigations in which secondary compounds were variously produced by plants to deter herbivores (Windle and Franz 1979, Dirzo and Harper 1982). Mechanical defenses are also associated with large costs to the plant, but the evidence is much less extensive than it is for chemical defenses (van der Meijden 1988, Björkman and Anderson 1990, but see Ågren and Schemske 1993).

Grazing resistance presumably evolved as individuals in a population allocate various amounts of resources to resistance mechanisms and thereby experience differing degrees of fitness. Since natural selection is driven by the relative contribution of individuals to the gene pool of subsequent generations within a population, fitness estimates must be based on sexual reproduction and associated fitness related characteristics rather than solely on estimates of biomass production. Grazing resistance is potentially maximized in an evolutionary context at the point where a plant realizes the greatest increase in fitness for the amount of resources allocated to resistance mechanisms. In other words, grazing resistance is maximized when the cost of resistance approximates the benefits of resistance (Coley et al. 1985, Simms and Rausher 1987) (Fig. 17). Therefore, plants do not become completely resistant to herbivores because the cost of resistance must, at some point, exceed the benefit conveyed by the resistance mechanisms (Pimentel 1988). The potential trade-off between the costs and benefits of herbivory resistance occur because competition is the predominant selective agent constraining the evolution of herbivory resistance (Herms and Mattson 1992).

The cost of herbivory resistance is influenced by both chemical (i.e., turnover rates and redistribution) and ecological considerations (i.e., resource availability and plant growth rate) (Skogsmyr and Fagerstrom 1992). Therefore, the cost of herbivory resistance will vary considerably given the wide range of defense mechanisms that are known to occur and the relative degree to which they are expressed. Trade-offs between herbivory resistance and competitive ability are assumed to be greatest in resource-rich environments (Coley et al. 1985, Herms and Mattson 1992). Alternatively,

herbivory resistance is assumed to be more compatible with competitive ability, and therefore, less costly, in resource-limited environments. The evolutionary models of herbivory resistance are reviewed by Herms and Mattson (1992).

An accurate evaluation of herbivory resistance requires an estimate of not only the fitness conferred by the associated resistance mechanism(s), but also some indication of the extent to which herbivory reduces fitness in individuals which do not possess resistance mechanisms. Unfortunately, the influence of resistance mechanisms on fitness related characteristics are difficult to quantify between grazed and ungrazed populations. The concept of herbivory resistance requires additional conceptual development and quantification in order to develop a greater understanding of how specific resistance mechanisms influence plant responses to herbivory.

COMPENSATORY   GROWTH

Grazing is generally perceived to have a detrimental impact on grassland productivity by natural resource managers. Ellison (1960) concluded from a thorough review of the early literature that the beneficial effects of grazing on herbaceous plant growth, if any, were difficult to discern. However, this perspective was markedly altered by Chew (1974) and Mattson and Addy (1975) who suggested that herbivores may influence the structure and function of ecosystems to a greater extent than indicated by their biomass or the amount of plant material they consume. These authors suggested that herbivores may act as regulators of energy flow and nutrient cycling through a series of feedback loops on vegetation function. Owen and Wiegert (1976) further hypothesized that herbivores may increase plant fitness and McNaughton (1976, 1979) proposed that grazing could potentially optimize grassland production. These viewpoints stimulated a lively debate which continued through much of the following decade and increased the popularity of plant-animal interactions.

Grazing optimization hypothesis

The grazing optimization hypothesis originated from this contemporary view of plant-animal interactions (Dyer 1975, McNaughton 1976, 1979). The hypothesis states that primary production increases above that of ungrazed vegetation as grazing intensity increases to an optimal level followed by a decrease at greater grazing intensities (Fig. 18). This perspective represents a dramatic departure from the alternative view that grazing decreases primary production or that production remains constant up to a moderate intensity of grazing beyond which production decreases. Unfortunately, the general applicability of the grazing optimization hypothesis has not yet been established.

Ambiguity of the term "compensatory growth" has added considerable confusion to the debate over whether or not grazing increases plant productivity (Belsky 1986). Compensatory growth has been used to describe plant responses ranging from a partial replacement of removed biomass to production exceeding that of ungrazed plants. It is often difficult to discern which definition of "compensatory growth" is being used when reviewing the literature. Belsky (1986) proposed specific terms to clarify these growth

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responses (Fig. 18). Overcompensation refers to instances where cumulative total weight, including biomass removed by defoliation, exceeds the cumulative total weight of undefoliated plants. Partial compensation defines instances where more growth is produced by defoliated plants than would be expected if no increase in growth rate, i.e., compensatory growth, had occurred.

Supporting evidence

Much of the evidence in support of the grazing optimization hypothesis has been derived from containerized plant investigations conducted under controlled conditions. Overcompensation has been documented in certain instances with <u>Kyllinga</u> <u>nervosa</u>, an African C_4 sedge, defoliated to a height of 4 cm at daily intervals (McNaughton 1979), <u>K</u>. <u>nervosa</u> defoliated to a height of 2 cm at 2 day intervals when grown with limited water and high nitrogen availability (McNaughton et al. 1983), <u>K</u>. <u>nervosa</u> defoliated to a height of 5 cm at 7 day intervals when grown with moderate nitrogen availability (Wallace et al. 1985), and <u>Sporobolus</u> <u>kentrophyllus</u> when infrequently defoliated to a height of 6 cm and grown with limited water and high nitrogen availability (Georgiadis et al. 1989). Complete compensation has also been reported in <u>Briza</u> <u>subaristata</u> and <u>Stipa</u> <u>bavioensis</u> in response to an exponential increase in relative growth rate of shoots with increasing defoliation intensity (Oesterheld 1992). Although these data substantiate the occurrence of overcompensation, they also demonstrate the specific growth conditions necessary to induce its response (Hilbert et al. 1981, Olson et al. 1989, Maschinski and Whitham 1989, Alward and Joern 1993, Belsky et al. 1993).

Examples of overcompensation by individual plants in field settings are less numerous and less definitive. Grazing by native ungulates or clipping increased total plant production of the biennial herb, scarlet gilia (<u>Ipomopsis</u> <u>aggregata</u>), 2 and 1.5 times, respectively, within the same growing season in comparison with undefoliated plants (Paige and Whitham 1987). Although, the intensities of both grazing and clipping were severe (95% of the shoot biomass was removed), defoliation was restricted to the phenological stage of plant development associated with stem elongation following vegetative growth, but prior to inflorescence production. Defoliation also increased flower and fruit production and did not detrimentally effect seed weight or germinability

in comparison with undefoliated plants. Root biomass of defoliated plants was comparable or greater than that of undefoliated plants demonstrating that overcompensation did not result from the reallocation of belowground resources. Ungrazed plants of this species may have been meristem limited (i.e., Watson 1984) and defoliation may have activated growth of additional meristems which contributed to the increase in biomass yield and sexual reproduction.

However, Bergelson and Crawley (1992) evaluated 14 populations of scarlet gilia and found no evidence for overcompensation following defoliation throughout much of it's range. They hypothesized that shade played a substantial role in the occurrence of compensatory growth reported by Paige and Whitham (1987). Defoliation may have released buds from apical dominance and promoted branching to a greater extent in shaded than in full sun habitats. Conflicting reports of compensatory growth within the same species clearly illustrates the involvement of specific environmental variables and our limited understanding of the mechanisms contributing to the process.

Overcompensation has also been documented in the Intermountain shrub bitterbrush (Purshia tridentata) under field conditions (Bilbrough and Richards 1993). Spring shoot growth of plants subjected to simulated winter browsing exceeded that of unbrowsed control plants following removal of terminal buds only, 60%, or 100% of the previous year's growth from all branches within a plant, but only the 60% defoliation intensity was significant. Overcompensation partially resulted from defoliation-induced meristem activation based on an increase in the frequency of short shoot and node production and the greater length of long shoots in defoliated plants.

Big bluestem and switchgrass on the Konza Prairie both compensated for bison grazing by increasing their relative growth rates in comparison with ungrazed plants (Vinton and Hartnett 1992). However, big bluestem tillers grazed repeatedly during the previous year had lower relative growth rates, tiller weights and tiller survival the following year than did ungrazed tillers. Overcompensation was only observed in switchgrass when all of the tillers within a plant were defoliated (Hartnett 1989). However, overcompensation in switchgrass plants was associated with a reduction in biomass partitioning to rhizomes. Therefore, the short-term increase in shoot growth in response to defoliation may occur at the expense of perennating organs and potentially

compromise plant production and survival over the long-term (Hartnett 1989, Vinton and Hartnett 1992).

Although not a direct documentation of overcompensation, relative growth rates of crested wheatgrass tillers grazed by cattle were greater than for tillers in ungrazed plants when grazing occurred prior to internode elongation in the spring (Olson and Richards 1988c, Olson et al. 1989). Compensatory growth was only maintained for a 2 -3 week period after which the relative growth rates of tillers on defoliated plants decreased to rates less than those of ungrazed plants. Compensatory growth was not observed in this species when spring precipitation was below normal or when grazing occurred during culm elongation or inflorescence emergence.

Definitive examples of overcompensation in plant communities are also limited, but information is becoming available for a greater number of diverse systems. McNaughton (1979) was among the first to indicate that moderate grazing intensities imposed by native ungulates doubled aboveground productivity of grasslands dominated by <u>Andropogon</u> <u>greenwayi</u> in the Serengeti Plains of east-central Africa. Although grazing intensity was the predominant variable affecting overcompensation, it occurred to the greatest extent when soil water was limiting. In another study, production of mixed prairie vegetation was 41% greater in a rotational grazing system in comparison to that of ungrazed vegetation during the second year of a 2 year investigation (Heitschmidt et al. 1982). Overcompensation primarily resulted from compensatory growth of warm-season grasses during the autumn when soil water was readily available. Aboveground herbaceous production on a diverse set of sites grazed by elk (<u>Cervus</u> <u>elaphus</u>) and bison (<u>Bison</u> <u>bison</u>) in Yellowstone National Park was found to be 47% greater than on comparable ungrazed sites over a 2-year period (Frank and McNaughton 1993). Overcompensation was documented in both vegetative and reproductive tissues of <u>Bouteloua</u> <u>gracilis</u> and <u>B</u>. <u>hirsuta</u> in response to grazing by grasshoppers (<u>Ageneotettix</u> <u>deorum</u>) in the mixed-prairie of southwestern Nebraska (Alward and Joern 1993). Overcompensation occurred most consistently under conditions of reduced competition on sites in which each species was naturally most abundant.

Perhaps the most definitive examples of overcompensation within plant communities are those where the production of intertidal vegetation near Hudson Bay

was monitored following grazing by lesser snow geese (<u>Chen</u> <u>caerulescens</u> <u>caerulescens</u>). Production increases of 60 - 80% and 35 - 80% occurred in grazed monocultures of <u>Carex</u> <u>subspathacea</u> (Cargill and Jefferies 1984a) and grazed stands of <u>C</u>. <u>subspathacea</u> and <u>Puccinellia</u> <u>phryganodes</u> (Cargill and Jefferies 1984b), respectively, in comparison with ungrazed vegetation during the same growing season (Fig. 19). This system is extremely nitrogen limited and the effect of grazing without the addition of nitrogen in goose feces did not result in overcompensation (Hik and Jefferies 1990, Hik et al. 1991). Compensatory growth of <u>P</u>. <u>phryganodes</u> was dependent upon the rapid recycling of N, a low to moderate grazing intensity, and grazing early in the growing season. The potential for compensatory growth decreased as the growing season and phenological development of the vegetation progressed. Additional field investigations of primary production responses to grazing in a variety of ecological systems are required to more thoroughly assess the general applicability of herbivore optimization.

Causal mechanisms

A wide variety of mechanisms have been proposed to explain compensatory growth responses. Intrinsic mechanisms, which are associated with herbivore-induced physiological processes, have received the greatest attention (McNaughton 1979, 1983) while extrinsic mechanisms, those involving herbivore-mediated environmental modifications, have been less thoroughly investigated, but may be of equal or greater importance (Table 6). For example, accelerated rates of nutrient cycling 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 occurs 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, Holland et al. 1992). Overcompensation in grasslands grazed during only the winter when plants are dormant also document the occurrence of extrinsic mechanisms (Frank and McNaughton 1993). However, intrinsic mechanisms must be the predominant

explanation for compensatory growth in individual plant investigations, especially those in which defoliation is imposed by clipping (e.g., Paige and Whitham 1987, Bilbrough and Richards 1993).

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 (e.g., Brown and Allen 1989. For example, compensatory growth in <u>Ipomopsis arizonica</u> decreased in response to increasing interspecific competition, decreasing nutrient availability, and grazing during the later portion of the growing season (Maschinski and Whitham 1989). Brief periods of intensive herbivory confined to the early portion of the growing season appear to be an important requirement for the occurrence of compensatory growth in several diverse systems (McNaughton 1976, Paige and Whitham 1987, Hik et al. 1991, Frank and McNaughton 1993). This pattern of grazing is most representative of the spatiotemporal patterns produced by migratory herbivores (Frank and McNaughton 1993).

Collectively, the currently available data does not support the conclusion that overcompensation is a widely occurring phenomena in grazed systems. Belsky (1986) reviewed 48 reports in the literature referencing the response of above-ground production to grazing and found that 34 documented a decrease in production, 5 reported no change and 9 reported an increase in production. Similarily, Milchunas and Lauenroth (1993) concluded that overcompensation occurred in only 17% of a total of 276 data sets representing 159 communities. In addition, the increase in aboveground production observed in the grazed communities was quite small relative to production in ungrazed communities. Differences in aboveground production between grazed and ungrazed communities, for all communities combined, were significantly and negatively related to increasing 1) years of grazing, 2) intensity of biomass utilization, and 3) community productivity. Nevertheless, these three variables only explained 25% of the variation among the communities evaluated. When only grassland or grassland and shrubland communities were evaluated, the differences in aboveground production between grazed and ungrazed communities were more sensitive to changes in ecosystem variables (i.e., production and history of grazing) than to variables associated with grazing (i.e., intensity of utilization, years of grazing).

However, various compensatory mechanisms may increase plant growth rates following defoliation, but only partially compensate for the total amount of biomass removed (Belsky 1986). Partial compensation determines that plant productivity is not suppressed in direct proportion to the frequency and intensity of defoliation imposed, even though total production does not exceed that of ungrazed vegetation (McNaughton 1983, 1985).

It is important to recognize that much of the data collected in support of the grazing optimization hypothesis were from grazed systems where herbivore density and movement were not directly regulated by humans (e.g., McNaughton 1979, 1985, Paige and Whitham 1987, Hik and Jefferies 1990, Frank and McNaughton 1993). In these systems, primary production and herbivore density often fluctuate widely in response to annual climatic variation. Conversely, herbivore density and movement are controlled in intensively managed systems and precautions are taken to minimize deleterious consequences on animal production. Consequently, the intensity of grazing in these systems may frequently exceed the optimal intensity required to consistently stimulate primary production as indicated by the grazing optimization hypothesis (Briske and Heitschmidt 1991, Oesterheld et al. 1992, McNaughton 1993). These differences between plant-animal systems may also partially explain why the grazing optimization hypothesis originated with researchers working in extensively managed, rather than intensively managed systems and why the hypothesis receives limited support from most natural resource managers.

The potential benefits of compensatory growth should not obscure the effects of grazing on the ecological processes governing the sustainability of grazed systems (Briske 1993). Overgrazing and site degradation frequently result from the attempt of humans to maintain a desired number of animals or to produce a sufficient amount of animal products for subsistence agriculture or economic profitability, rather than from the inherent instability of grazed systems. While compensatory plant growth may potentially optimize primary production in some systems given the appropriate environmental conditions, it very likely has a negligible effect on the threshold limits defining system stability. In this context, the sustainability of grazed systems is a more fundamental ecological issue than is grazing optimization.

SUMMARY

The following dichotomous model and summary statements are intended to emphasize the most important conclusions concerning the morphological, physiological and demographic responses of plants to grazing. Responses of plants to grazing span temporal scales beginning with the disruption of steady-state growth within minutes, to the expression of compensatory physiological processes within days, followed by the progressive development of regrowth over a period of weeks, and conclude with demographic processes spanning months and years. Morphological, physiological and demographic responses to defoliation encompass the ecological scales of tillers, plants and populations within grassland communities.

Dichotomous model for analyzing regrowth responses

The ability of individual plants to regrow following defoliation is a multi-facetted process involving the meristematic potential and compensatory physiological processes of individual plants, intra- and interspecific competition among plants, and abiotic variables within the environment. The inherent morphological and physiological attributes of individual plants establish the potential for regrowth while the intensity of plant competition, resource availability and environmental conditions constrain the extent to which this regrowth potential is realized. The following dichotomous model is presented as a concise summary of the plant attributes and environmental variables that must be considered when predicting and/or analyzing regrowth responses of individual plants following defoliation.

I. Active meristems intact (dependent upon plant architecture, phenology, and defoliation intensity and pattern). [If not, go to II.]

A. Environmental conditions appropriate for growth (consider both abiotic, e.g., light intensity, temperature, water and nutrient availability, and biotic variables, e.g., competitive interactions and pathogens). [If not, go to I. B.]

1. High plant capacity for compensatory photosynthesis and/or reallocation of photosynthetic carbon to new shoot tissues (dependent upon sink strength and number of active apical and intercalary meristems).

These conditions lead to rapid canopy reestablishment; rapid recovery of photosynthetic capacity and recharge of carbohydrate and nutrient pools;

root growth and function begins to recover within 2-4 days after defoliation; dependence on stored carbohydrates and nutrients is limited to several days.

2. Low plant capacity for compensatory photosynthesis and/or reallocation of photosynthetic carbon.

Canopy reestablishment occurs more slowly than I.A.1. because less current photosynthetic carbon is reinvested in shoot regrowth.   Predefoliation root/shoot ratios are reestablished more slowly.

B. Environmental conditions are suboptimal for growth (consider both abiotic, e.g., light intensity, temperature, water and nutrient availability, and biotic variables, e.g., competitive interactions and pathogens).

The potential for canopy reestablishment is great, but it is not realized.   In some cases (e.g., defoliation during winter) environmental conditions may both prevent regrowth and induce quiescence so that stored carbohydrates and nutrients remain in the plant until optimal environmental conditions for growth occur.

II. Active meristems removed (regrowth dependent on activation of shoot sinks, i.e., axillary bud growth).

A. Quiescent axillary meristems absent or necrotic.   [If present, go to II. B.]

Canopy reestablishment does not occur; plants respire available substrate and die.

B. Quiescent axillary meristems present.

1. Rapid activation of axillary meristems.   [If slow, go to II. B.2.]

Canopy reestablishment is relatively rapid, but less than in I.A.1. because of time lag required for bud activation. Regrowth is dependent on available carbohydrate pools at the time growth is initiated and on the reinvestment of photosynthetic carbon into shoot growth. Presence of residual leaf area or resource reallocation from within the plant are critical for rapid regrowth.

2. Slow activation of axillary meristems.

Potential loss of stored carbohydrates and nutrients within the plant and potential loss of water, nutrient and light resources to competitors.

(1)   "Dormant" season:

Low metabolic activity of plants and inactivity of competitors preserves stored carbohydrates and nutrients within plants and access to environmental resources, respectively, until quiescence or dormancy is alleviated. Regrowth rate may be rapid depending on the number and sink strength of activated shoot meristems and on the availability of carbohydrates to promote the initial growth of leaves.

(2) Growing season:

High metabolic activity of plants reduces resources to a level that may severely limit regrowth rates when shoot meristems are activated. Competitors may preempt environmental resources and minimize the potential for canopy reestablishment and plant survival.

Summary statements

1. Steady-state plant growth is immediately disrupted by defoliation in response to a substrate limitation imposed by a reduction in photosynthetic area. A reduction in whole-plant photosynthesis and preferential carbon allocation to active shoot sinks reduces root growth and nutrient absorption as root carbohydrates are depleted. The extent to which these physiological processes are suppressed and their potential rates of recovery directly affect the grazing resistance, competitive ability and productivity of defoliated plants.

2. The reduction of carbohydrate pools within root systems following defoliation primarily results from the combined effects of a reduction in the amount of photosynthetic carbon allocated to the root system and the continued utilization of carbohydrates in root respiration, rather than the remobilization of carbohydrates to support shoot regrowth. Although, carbohydrate pools within the remaining shoot system are important for initiating plant growth when photosynthetic capacity is severely limited, the relative inaccessibility of root carbohydrates to support shoot growth, the limited amount of carbohydrates stored in tiller bases, and poor correlations between shoot regrowth 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.

3. Compensatory photosynthesis is a very consistent physiological response following defoliation that has been documented in numerous species. The process involves the rejuvenation of leaves and/or the postponement of the normal decline in photosynthetic capacity that occurs as leaves age and senesce. Although the occurrence of compensatory photosynthesis is partially influenced by increased light availability following partial canopy removal, indirect mechanisms presumably mediated by cytokinins or other root produced signals, appears to be the predominant mechanism inducing the response. Compensatory photosynthesis occurs in defoliation-sensitive as well as defoliation-tolerant species and it often does not persist throughout the recovery period. Therefore, the rate of leaf area expansion following defoliation plays a greater role than does the increase in photosynthetic rate per unit leaf area in the reestablishment of whole-plant photosynthetic capacity.

4. Canopy reestablishment is a function of the source, number, and activity of remaining meristems; the availability of photosynthetic carbon, and the amount of stored carbohydrates and nutrients. Growth following defoliation is most rapid from intercalary meristems, intermediate from apical meristems and slowest from axillary buds. Canopy reestablishment is delayed when a large portion of the active meristems are removed by defoliation, or when suboptimal environmental conditions or intense competition limit growth, photosynthesis, or nutrient acquisition. A series of compensatory processes, including increased resource allocation to shoots, increased photosynthetic rates, and enhanced rates of nutrient absorption by roots, may occur within several days of defoliation to increase relative growth rates over those of undefoliated plants.

5. The widely held assumption that apical meristem removal stimulates tiller initiation in grasses is not consistently supported by either traditional or contemporary experimental data demonstrating that the process is more complex than the direct inhibition of axillary buds by auxin produced in the apical meristem. Although tiller recruitment may increase for a short period following defoliation, tiller recruitment

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or longevity is often reduced over the course of one or more growing seasons in comparison with undefoliated plants. Defoliation-induced reductions in tiller recruitment and longevity suppress tiller numbers per plant and per unit area when evaluated over one or more growing seasons in even the most grazing resistant rangeland grasses.

6. Radiation quality has been hypothesized to function as an environmental signal capable of regulating tiller recruitment in grasses. Reductions in the red:far-red ratio, resulting from greater attenuation of red than far-red wavelengths as radiation passes through a plant canopy, may function as a signal to reduce tiller recruitment before tiller densities exceed the carrying capacity of the environment. However, supplemental red or far-red radiation applied to the base of plants does not consistently modify the rate or magnitude of tiller recruitment under field conditions. Reductions in the red:far-red ratio are probably of greater ecological significance as a signal of impending competition for light than they are as a density-dependent signal capable of directly regulating tiller recruitment. These findings demonstrate that additional research is required before definitive ecological or managerial conclusions can be established concerning the significance of radiation quality as an environmental signal capable of regulating tiller recruitment.

7. Grazing-induced modifications of tiller demography are eventually manifested in plant demography and population structure. Individual plant basal areas decrease and plant densities increase following the fragmentation of individual bunchgrass plants subjected to grazing. Total basal area and tiller number per unit area may be substantially reduced by continued severe grazing. Grazing-induced modifications in population structure reduce the potential for population maintenance and decrease competitive ability thereby increasing resource availability for more grazing resistant species populations within the community. Grazing appears to decrease plant longevity by placing the most severely grazed plants at a competitive disadvantage with associated species which are grazed less severely.

8. Grazing or mowing is known to select against morphotypes possessing an erect canopy architecture and increase the proportion of decumbent growth forms, commonly referred to as grazing morphs, within species populations. Decumbent growth forms are characterized by a large number of small tillers with reduced leaf numbers and blade areas which are better able to avoid grazing because less biomass is removed by herbivores and a greater number of meristems remain to facilitate growth following defoliation. A majority of the evidence indicates that grazing-induced selection among growth forms is genetically based. Selection has been documented to occur within $\leq$ 25 years in response to grazing by cattle and in 2-12 years in response to intensive grazing by prairie dogs.

9. Grazing resistance consists of avoidance and tolerance mechanisms which reduce the probability and/or severity of grazing and increase the rate of growth following grazing, respectively. Although plants possess components of both mechanisms, avoidance mechanisms appear to dominate the relative expression of grazing resistance among grasses. Grazing resistance is maximized in an evolutionary context when a plant attains the greatest increase in fitness for the amount of resources allocated to resistance mechanisms. However, the relative costs and benefits associated with avoidance and tolerance mechanisms require additional investigation if the concept of grazing resistance is to be of greater value in anticipating and predicting plant responses to defoliation.

10. Plants rarely respond to defoliation as isolated individuals in the field. Competition from undefoliated plants has been demonstrated to constrain growth of defoliated plants to as great an extent as the direct effects of defoliation. Defoliation reduces the competitive ability of plants by decreasing resource acquisition from the environment. The significant influence of competitive interactions on canopy reestablishment indicate that grazing tolerance (i.e., regrowth ability following defoliation) and competitive ability are distinct processes regulating the regrowth capacity of plants.

11. Compensatory growth following defoliation has been documented in both individual plants and plant communities. Intrinsic mechanisms, which are associated with herbivore-induced physiological processes of individual plants, and extrinsic mechanisms, which involve herbivore-mediated environmental modifications, both contribute to compensatory growth, but their relative contributions appear to vary with species or community, associated environmental variables, defoliation regime, and the ecological scale investigated. Compensatory growth appears to be promoted by limited competition, increased nutrient availability, and grazing only during the early portion of the growing season. Current information indicates that grazing only infrequently increases total growth of grazed plants above that of ungrazed plants in managed systems. However, greater growth rates of grazed plants very likely prevent growth from being suppressed in direct proportion to the severity of defoliation imposed even though complete compensation does not occur.

12. Plant communities are composed of several hierarchical scales possessing unique temporal and spatial characteristics. Lower scales (i.e., tillers and plants) contribute to the structure of higher scales (i.e., populations and communities) while higher scales can modify responses of the scales below in ways which are not predictable from the investigation of lower scales in isolation. Consequently, it is essential that several hierarchical scales be evaluated simultaneously to develop an accurate interpretation of plant and vegetation responses to grazing.

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Table 1.   Growth rate following defoliation is most rapid from intercalary meristems,intermediate from apical meristems and slowest from axillary buds. However, the relative contribution of these meristematic sources to total biomass production occurs in the reverse order.   (Adapted from Briske 1986).

	Meristematic Source		
Growth Response	Intercalary	Apical	Axillary
Growth Rate	Rapid	Intermediate	Slow
Total production	Low	Intermediate	High

Table 2. Maximum longevity (years) of perennial grasses in ungrazed communities at the Santa Rita Experimental Range (Canfield 1957), Jornada Experimental Range (Wright and Van Dyne 1976), and the U.S. Sheep Experimental Station (West et al. 1979).

Santa Rita Experimental Range		Jornada Experimental Range		Sheep Experimental Station	
Species	Longevity	Species	Longevity	Species	Longevity

Aristida hamulosa
  Mesa threeawn
	13	Aristida divaricata
		  Poverty threeawn
			9	Koeleria cristata
				  Prairie junegrass
					27

Bouteloua curtipendula
  Sideoats grama
	7	Aristida longiseta
		  Red threeawn
			9	Oryzopsis hymenoides
				  Indian ricegrass
					19

Bouteloua eriopoda
  Black grama
	14	Bouteloua eriopoda
		  Black grama
			27	Poa spp.[1]
				  Bluegrasses
					41

Bouteloua hirsuta
  Hairy grama
	6	Hilaria mutica
		  Tobosa grass
			7	Pseudoroegneria spicata
				  Bluebunch wheatgrass
					42

Heteropogon contortus
  Tanglehead
	6	Muhlenbergia arenacea
		  Ear muhly
			9	Stipa comata
				  Needle-and-thread
					43

Hilaria belangeri
  Curly mesquite
	4	Scleropogon brevifolius
		  Burro grass
			12		

Trichachne californica		_Sporobolus flexuosus_	
Arizona cottontop	8	Mesa dropseed	19

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[1] Includes _Poa secunda_, _Poa nevadensis_, and _Poa cusickii_.

Table 3. Mechanisms of grazing avoidance in grasses at the leaf, tiller, plant and community levels of grassland organization. The herbivore(s) and selected reference(s) are indicated for each mechanism.

	Mechanism	Herbivore	Reference
Leaf			
	Presence of vascular bundles	Grasshoppers	Caswell et al. 1973, Boutton et al. 1978, Heidorn and Joern 1984
		Cattle	Wilson et al. 1983, Akin et al. 1983
	Silicification	Slugs	Wadham and Parry 1981
		Stem-boring larvae	Moore 1984
		Serengeti ungulates	McNaughton et al. 1985, but see Shewmaker et al. 1989
		Prairie vole	Gali-Muhtasib et al. 1992
	Secondary compounds	Sheep	Marten et al. 1973, 1976
		Geese	Buchsbaum et al. 1984, but see Gauthier and Bédard 1990
		Cattle	Georgiadis and McNaughton 1988
Tiller			
	Height and angle	Clipping	Westoby 1980
		Prairie dogs	Detling and Painter 1983, Painter et al. 1989
		Cattle	Heitschmidt et al. 1990
	Height of apical meristem	Clipping	Branson 1953, Booysen et al. 1963, Westoby 1980
	Culm elongation/flowering	Cattle	Gammon and Roberts 1978
Plant			
	Accumulation of culms	Cattle, Deer	Willms et al. 1980
		Cattle	Norton and Johnson 1983, Truscott and Currie 1989, Ganskopp et al. 1992
	Large or small basal area	Cattle	Norton and Johnson 1983, Truscott and Currie 1989, Ganskoff and Rose 1992
Community			
	Interspecific association	Serengeti ungulates	McNaughton 1978
		Cattle	Davis and Bonham 1979
		Rabbits	Jaksi and Fuentes 1980

Table 4. Mechanisms of grazing tolerance in grasses at the leaf, tiller, and plant levels of grassland organization. The physiological process(es) and selected reference(s) are indicated for each mechanism.

Mechanism	Physiological Processes	Reference
Leaf		
Compensatory photosynthesis	Increased nitrogen content	Hodgkinson 1974, Nowak and Caldwell 1984
	Increased carboxylase activity or amount	Yamashita and Fujino 1986, von Caemmerer and Farquhar 1984
	Increased electron transport capacity	Jenkins and Woolhouse 1981
	Increased stomatal conductance	Gifford and Marshall 1973, Wallace et al. 1984
Rapid elongation rate	Intercalary meristem activity	Volenec and Nelson 1983, Coughenour et al. 1985a, 1985b
	Enhanced water status	Wolf and Parrish 1982, Toft et al. 1987
Increased blade:sheath ratio	Increased photosynthetic rate	Detling et al. 1979b, Painter and Detling 1981
Tiller		
Rapid leaf recruitment	Apical meristem activity	Youngner et al. 1976, Kotanen and Jeffries 1987
Rapid tiller recruitment	Axillary bud activation	Stur and Humphreys 1988, Richards et al. 1988
Increased C allocation to shoots	Source-sink activity	Ryle and Powell 1975, Richards 1984
Increased N allocation to shoots	Source-sink activity	Ourry et al. 1988, Millard et al. 1990
Plant		
Compensatory shoot growth	Potentially all processes above and a modified canopy age-structure	Dyer and Bokhari 1976, Georgiadis et al. 1989, Gold and Caldwell 1990, Oesterheld 1992
Compensatory root activity	Nutrient reallocation to roots	Jaramillo and Detling 1988
	Increased sink activity of shoots	Polley and Detling 1988, Chapin and McNaughton 1989
Inter-tiller resource allocation	Source-sink activity	Watson and Ward 1970, Welker et al. 1987, 1991, Jónsdóttir and Callaghan 1989
Inherent competitive ability	Maintenance of resource acquisition	Mueggler 1972, Caldwell et al. 1985, 1987, Wallace and Macko 1993

Table 5. Species populations in which defoliation has been documented to induce morphotypic selection. The herbivore(s), time interval grazing was imposed and reference(s) are indicated for each species.

Plant species	Herbivore	Time interval	Reference
Andropogon gerardii Big bluestem	prairie dogs/bison	2-100 yrs	Painter et al. 1993
Agropyron smithii Western wheatgrass	prairie dogs/bison	12 yrs	Detling and Painter 1983, Painter et al. 1989, 1993
Agrostis tenuis Colonial bentgrass	rabbits/sheep	unknown	Bradshaw 1959
Arrhenatherum elatius Tall oatgrass	sheep/cattle	unknown	Mahmoud et al. 1975

Bouteloua gracilis
  Blue grama
	prairie dogs/bison	12 yrs
		  2-100 yrs
			Jaramillo and Detling 1988,
			  Painter et al. 1989

Dactylis glomerata Orchardgrass	sheep/rabbits sheep	unknown unknown	Gregor and Sansome 1926 Etherington 1984
Danthonia linkii D. richardsonii D. racemosa Oatgrasses	sheep	30 - >100 yrs	Scott and Whalley 1984
Lolium perenne Perennial ryegrass	sheep/rabbits	unknown	Gregor and Sansome 1926

Poa annua
  Annual bluegrass
	clipping
	  clipping/sheep
		unknown
		  unknown
			Warwick and Briggs 1978
			  McNeilly 1981

Poa pratensis Kentucky bluegrass	livestock	37 yrs	Kemp 1937

Schizachyrium scoparium
  Little bluestem
	cattle/bison
	cattle
	prairie dogs/bison
		56 - >100 yrs
		20 yrs
		2 - 100 yrs
			Carman and Briske 1985
			Briske and Anderson 1992
			  Painter et al. 1993

Stipa comata Needle-and-thread	livestock	13 yrs	Peterson 1962

Table 6. Two categories of mechanisms potentially contributing to compensatory plant growth following defoliation. Intrinsic mechanisms are associated with herbivore-induced physiological processes while extrinsic mechanisms result from herbivore-mediated environmental modifications (Modified from McNaughton 1983).

Mechanism	Reference
Intrinsic category	
Accelerated photosynthetic rate per leaf area	Detling et al. 1979b, Nowak and Caldwell 1984, Wallace 1990
Accelerated nutrient absorption per unit root mass	Ruess et al. 1983, Polley and Detling 1988, Chapin and McNaughton 1989
Greater resource allocation to shoots	Hartt et al. 1964, Ryle and Powell 1975, Richards 1984
Increased tiller initiation	Jameson and Huss 1959, Oesterheld and McNaughton 1988, Richards et al. 1988, but see text
Improved water status	Wolf and Parrish 1982, Toft et al. 1987, Briske and Anderson 1990
Extrinsic category	
Increased irradiance on remaining leaf tissue	Woledge 1977, Caldwell et al. 1983, Wallace 1990, Senock et al. 1991
Conservation of soil water following leaf area removal	Caldwell et al. 1983, Wraith et al. 1987 Svejcar and Christiansen 1987, but see Naeth et al. 1991, Miller and Rose 1992
Accelerated rate of nutrient cycling	Floate 1981, Hik and Jefferies 1990, Holland et al. 1992
Increased activity of decomposer organisms	Ruess and McNaughton 1987, Holland and Detling 1990

Figure 1. Root growth and function in orchardgrass plants defoliated to a height of 2.5 cm. Root respiration (solid line), root length extension (dashed line), and relative uptake of ^{32}P during 4-hour exposures (histograms) prior to and for 8 days following defoliation imposed on day 0. Plants were grown in solution culture to allow continuous physiological measurements (From Davidson and Milthorpe 1966b).

Figure 2. Daily net photosynthetic carbon uptake and carbon utilization for plants of (a) crested wheatgrass and (b) bluebunch wheatgrass on the day of defoliation (day zero) and 1, 2, 3, 4, and 16 days following defoliation. The daily availability of photosynthetic carbon exceeded the amount of carbon utilized for growth and respiration within 3 days of defoliation in both species (From Richards and Caldwell 1985).

Figure 3. Relationship between root and crown TNC (total nonstructural carbohydrate) pools and regrowth of crested and bluebunch wheatgrass 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 4. Relative allocation of ^{14}C to various components of defoliated and undefoliated barley plants. Plants were labelled for 25 minutes and harvested at 1, 2, 4, and 7 days. Defoliated plants were cut at the ligule of the 3rd leaf at the beginning of day 1. Allocation to meristematic leaf tissue (apical meristem, leaf primordia, and unexpanded leaves) increased and allocation to roots decreased at day 4 and 7 of regrowth (From Ryle and Powell 1975).

Figure 5. Total amount of N allocated to regrowing leaves of perennial ryegrass following defoliation to a height of 4 cm. The contribution of remobilized N from within the plant was greater than that of N absorption from the growth medium for 6 days

following defoliation, after which N absorption supplied the majority of N for regrowth (From Ourry et al. 1988).

Figure 6. Net photosynthetic rate per unit leaf area for alfalfa leaves with increasing age on undefoliated plants and for undefoliated leaves on plants subjected to partial defoliation. Compensatory photosynthetic responses of leaves of three different ages are shown in comparison with leaves of the same chronological age on undefoliated plants. Maximum photosynthetic rates of leaves on undefoliated plants were achieved 10-20 days after leaf appearance and several days after maximum leaf expansion (From Hodgkinson 1974).

Figure 7. Longitudinal view of the crown of a grass tiller illustrating three meristematic sources contributing to growth and development in grasses. The magnitude of biomass production and rate of growth following defoliation differ for intercalary, apical and axillary meristems, but all three contribute to canopy reestablishment (Modified from Jewiss 1972).

Figure 8. (a) Number of tillers per plant and (b) daily rates of tiller appearance per plant for Dallisgrass (Paspalum dilatatum) as affected by red light enrichment in the lower portion of the canopy. Asterisks indicate significant differences between red light enriched and control plants (From Deregibus et al. 1985).

Figure 9. (a) Mean red:far-red ratios beneath canopies of little bluestem plants and (b) cumulative mean number of tillers recruited per plant in each of four treatments. Arrows indicate the dates of partial canopy removal to a height of 15 cm on plants assigned to defoliation treatments. The two values shown for the red:far-red ratios on 9 April and 20 May for plants in the defoliated and defoliated plus far-red treatments indicate the values measured immediately before and after partial canopy removal (From Murphy and Briske 1994).

Figure 10. Tiller recruitment in little bluestem populations that had been moderately or severely grazed by cattle in a rotational grazing system for 4 years. Control populations

had been protected from livestock grazing for 25 years. Values are a mean of 10 permanently marked tillers per each of 20 plants in each of the grazed populations and 10 plants in the ungrazed population. Asterisks indicate a significant difference between the grazed and ungrazed populations (From Butler and Briske 1988).

Figure 11.   Rate of juvenile tiller recruitment (juvenile tillers/parent tiller/time interval) in response to the intensity and timing of a single grazing event. Crested wheatgrass plants were moderately or severely grazed by cattle at each of four stages of culm elongation during a 3 year period. Tiller counts were made at 5 - 8 day intervals following grazing in each experiment (From Olson and Richards 1988c).

Figure 12. Densities of two size classes of little bluestem plants that were moderately or severely grazed by cattle in a rotational grazing system for 4 years.   Control populations had been protected from livestock grazing for 25 years.   Values are a mean of 20 plants in each of the grazed populations and 10 plants in the ungrazed population (From Butler and Briske 1988).

Figure 13. Tiller densities and total basal areas of little bluestem populations that had been moderately or severely grazed by cattle in a rotational grazing system for 4 years. Control populations had been protected from grazing for 25 years. Values are a mean of 20 plants in each of the grazed populations and 10 plants in the ungrazed population. Only plants with basal areas of 25 cm^2 or greater were monitored to calculate these variables. Asterisks indicate significant differences between grazed and ungrazed populations (From Butler and Briske 1988).

Figure 14. Maximum longevity of ungrazed and grazed black grama (<u>Bouteloua eriopoda</u>) and curly mesquite (<u>Hilaria belangeri</u>) plants on the Santa Rita Experimental Range near Tuson, Arizona. Grazing reduced the longevity of the late-successional dominant (black grama), but increased the longevity of the mid-successional species (curly mesquite) (Modified from Canfield 1957).

Figure 15.   Response of bluebunch wheatgrass to three defoliation intensities in the presence of full, partial or no competition from association vegetation. Competition

from associated species exerted a greater influence on growth following defoliation than did defoliation intensity (Modified from Mueggler 1972).

Figure 16. Mean importance values (relative cover x relative frequency) of four graminoids along mixed prairie toposequences (swale, mid-slope or ridge) subjected to different grazing intensities (N=none, L=light, M=moderate and H=heavy). The relative grazing resistance of western wheatgrass and buffalograss varied with topographic position and grazing intensity while the grazing resistance of sun sedge and blue grama remained relatively constant (From Archer and Tieszen 1986).

Figure 17. Schematic presentation of the costs and benefits of grazing resistance when treated as a quantitative trait. Plants experience maximum fitness at a point where the greatest grazing resistance is attained with minimum resource allocation to resistance. Plants do not become completely resistant to herbivores because at some point the cost of resistance exceeds the benefits to plant fitness (From Simms and Rausher 1987).

Figure 18. Three potential responses of primary production to increasing grazing intensity as proposed by the grazing optimization hypothesis. Primary production may: a) decrease with increasing grazing intensity, b) remain unaffected until intermediate levels of grazing intensity are attained and then decrease, or c) increase with increasing grazing intensity to an optimal level and then decrease at greater grazing intensities. The concepts of over- and undercompensation are also illustrated (From Belsky 1986).

Figure 19. Cumulative net aboveground primary production of grazed and ungrazed swards of (a) Puccinellia phryganodes and (b) Carex subspathacea in response to early season grazing by geese near Hudson Bay, Canada. Productivity of both the grazed and ungrazed swards were similar early in the season, but grazed swards maintained a high growth rate throughout the season in comparison with ungrazed swards (From Cargill and Jefferies 1984b).