

## ADAPTIVE TOLERANCE MECHANISMS IN GRASS PLANTS

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Graminoid plant species respond differently to defoliation by grazing, mowing, and fire at various times during their growth cycles and stages of phenological development. These various responses are a result of compensation to defoliation during the long period of coevolution with herbivores and fire. Grass plants and grazing mammals appeared in the fossil record at the same time in the lower Miocene Epoch about 20 million years ago. Grass plants, grazing mammals, and grassland plant communities have evolved together. The adaptive tolerance mechanisms that grass plants developed to compensate for defoliation can be understood and manipulated with defoliation management at specific times or phenological growth stages to produce beneficial effects to grassland ecosystems. Sampson (1914 and 1954) recognized the importance of basing grazing management on the growth requirements and life history of the vegetation. Recently, several greenhouse and laboratory studies (Anderson *et al.* 1981, Clarholm 1985, Coleman *et al.* 1983, Ingham *et al.* 1985) have opened the way to a better understanding of the adaptive tolerance mechanisms that grassland plants have developed. These adaptive tolerance mechanisms can be separated into two general categories that function interrelatively. The first tolerance mechanism is numerous changes in the physiological responses within the grassland plant caused by defoliation. The second tolerance mechanism is numerous changes in the activity levels of the symbiotic soil organisms in the rhizosphere caused by defoliation.

The physiological responses within the plant caused by defoliation have been reviewed and grouped into nine categories by McNaughton (1983). Physiological responses to defoliation do not occur at all times, and the intensity of the response is variable. Responses can be related to different phenological stages of growth of the grass plants. The key to ecological management by effective defoliation is to match the timing of the defoliation to the phenological stage of growth that triggers the desired outcome. All of the relationships between the physiological

responses and the application of the management treatment have not been fully developed with scientific research. One of the main physiological effects of defoliation is the temporary reduction in the production of the blockage hormone, auxin, within the meristem, and young developing leaves (Briske and Richards 1994). This reduction of plant auxin in the lead tiller allows either for cytokinin synthesis in the roots or crown, or its utilization in axillary buds, which stimulate the development of vegetative tillers (Murphy and Briske 1992, Briske and Richards 1994). Partial defoliation of young leaf material reduces the hormonal affects of apical dominance by the lead tiller, and allows some secondary tillers to develop from the previous year's axillary buds. Secondary tillers can develop without defoliation manipulation after the lead tiller has reached anthesis phenophase, but usually only one secondary tiller develops from the potential of five to eight buds because this secondary tiller suppresses additional axillary bud development hormonally by apical dominance. When the lead tiller is partially defoliated at an early phenological growth stage, several axillary buds can develop subsequently into secondary tillers. Apparently, no single secondary tiller is capable of developing complete hormonal apical dominance following defoliation of the lead tiller at this time. Some level of hormonal control from the older axillary buds still suppresses development of some of the younger axillary buds' development. With our present level of knowledge of this mechanism, we are unable to achieve the full potential for all axillary buds to develop into secondary tillers.

The second type of influence by defoliation on grassland plants are the changes in activity levels within the components of the rhizosphere. The rhizosphere is that narrow zone of soil around living roots of perennial grassland plants where the exudation of sugars, amino acids, glycosides, and other compounds affect microorganism activity (Curl and Truelove 1986, Whipps 1990, Campbell and Greaves 1990). Bacterial growth in the rhizosphere is stimulated by the presence of carbon from the exudates (Elliott 1978, Anderson *et al.* 1981, Curl and Truelove 1986, Whipps 1990). Protozoa and nematodes graze increasingly on the increased bacteria (Curl and Truelove 1986), and accelerate the overall nutrient cycling process through the "fast" pathway of substrate decomposition as postulated by Coleman *et al.* (1983). The activity of the microbes in the rhizosphere increases the amount of nitrogen available for plant growth (Ingham *et al.* 1985 a.b., Clarholm 1985, Allen and Allen 1990). The presence of vasicular-arbuscular mycorrhizal (VAM) fungi enhances the absorption of ammonia, phosphorus, other mineral nutrients, and water (Moorman and Reeves 1979, Harley and Smith 1983, Allen and Allen 1990, Box and Hammond 1990, Marschner 1992). Rhizosphere activity can be manipulated by defoliation at early phenological growth stages when a higher percentage of the total nitrogen of the plant is in the aboveground parts and a higher percentage of the total carbon of the plant is in the belowground parts. At that time, partial defoliation disrupts the plant's carbon to nitrogen

ratio, leaving a relatively high level of carbon in the remaining plant. Some of this carbon is exudated through the roots into the rhizosphere in order to readjust the carbon-nitrogen ratio. Bacteria in the rhizosphere are limited by access to simple carbon chains under conditions with no defoliation (Curl and Truelove 1986). The rhizosphere bacteria increase in activity in response to the increase in exudated carbon under conditions with defoliation (Lynch 1982, Ingham *et al.* 1985). The increases in activity by the bacteria triggers increases in activity in the other trophic levels of the rhizosphere organisms (Curl and Truelove 1986). This ultimately increases available nutrients for the defoliated grass plant (Ingham *et al.* 1985, Clarholm 1985). During middle and late phenological stages of growth, carbon and nitrogen are distributed more evenly throughout the plant. Defoliation at that time does not remove a disproportionate amount of nitrogen, and very little or no carbon is exudated into the rhizosphere. Soil water levels generally decrease during middle and late portions of the grazing season and also limit rhizosphere organism activity levels (Curl and Truelove 1986, Bazin *et al.* 1990).

Interpretation of data from these studies strongly suggests compensatory growth mechanisms on plants subjected to defoliation by grazing. One school of thought suggests that these plants may be dependent on grazing to optimize production (McNaughton 1983, Pieper 1994). Data from McNaughton (1979, 1985) indicate that grazing exclusion leads to a drastic decline in net primary productivity (NPP) and to a rapid ecotypical selection toward less productive, and less grazing resistant plants. McNaughton (1983) theorizes that grazing exclusion may lead to a net diminution of total energy and nutrient flow through the system. Plants capable of compensating for herbage removal may support a dense and complex trophic web which in turn may be essential to their existence. This in turn implies a critical role for the belowground trophic level (belowground NPP, soil microflora and soil fauna) in ecosystem function. Understanding the adaptive tolerance mechanisms at work in the physiology within a grassland plant and in the activity levels of the symbiotic soil organisms in the rhizosphere following defoliation and the beneficial manipulation of these mechanisms under field conditions are the key to the further development of ecologically sound recommendations for management of our grassland natural resources.

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