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# Plant Responses to Different Grazing Intensities in the Missouri Coteau of North Dakota

## Introduction

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Grasses and herbivores have a long co-evolutionary history, which has resulted in a number of mechanisms that contribute to the response of grasses to grazing (Mack and Thompson, 1982; Coughenour, 1985). Many studies have focused on the problem of plant-animal interactions (Milchunas and Laurenroth, 1993). The grazing optimization theory, which hypothesizes that herbivores may increase plant productivity, raised widespread controversy in some situations (Belsky, 1986; McNaughton, 1986; Crawley, 1987; Hobbs and Swift, 1988). The grazing optimization hypothesis (Dyer, 1975; McNaughton, 1979, 1983) and the generalized model of changes in species composition and diversity with grazing (Milchunas et al., 1988) are generally qualitative studies. They explain potential responses based on a large number of data sets coupled with ecological theories. However, McNaughton (1979, 1985) indicated 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.

In some North American grasslands, plants can experience pressure from ungulate grazing, which severely reduces above- and below-ground biomass. Many range plants can suffer moderate to extreme stress from leaf loss due to herbivory. Heavy grazing can function as a selection pressure on grass plant morphology, causing some species to change and grow low to the ground. Since grazed and ungrazed populations of grasses react differently to selective pressures (i.e., herbivory and competition), it is reasonable to hypothesize that the population characteristics of plants from grazed and ungrazed sites will be accompanied by distinct morphological patterns and physiological functions.

Herbivore-induced changes in the population structure of plants, such as aboveground biomass, density, and frequency of occurrence, can be expected to affect the physiological functions such as photosynthetic rate,  $V_{cmax}$  and  $J_{max}$ . These specific physiological responses are often difficult to predict and may change over time. Harvesting leaves directly reduces photosynthesis, potentially impeding growth and reproduction. Adequate leaf area is the main consideration for photosynthesis and storage of non-structural carbohydrates. Reduced leaf area implies the loss of photosynthetically active leaf area and may reduce growth, reproduction, and survival of the plants because of loss of carbohydrates. Plants from sites where long-term grazing has taken place may have a limited ability to acquire sufficient light for photosynthesis and accumulation of carbohydrates. Most plants possess compensatory mechanisms by which they can mitigate the effects of photosynthetically active leaf loss. One of these mechanisms is an increased photosynthetic rate per unit area of remaining leaves. Also, plants on grazed areas may have more light available to them than those on un-grazed sites because of less shading from other plants. This enables them to more effectively use all leaf area in photosynthesis (Jameson, 1963; McNaughton, 1979).

Species of different life-forms (i.e. grasses, forbs, shrubs, etc.) typically differ in their tolerance to foliage loss as a result of grazing. Some plant species are more adapted to significant grazing pressure. Responses that plants make to grazing include higher photosynthetic rates, reduced foliage longevity, lower proportion of reproductive shoots, lower height, greater density, and faster rates of leaf replacement (Caldwell et al., 1981; Archer and Tieszen, 1983). The optimal defoliation intensity varies with species, stage of phenological development, and associated environmental conditions (Langer, 1963). For example, grazing some native bunchgrass populations decreases the individual plant basal area (the area occupied by the plant at ground level) and increases total plant density (plants/per unit area).

Specific leaf area (SLA) is important in the regulation and control of plant functions, such as carbon assimilation and allocation, and is related to growth rates (Lambers and Poorter 1992). SLA may be important in determining the responses of the five selected species in different grazing environments. Several studies (Garnier, 1992; Lambers and Poorter, 1992; Reich et al., 1992; Westoby, 1998; Hodgson et al., 1999) highlight the importance of SLA as a simple measurement that integrates investment of energy and resources into growth as opposed to defense mechanisms and storage of energy and resources. Westoby (1999) has proposed that SLA and plant height play a major role in responding to disturbance, particularly grazing. High SLA was predicted for heavily grazed

areas (Westoby, 1999) and indicated higher growth rate as a mechanism (Briske, 1996, 1999).

Among the leaf nutritional characteristics that respond significantly to the environmental stress and influence of grazing, nitrogen content is one of the most important because it is typically the most limiting resource for plant growth. This is partly because nitrogen is a key constituent of photosynthetic enzymes. In the past, the complexity of reactions involving nitrogen has been difficult to study in the field. Despite the complexities, we can now gain valuable insights on the functioning of several important components of the photosynthetic mechanisms using non-destructive measurements under field conditions. The main pathway of photosynthesis involves fixing of  $\text{CO}_2$  by the enzyme named Rubisco using 5-C sugar phosphates (called RuBP) as substrates. This reaction is called the RuBP carboxylation and its maximum capacity is called  $V_{\text{cmax}}$ . To make photosynthetic carbon-fixation progress continuously, the molecules of RuBP have to be regenerated, which is largely dependent on light-requiring electron transport and energy conversion. The maximum capacity of RuBP regeneration is called  $J_{\text{max}}$ . Using a gas exchange measurement system, the values of both  $V_{\text{cmax}}$  and  $J_{\text{max}}$  can be estimated by the construction of  $A/C_i$  (photosynthesis-internal  $\text{CO}_2$  response) curves relating photosynthesis to internal  $\text{CO}_2$  partial pressure (Sharkey, 1985). With the purpose of detecting the influence of grazing on the physiological level, we sampled these two values,  $V_{\text{cmax}}$  and  $J_{\text{max}}$ . They helped us to learn more information on the plant's mechanism.

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