BIOLOGICAL EFFECTS OF DEFOLIATION ON GRASS PLANTS

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Defoliation is the removal of plant leaf material by grazing, mowing, burning, hail, frost, or chemical action. Grass plants have developed adaptive tolerance mechanisms in response to defoliation during the long period of coevolution with herbivores and from the evolutionary selective forces of fire and drought. Plants that have developed these adaptive processes, or resistance mechanisms, have the ability to persist in a grazing plant community.

The effect of grazing is not simply the removal of herbage from grass plants (Langer 1972): grazing also changes physiological processes in all parts of the plants; alters the plant community microclimate (the climatic conditions around parts of a plant or within a small area of a plant community) by changing light transmission, moisture relations and temperature; and changes the soil environment, thereby affecting soil organism activity. Defoliation by livestock can be used to sustain healthy native prairie ecosystems when grazing is applied at phenological growth stages (identifiable growth stages related to the climate and/or time of the year) during which resistance mechanisms that beneficially manipulate grass growth and development can be stimulated.

Grazing resistance mechanisms are described in two categories. External mechanisms involve herbivore-induced environmental modifications (Briske and Richards 1995). Internal mechanisms are associated with herbivore-induced physiological processes (McNaughton 1979, McNaughton 1983) and are divided into two subcategories: tolerance mechanisms and avoidance mechanisms (Briske 1991). Grazing tolerance mechanisms facilitate growth following defoliation and include increased activity within the plant meristem (the growth-point tissue where new cells are produced by cell division) and compensatory (or counteractive) physiological processes (Briske 1991). Grazing avoidance mechanisms reduce the probability and severity of grazing and include the modification of anatomy and growth form. Grazing resistance in grass is maximized when the cost of resistance approximates the benefits. Plants

do not become completely resistant to herbivores because the cost of resistance at some point exceeds the benefits conveyed by the resistance mechanisms (Pimentel 1988).

Defoliation removes leaf area, immediately disrupting plant growth and photosynthesis (the process which occurs in the presence of light and by which plants take carbon dioxide from the air, build carbohydrates, and emit oxygen into the air). Defoliation by large herbivores triggers internal tolerance mechanisms that become engaged immediately following foliage removal and occur over a period of several days. The resulting increases in leaf photosynthetic capacity and carbon and nitrogen allocation (redistribution of carbon and nitrogen from remaining plant structures) enable defoliated plants to compensate for foliage losses.

Carbon and nitrogen are necessary to many physiological processes within the plant. When a plant is defoliated, carbon and nitrogen levels decrease because the processes through which the plant normally acquires these elements are affected (Coyne et al. 1995). Carbon and nitrogen are allocated from alternative sources to maintain the physiological processes of the plant. Because the compensatory growth process requires greater amounts of carbon and nitrogen, the defoliated plant requires greater amounts of these elements to restore leaf area lost to defoliation. The carbon that may be utilized by plants for shoot growth comes not from the roots but from the remaining leaf tissue, stems, and rhizomes and from alternative substrates, including hemicellulose, proteins, and organic acids (Richards and Caldwell 1985, Briske and Richards 1995). Current photosynthetic carbon from the remaining shoot is preferentially allocated to areas of active shoot meristematic tissue (Ryle and Powell 1975, Richards and Caldwell 1985, Briske and Richards 1995). Carbon allocation from undefoliated tillers to defoliated tillers increases following defoliation until the defoliated tillers reestablish their own photosynthetic capacity (Welker et al. 1985, Briske and Richards 1995). Most of the nitrogen remobilized to support shoot growth following defoliation is allocated from remaining shoot tissue; a smaller portion is allocated from the root system (Briske and Richards 1995).

Defoliated plants increase photosynthetic rates of remaining foliage (Briske and Richards 1995). This compensatory photosynthesis can be induced by modifications of physiological functions and by changes in light intensity and quality that result from grazing modifications to the microhabitat (Briske and Richards 1995). Through these changes, the photosynthetic apparatus is rejuvenated, the rate of leaf senescence (the process of leaf aging, which begins at the tip and moves to the base and during which, as cell material is moved from the leaf to other plant

structures, the leaf acquires a dry appearance) is inhibited or reduced, and the life span of the leaf is increased (Briske and Richards 1995). Remaining mature leaves on defoliated plants frequently develop increased leaf mass per unit area within 1-14 days after defoliation (Briske and Richards 1995). Leaves exhibiting compensatory photosynthesis after defoliation may have higher rates of dark respiration (a nocturnal process by which plants draw oxygen from the air and emit carbon dioxide), a characteristic which is exhibited by leaves with higher protein contents (Atkinson 1986) and which therefore suggests that foliage at the same growth stage is higher in protein content and nutritional quality on defoliated plants than on undefoliated plants.

The growth rate of replacement leaves and shoots increases following defoliation. Expanding leaves tend to grow longer on defoliated plants than on undefoliated plants (Langer 1972), and the photosynthetic rate of the regrowth leaves is higher than that of same-age foliage on undefoliated plants (Briske and Richards 1995). Enhanced leaf and tiller growth rates usually persist for only a few weeks following defoliation and are not consistently expressed in all environmental conditions or phenological stages within the growing season.

Defoliation applied at the appropriate phenological growth stages can stimulate tillering by reducing the influence of apical dominance, the physiological process by which the apical meristem (the meristem located at the top of a stem) of a lead tiller exerts hormonal control over the growth of axillary buds (the meristematic portions of phytomers, the structural shoot units, each of which comprises a leaf, an internode, an axillary bud, and a node) and inhibits axillary buds from developing into tillers (Briske and Richards 1994, Briske and Richards 1995). Partial defoliation of the lead tiller at an early phenological growth stage reduces the hormonal effects of apical dominance asserted by that 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 flowering phenophase, but usually only 1 secondary tiller develops from the potential of 5 to 8 buds because this secondary tiller hormonally suppresses additional axillary bud development 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 early partial defoliation of the lead tiller. Defoliation that removes the apical meristem has been shown to increase tillering in several warm-season grasses and some cool-season grasses (Richards et al. 1988, Murphy and Briske 1992) and not to stimulate tillering in some other cool-season grasses (Branson 1956, Richards et al. 1988).

Stimulation of tillering by defoliation is not consistent throughout the growing season and varies with stage of phenological development, environmental conditions, and frequency and intensity of defoliation. Influence of the physiological stage of plant development at the time of defoliation is not completely understood; however, some studies have reported effects of defoliation at several phenological stages. Defoliation during early spring, before plants have reached the third-leaf stage, exerts a negligible stimulatory effect on tillering (Olson and Richards 1988, Vogel and Bjugstad 1968) and negatively affects potential peak herbage biomass production (Campbell 1952, Rogler et al. 1962, Manske 1994). In some grasses defoliation during later vegetative growth (stages of asexual reproduction in which tillers grow from axillary buds) promotes tiller recruitment to a greater extent than does defoliation during any other phenological stage (Briske and Richards 1995). Defoliation during stem elongation but prior to the emergence of the inflorescence (the flower-and-seed-bearing portion of a stem) stimulates tillering in several grass species (Olson and Richards 1988). Defoliation at the boot stage suppresses tillering in some warm-season grasses that are stimulated to tiller by defoliation applied at the inflorescence emergence stage (Vogel and Bjugstad 1968). Defoliation alters the timing or seasonality of tiller recruitment. Vegetative reproduction through increase in tiller development from axillary buds can be beneficially stimulated by partial defoliation of lead tillers between the third-leaf stage and flowering. Severe fall and winter defoliation has the potential to reduce grass density and production greatly the following year because late-stimulated tillers remain viable over winter, and cool-season species initiate tillers the previous fall. Defoliation of these tillers reduces their contribution to the ecosystem the following summer.

Tiller development decreases with increasing frequency and intensity of defoliation. Low levels of grazing also reduce tiller densities by decreasing tiller development and increasing tiller mortality through shading (Grant et al. 1983). The optimal defoliation intensity varies with species, stage of phenological development, and associated environmental conditions (Langer 1963). Grazing some native bunchgrass populations decreases individual plant basal area (the area occupied by the plant at ground level) and increases total plant density (Butler and Briske 1988). However, severe grazing may reduce total basal area and tiller numbers (Olson and Richards 1988).

An internal avoidance mechanism reduces plant tissue accessibility by changing the morphology (shape, form, or structure) of a plant. Grass plants exhibit two strategies of stem elongation: short shoots and long shoots. In short shoots, the apical meristem remains below cutting or grazing height during vegetative growth, continuing to produce new leaves until the stem enters the reproductive phase (the stage of sexual reproduction) and the flower stalk

elongates (Dahl 1995). In long shoots, the apical meristem is elevated while the tiller is still in the vegetative phase (Dahl 1995). Both heavy grazing and frequent mowing can function as selection pressure on grass plant morphology, causing forms to change and grow low and close to the ground. This genetically based change in growth form can occur in less than 25 years (Briske and Anderson 1992). The grazing-induced growth forms are characterized by a large number of small tillers with reduced leaf numbers and blade area (Briske and Richards 1995). This growth form is better able to avoid grazing because less biomass is removed and a greater number of meristems remain to facilitate growth. Many grass species with long shoots are stimulated to increase tiller production by moderate defoliation prior to flowering (Richards et al. 1988). Long shoot plants are nearly always decreased in pastures that are heavily grazed continuously (Branson 1953).

External mechanisms contribute to compensatory grass growth following defoliation. Long-term ungrazed grass plants shift to erect growth forms with a small number of larger tillers because the shading from other plants reduces the light intensity reaching the lower leaves of an individual plant (Briske and Richards 1995). Grass leaves grown under shaded conditions become longer but narrower, thinner, (Langer 1972, Weier et al. 1974) and lower in weight (Langer 1972) than leaves in sunlight. Root growth is reduced because roots are very sensitive to reduction in light intensity suffered by the leaves. Grazing removes some of the aboveground herbage and increases the amount of solar radiation reaching remaining tissue. Defoliation improves plant water status as the result of an increase in root-shoot ratio and reduction of the transpiration surface. Increasing the root-shoot ratio also increases nutrient supply to remaining tissue.

An important external resistance mechanism stimulated by defoliation of grassland plants is manipulation of the activity of symbiotic (mutually beneficial) soil organisms within the rhizosphere, the narrow zone of soil surrounding the living roots of perennial grassland plants (Manske 1996). The exudation of organic substances from the grass plants' roots affects microorganism activity (Curl and Truelove 1986, Whipps 1990, Campbell and Greaves 1990). Under conditions with no defoliation, rhizosphere microorganisms are limited by access to simple carbon chains (Curl and Truelove 1986). At early phenological growth stages, defoliation stimulates the roots of the grass plant to exude carbon into the rhizosphere. The elevated level of carbon leads to increased activity of the soil microorganisms (Elliott 1978, Anderson et al. 1981, Curl and Truelove 1986, Whipps 1990) and to the acceleration of the overall nutrient cycling process (Coleman et al. 1983), thereby increasing the amount of nitrogen available for the growth of the plant (Ingham et al. 1985a, Ingham et al. 1985b, Clarholm 1985, Allen and Allen 1990). Defoliation

during the middle and late portions of the grazing season produces less beneficial results in the rhizosphere. During this period, when grass plants have entered the middle and late phenological stages, defoliation stimulates the release of very little or no carbon into the rhizosphere. Moreover, the general decreases in soil water level typical of this time also limit rhizosphere organism activity (Curl and Truelove 1986, Bazin et al. 1990).

Defoliation management designed to enhance sexual reproduction through seed production does not improve the prairie ecosystem. Seedlings contribute very little to plant production, and the energy and resources used in seed production could be manipulated into vegetative tiller production, which could improve the prairie ecosystem. Management by defoliation with herbivores has the greatest beneficial effect if planned to stimulate two mechanisms: vegetative tillering from axillary buds and activity of symbiotic soil organisms. The phenological growth stages during which these two mechanisms can be manipulated are the same, between the third-leaf stage and flowering phenophase. Little evidence has been found to suggest that defoliation at other stages has beneficial stimulatory effects on grass growth.

Along with properly timed defoliation, periods with no defoliation should be provided to allow defoliated plants to complete the entire resistance mechanism process before successive defoliation events are permitted. Because the carbon and most of the nitrogen for recovery from defoliation are allocated not from the roots but from remaining shoot tissue, each defoliation event should be regulated to ensure that plants retain sufficient leaf surface to provide adequate assimilates for regrowth. Grass plants subjected to continuous severe defoliation do not completely recover and can not produce at their potential levels.

Sustainable prairie management requires that grass plant needs and biological processes be given the highest priority in the planned strategy. Management strategies that give primary consideration to other goals may have short-term benefits but can not be sustained over the long term if they fail to incorporate consideration of grass plant growth.

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