Management of Northern Great Plains Prairie
Based on Biological Requirements of the Plants

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Properly managed prairie can provide a multitude of uses. Rangelands and grasslands provide forage for livestock, habitat for wildlife and plants, clean air, clean water, open spaces for recreation and sightseeing, and food, fiber, and energy for people. The unique attribute of healthy prairie ecosystems is that they can provide all these benefits simultaneously. However, if management practices are designed to enhance only a single use, a healthy, productive prairie ecosystem will not be maintained over time. Prairie ecosystem health and productivity can be sustained only when grass plant requirements and biological processes are given the highest priority in management strategies.

The key factor in meeting grass plant biological requirements is the proper timing of defoliation. The effect of defoliation is not simply the removal of herbage from grass plants (Langer 1972): defoliation also changes physiological processes in all parts of the plants; alters the plant community microclimate by changing light transmission, moisture relations, and temperature; and changes the soil environment, thereby affecting soil organism activity. Grass plants have developed defoliation resistance mechanisms in response to grazing during the long period of coevolution with herbivores and from the evolutionary selective forces of fire and drought. Grass plants developed these biological processes 20 million years ago in areas outside the Northern Great Plains and in conjunction with early herbivores that are now extinct. The biological processes within prairie plants are old, but the prairie plant communities in the Northern Great Plains and the interactions that affect plant growth and development are relatively young. Grass plants migrated from numerous types of environments into the region by different mechanisms and at different times and rates (Manske 1994b). Plants initiated development of the current dynamic plant communities only about 5,000 years ago when the climate of the Northern Great Plains changed to conditions like those of the present, with cycles of wet and dry periods (Bluemle 1977, Bluemle 1991, Manske 1994b). Plants that have developed adaptive biological processes, or resistance mechanisms, and have maintained a niche in a prairie community have the ability to thrive in a grazed plant community. Therefore, defoliation by livestock can be used to sustain healthy native prairie ecosystems when grazing is applied at phenological growth stages during which resistance mechanisms that beneficially manipulate grass growth and development can be stimulated.

Grass Leaf Development

The grass shoot is made up of repeated structural units called phytomers (Beard 1973, Dahl 1995), each comprising four parts: 1) a leaf, consisting of a blade and sheath, with a collar separating the two structures; 2) a node, the location of leaf attachment to the stem; 3) an internode, the length of stem between two successive nodes; and 4) an axillary bud, the concentration of meristematic tissue capable of developing into a tiller (Hyder 1974, Dahl and Hyder 1977). Meristematic tissue is a collection of undifferentiated cells concentrated in growth point areas called meristem. Each shoot generally has five or six phytomers but may have seven or more. Collectively the nodes and internodes of the phytomers are called the stem. The vegetative stem consists of a few to several nodes and unelongated internodes, with the apical meristem located at the highest node, at the top of the stem (Langer 1972). The crown of a grass plant is the lower portion of a shoot and has two or more nodes (Dahl 1995).

Young grass leaves develop from leaf bud primordia produced in the apical meristem. Almost all cells of the leaf are formed while the leaf is a minute bud (Langer 1972). Growth of the leaf results from expansion in cell size (Esau 1960, Dahl 1995) and increase in weight (Coyne et al. 1995). The new growing leaf draws carbohydrates from roots, stems, or older leaves until its maintenance and growth requirements can be met by assimilates produced by the new leaves (Langer 1972, Coyne et al. 1995). When the tiller is between the 3.0 and 3.5 leaf stage, the apical meristem ceases to produce leaf bud primordia and begins to produce flower bud primordia (Frank 1996, Frank et al. 1997). The previously formed leaf bud primordia continue to grow and develop (Esau 1960, Langer 1972), with the oldest cells at the tip (Langer 1972, Dahl 1995) and the oldest leaf outermost (Rechenthin 1956, Beard 1973). Defoliation of leaf material before the tiller has reached the third-leaf stage has the potential to disrupt the formation of leaf bud primordia for the tiller. However, defoliation of the tiller after the third-leaf stage functions beneficially, stimulating resistance mechanisms. In the Northern Great Plains, most native cool-season grasses reach the third-leaf stage around early June, and most native warm-season grasses reach the third-leaf stage around mid June. Many domesticated cool-season grasses reach the third-leaf stage around late April and early to mid May.

Defoliation Resistance Mechanisms

Defoliation 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). Defoliation tolerance mechanisms facilitate growth following grazing and include both increased activity within the plant meristem and compensatory physiological processes (Briske 1991). Defoliation 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 derived from the resistance mechanisms (Pimentel 1988).

Internal Tolerance Mechanisms

Defoliation removes leaf area, immediately disrupting plant growth and photosynthesis. 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 allocation of carbon and nitrogen, leaf photosynthetic capacity, and stimulated tiller development 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 then allocated from alternative sources to maintain the physiological functions of the plant. The compensatory growth process requires greater amounts of carbon and nitrogen. The carbon that may be utilized for compensatory 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). Following defoliation, carbon allocation from undefoliated tillers to defoliated tillers increases 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 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 one to fourteen days after defoliation (Briske and Richards 1995). Leaves exhibiting compensatory photosynthesis after defoliation may have higher rates of dark respiration, a characteristic which is exhibited by leaves with higher protein content (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.

Partial defoliation of young grass leaf material at the appropriate phenological growth stages can stimulate tillering by reducing the influence of apical dominance, the physiological process by which the apical meristem of a lead tiller exerts hormonal control over the growth of axillary buds 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 one secondary tiller develops from the potential of five to eight buds because this secondary tiller asserts apical dominance and hormonally suppresses additional axillary bud development. 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, previously the only process known to influence apical dominance, 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 condition, 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 1994c). In some grasses, defoliation during later vegetative growth 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 stimulates tillering in several grass species (Olson and Richards 1988). Some warm-season grasses 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. Severe fall or winter defoliation has the potential to reduce grass density and production greatly the following year because late-stimulated tillers remain viable over the 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). Grazing decreases individual plant basal area and increases total plant density of some native bunch grass populations (Butler and Briske 1988). However, severe grazing may reduce total basal area and tiller numbers (Olson and Richards 1988). The optimal defoliation intensity varies with species, stage of phenological development, and associated environmental conditions (Langer 1963). Partial defoliation of lead tillers between the third-leaf stage and flowering can beneficially stimulate vegetative reproduction through an increase in tiller development from axillary buds.

Internal Avoidance Mechanisms

Internal avoidance mechanisms reduce plant tissue accessibility to herbivores by changing the morphology of a plant, producing secondary compounds for chemical defense, and depositing mineral silica in epidermal cells. Grass plants exhibit two strategies of stem elongation: short shoots and long shoots. In plants with 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 and the flower stalk elongates (Dahl 1995). In plants with 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 exert selective pressure on grass plant morphology, causing forms to change and plants to 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 meristem 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). Plants with long shoots are nearly always decreased in pastures that are heavily grazed continuously (Branson 1953).

External Resistance Mechanisms

External mechanisms contribute to compensatory grass growth following defoliation. In ungrazed areas, shading from upper leaves reduces the intensity of light reaching the lower leaves and causes a change in growth form. Grass leaves become long and thin, and lower in weight. Shading also causes reduced root growth (Langer 1972). Grazing removes some aboveground herbage and increases the amount of solar radiation that reaches remaining tissue. Defoliation improves plant water status as the result of a higher root-shoot ratio and reduced transpiration surface. The higher root-shoot ratio also results in increased nutrient supply to remaining tissue.

An important external resistance mechanism stimulated by defoliation of grassland plants is manipulation of the activity of symbiotic soil organisms within the rhizosphere, the narrow zone of soil surrounding the living roots of perennial grassland plants (Manske 1996a). The exudation of organic substances from grass plant 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 carbon level 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 plant growth (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).

Stimulation of Resistance Mechanisms

The 3.0 to 3.5 leaf phenological growth stage is the best indicator of grass plant grazing readiness. Grazing grass plants prior to the third-leaf stage negatively affects grass growth. Starting grazing after the third-leaf stage allows plants to establish sufficient leaf area to produce adequate photosynthetic assimilate to meet leaf growth requirements and allows leaf bud primordia in the apical meristem to develop completely.

Partial defoliation between the third-leaf stage and flowering phenophase stimulates defoliation resistance mechanisms. The two mechanisms of primary concern to grassland managers are vegetative reproduction by secondary tiller development from axillary buds and increased symbiotic soil organism activity in the rhizosphere. 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.

Grazing before Third-Leaf Stage

Cool-season grasses initiate lead tiller growth during the fall and resume active growth the next spring. Spring growth of cool-season grass leaves depends both on carbohydrate reserves and on photosynthetic products from the portions of fall-initiated tiller leaves that have overwintered and regreened. Spring growth of warm-season grass leaves depends initially on carbohydrate reserves and later both on carbohydrate reserves and on photosynthetic product from young leaves. Grass plant growth and development depend on adequate carbohydrate reserves in early spring because the amount of photosynthetic product synthesized by early growing leaves is insufficient to meet the requirements for leaf growth (Heady 1975, Coyne et al. 1995). Grass growth also requires that the plant have adequate leaf area to provide photosynthetic product for early growing leaves. The total nonstructural carbohydrates of a grass plant are at low levels following the reduction of reserves during the winter respiration period, and the carbohydrate reserves remaining in the roots and stems are needed for both root growth and initial leaf growth during early spring. The low quantity of reserve carbohydrates may not be adequate to supply the entire amount required to support root growth and also support leaf growth until sufficient leaf area is produced to provide the photosynthetic assimilates required for plant growth and other processes (Coyne et al. 1995). Removal of aboveground material deprives plants of foliage needed for photosynthesis and increases the demand upon already low levels of carbohydrate reserves when sequential leaves grow. The quantity of herbage produced by a grass plant after it has been grazed is dependent on the levels of carbohydrates present in the remaining herbage at the time of defoliation (Coyne et al. 1995). Defoliation of the tiller before the third-leaf stage, when the plant is low in carbohydrates, results in reduced growth rates of herbage production (Coyne et al. 1995) and negatively affects peak herbage biomass production later in the year (Manske 1994c).

Grazing after Third-Leaf Stage

Defoliation of leaf material after the third-leaf stage affects herbage biomass production in relation to the amount of leaf material removed. The amount of leaf area remaining after defoliation and capable of conducting photosynthesis is an important factor affecting the quantity of herbage produced by grazed grass plants. Replacement of leaf tissue from current assimilates has a lower cost to the plant than growth from stored carbohydrates and results in higher growth rates and increased production of herbage biomass (Coyne et al. 1995). Plants with sufficient leaf area remaining after defoliation utilize some stored carbohydrates for development of new leaf tissue (Briske and Richards 1995, Coyne et al. 1995), but the source of carbohydrates for most new growth is current photosynthates, which are preferentially allocated to areas of active shoot growth (Richards and Caldwell 1985, Briske and Richards 1995). Severely defoliated plants depend upon stored carbohydrates for new plant growth (Briske and Richards 1995), and dependance on stored carbohydrate for replacement of the photosynthetic system occurs at an additional cost to the plant. This implied reduction in efficiency results in low growth rates and reduced production of herbage biomass (Coyne et al. 1995). Additional restrictions inhibit herbage production when the stored carbohydrates are at low levels (Coyne et al. 1995).

Defoliation after the third-leaf stage stimulates vegetative reproduction from axillary buds by reducing apical dominance (Manske 1998). Partial defoliation of grass plants between the third-leaf and flowering stages stimulates growth of secondary tillers and stimulates rhizosphere organism activity (Manske 1998). The presence of higher levels of carbohydrate reserves before defoliation increases the number of stimulated tillers that grow (Coyne et al. 1995), and the resulting development of secondary tillers increases herbage biomass. Rate of growth of secondary tillers is variable depending on the growing season period during which axillary bud growth is stimulated. Early stimulated secondary tillers require less time to reach the third-leaf stage than do late-stimulated tillers. Grazing periods should be synchronized with the growth rate of the stimulated secondary tillers so that defoliation is applied only after they reach the third-leaf stage.

Grazing during Late Season

In the fall, cool-season grass species initiate lead tillers that overwinter. The following spring, the tiller leaf cells with intact cell walls regreen, resume active growth, and provide photosynthetic product for new leaf growth (Briske and Richards 1995, Manske 1998). Late-stimulated secondary tillers that start development during late June or early July usually do not produce flower heads and also frequently overwinter, resuming active growth the subsequent growing season (Briske and Richards 1995, Manske 1998). Therefore, secondary tillers should be allowed to reach the third-leaf stage before they are grazed. Late-stimulated secondary tillers and fall-initiated lead tillers should be managed in the fall so that they retain adequate leaf material to produce sufficient carbohydrate reserves. Selective severe fall and winter defoliation of late-stimulated secondary tillers and cool-season fall-initiated lead tillers reduces their contribution to the ecosystem and results in greatly reduced grass density and herbage production the following year (Manske 1998) because with late-season defoliation, plants are unable to replenish sufficient reserve carbohydrates to support active growth (Coyne et al. 1995).

Deferred Grazing after Seed Development

The concept of deferring the start of grazing on a pasture until after seed production was developed shortly after 1900. The intended goal was to increase grass density by promoting seedling development from increased seed stalk development and using trampling of the livestock to scatter and plant the resulting seeds. However, Sarvis (1941) was not able to determine any benefit from reseeding of the grasses after 23 years of grazing treatment on a three-pasture, once-over, deferred rotation system. Through three years of research Manske et al. (1988a) found that after only one year the total basal cover and the basal cover of warm-season grasses showed significant negative effects from the three-pasture, once-over, deferred treatments compared to ungrazed treatments. The basal cover of cool-season grasses and upland sedges showed trends of reductions after one year of deferred treatments. Kentucky bluegrass showed a trend of increased basal cover on the deferred treatments.

Plant populations persist through both asexual reproduction and sexual reproduction (Briske and Richards 1995). Sexual reproduction is necessary for a population to maintain genetic diversity to withstand large-scale changes (Briske and Richards 1995). However, production of viable seed each year is not necessary for perpetuation of a healthy grassland. Reproductive shoots are adapted for seed production rather than for tolerance to defoliation (Hyder 1972). Grass species that produce a high proportion of reproductive shoots are less resistant to grazing than are those species in which a high proportion of shoots remain vegetative (Branson 1953). The frequency of true seedlings is low in functioning grasslands, and establishment of seedlings occurs only during years with favorable moisture and temperature conditions (Wilson and Briske 1979, Briske and Richards 1995), in areas of reduced competition from older tillers, and when resources are readily available to the growing seedling. Vegetative growth is the dominant form of reproduction in semiarid and mesic grasslands (Belsky 1992, Chapman and Peat 1992, Chapman 1996), including the tallgrass, midgrass, and shortgrass prairies of North America (Briske and Richards 1995).

Since seedlings contribute very little to plant production, defoliation management designed to enhance sexual reproduction through seed production, like the deferred grazing system or full season rest system, does not improve the prairie ecosystem. The energy and resources used in seed production could be manipulated into vegetative tiller production through more effective grazing management.

Short-Term Severe Defoliation

Short-term severe defoliation results from practices that remove a high proportion of leaf material during a relatively short period (one to a few days). Such practices include fire, flash grazing, or mowing close to the ground. If the plants are healthy and have relatively high levels of stored carbohydrates, prairie ecosystems can tolerate periodic short-term severe defoliation events. The interval between short-term severe defoliation events and the seasonal periods during which they are effective require additional research. Current guidelines for determining the seasonal periods and the interval between severe defoliation events are based on interpretation of historical information. The interval between short-term severe defoliation events was extrapolated from the fire return interval, which is 3 to 4 years for tallgrass prairie, 5 to 10 years for moist mixed grass prairie, and up to 25 years for dry mixed grass prairie (Wright and Bailey 1982, Bragg 1995). The seasonal period when short-term severe defoliation occurred was interpreted from historical grassland fire information about Indian- and lightning-set fires (Higgins 1986). The Indian-set fires occurred primarily during two periods, March through May with a peak in April, and July through early November with a peak in October; the probable practice was burning the mixed grass prairie in late summer and fall and the tallgrass prairie in spring. Lightning-set fires occurred during summer and early fall, with 73% occurring in July and August.

Healthy vigorous plants will be able to recover from short-term severe defoliation in a relatively short period, one to a few years. Severely defoliated plants have little or no leaf area capable of conducting photosynthesis and will depend on stored carbohydrates for new growth, an inefficient process that results in reduced herbage production. Some plants that are not vigorous will undergo greater stress from severe defoliation and require several years to recover. The additional stress from severe defoliation will cause serious damage from which plants previously stressed by small leaf area, low carbohydrate reserves, and/or water stress may not recover.

Mowing close to the ground is short-term severe defoliation because a high proportion of the leaf area is removed. Mowing height, however, can be adjusted. The severity of mowing decreases when a greater amount of leaf area remains after defoliation. Mowing at a moderate height that leaves adequate leaf area capable of conducting photosynthesis and that is conducted during the period between the third-leaf stage and flowering phenological growth stage can be used to stimulate resistance mechanisms.

Short-term severe defoliation can have beneficial effects. Conducted at a seasonal period when undesirable species are experiencing greater levels of stress than desirable species, the practice can selectively modify plant species composition. Management practices that result in short-term severe defoliation can also be used in grassland ecosystems to alleviate the ecological problems of slowed nutrient cycling processes and inhibited herbage production that are caused by excessive litter accumulation. Even though short-term severe defoliation practices can increase nutrient cycling, it is doubtful that healthy prairie ecosystems can be sustained over time with only short-term severe defoliation management. Severe defoliation stresses plants by draining carbohydrate reserves; even healthy plants require a few to several years to recover from this practice. Consequently, grassland ecosystems without excess accumulated litter are not benefited ecologically from short-term severe defoliation practices.

Long-Term Severe Defoliation

Long-term severe defoliation is continued heavy defoliation that exceeds the recovery capacity of the plants. Prolonged severe defoliation that results in biological damage to plants is technically overgrazing. Overgrazing reduces the total leaf area and photosynthetic capacity

so that the affected grassland has reduced potential herbage yield, reduced plant root systems, distorted plant growth patterns with decumbent forms, delayed growth response, and reduced plant vigor causing death to some plants and resulting in a shift in plant species composition to a deteriorated range condition. When these conditions start to occur, a change in management practices is in order. These problems could result from excessively high stocking rates, but they also could result from defoliation during periods that plants are at or near stressful stages of development; from defoliation that is too severe and removes too much leaf area, forcing plants to use the limited stored carbohydrates for new growth; or from defoliation too frequent to allow plants adequate recovery time between defoliation events.

Application of the term "overgrazed" to pasture conditions that may be below an arbitrary critical standard but that have not been damaged biologically is incorrect. The assumption that overgrazing is caused only by overstocking is also incorrect. The term "overgrazed" correctly refers to the status of the plants managed over a period of time with defoliation practices that have caused biological damage to those plants. Stocking rate may not be the cause of the problems. Proper stocking levels for a parcel of land are variable with different grazing systems. Grazing systems based on plant requirements and coordinated with plant phenological growth stages can be properly stocked at levels that would be considered overstocked on a given parcel of land managed with another type of grazing system.

Long-Term Non-Defoliation

Long-term non-defoliation (idle) management is a management choice that withholds defoliation from a grassland for a considerable length of time. Non-defoliation treatments increase the level of shading in a grassland ecosystem and thereby reduce the intensity of the light that reaches the leaves. 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. Shaded leaves have a reduced rate of photosynthesis, which decreases the carbohydrate supply and causes a reduction in growth rate of leaves and roots (Langer 1972). Root growth is reduced because roots are very sensitive to reductions in light intensity reaching the leaves. Shading increases the rate of senescence in the lower older leaves.

Decomposition of leaf material through microbial activity can take place only after the leaves have made contact with the soil. Standing dead material not in contact with the soil does not decompose but breaks down slowly as a result of leaching and weathering. Accumulation of standing dead leaves reduces availability of carbon and nitrogen. Under ungrazed treatments dead leaves remain standing for several years. Increased mulch biomass resulting from long-term non-defoliation (Brand and Goetz 1986, Manske 1995d) negatively affects the soil. Excessive mulch reduces water infiltration and early season soil temperatures, causing reduced soil bacterial activity in the top 12 inches of soil. Excess mulch accumulation also causes conditions that decrease mycorrhizal fungi and rhizosphere organism activity, slow nutrient cycles, and reduce available nutrients. Standing dead leaves shade early leaf growth in spring, slowing the rate of growth, reducing the leaf area, and causing a reduction in the net primary productivity. Long-term effects of shading in ungrazed grasslands include reduced total plant densities and native grass species composition (Manske 1995d) and increased composition of shade-tolerant or shade-adapted replacement species like smooth bromegrass and Kentucky bluegrass.

Management Implications

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.

The twice-over rotation system was developed for use in the Northern Great Plains and was designed to manipulate processes that result in beneficial changes to the prairie ecosystem. The twice-over rotation system on native range with complementary domesticated grass spring and fall pastures coordinates defoliation with grass phenological growth stages to maximize vegetation and animal performance. In the twice-over rotation system, a spring pasture of crested wheatgrass or other early growing domesticated cool-season grass is grazed during the month of May. A three- or four-pasture native range rotation system is used from early June until mid October, with each pasture grazed for two periods. The first period is grazed for 15 or 11 days in each pasture of a three- or four-pasture system, respectively, during the 45-day period when grasses can be stimulated to tiller, from the third-leaf stage to flowering stage (1 June to 15 July). The second period is grazed for 30 or 22 days in each pasture of a three- or four-pasture system, respectively (after mid July and before mid October). A fall pasture of Altai wildrye or other type of wildrye is grazed with cows and calves from mid October until weaning in early or mid November and grazed by dry cows from mid November until mid or late December.

The twice-over rotation grazing management system with complementary domesticated grass pastures has a grazing season of over 7.5 months with the available forage above, at, or only slightly below the requirements for a lactating cow for nearly the entire grazing season. This system requires fewer than 12 acres per cow-calf pair for the entire 7.5-month grazing season on grassland that when grazed for 6.0 months seasonlong requires 24 acres per cow-calf pair. The cow-calf weight performance on the twice-over rotation grazing system with complementary domesticated grass pastures is improved over the performance on other systems (Manske 1994a, Manske 1996b).

The twice-over rotation grazing management system applies defoliation treatment to grass plants at the appropriate phenological growth stages to stimulate the defoliation resistance mechanisms and the activity of the symbiotic rhizosphere microorganisms. This stimulation increases both secondary tiller development of grasses and nutrient flow in the rhizosphere, resulting in increased plant basal cover and aboveground herbage biomass and improved nutritional quality of forage. The increase in quantity and quality of herbage permits an increase in stocking rate levels, improves individual animal performance, increases total accumulated weight gain, reduces acreage required to carry a cow-calf pair for the season, improves net return per cow-calf pair, and improves net return per acre (Manske et al. 1984, Manske and Conlon 1986, Manske et al. 1988b, Manske 1994a, Biondini and Manske 1996, Manske 1996b, Manske and Sedivec 1999). The increase in basal cover and herbage biomass reduces the number and size of bare soil areas and increases the quantity of residual vegetation. These changes in vegetation produce conditions favorable to the limitation of grasshopper pest species populations (Manske 1995a, 1995b; Manske and Onsager 1997; Onsager 1998). The increase in plant density, herbage production, residual vegetation, and ecosystem health improves the habitat for prairie grouse, ducks, waterfowl, and ground nesting birds (Manske and Barker 1981a, 1981b, 1988; Manske et al. 1988a; Sedivec et al. 1990, Manske 1995c). These beneficial effects of improved vegetation condition, livestock performance, wildlife habitat, and grasshopper control demonstrate the potential of the twice-over rotation grazing system for successful implementation in this region.

Acknowledgment

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