

Biological Management of Western Snowberry

Llewellyn L. Manske PhD
Range Scientist

North Dakota State University
Dickinson Research Extension Center

Report DREC 05-1060

Biological management is the use of an agent organism to cause an intentional reduction of an undesirable organism. A recent example of biological management is the reduction of leafy spurge, an introduced undesirable plant, by the flea beetle, a natural enemy that was brought into North America from the weed's original habitat. Biological management of problem native plants is not as straightforward or as dramatic as that of introduced plants. Effective biological management of western snowberry requires the identification and enhancement of an agent organism whose detrimental action leads to the reduction or containment of western snowberry colonies.

A number of biotic agents are injurious to western snowberry. Many insects attack the vegetative parts. Several butterfly and moth larvae chew the leaves, and aphids injure leaves and shoots. At least 42 genera and 50 species of fungi are known to occur on various parts of the plant (Pelton 1953). A wide variety of animals use western snowberry as food. Mice and other rodents girdle stems. Rabbits browse the stems. Wild ungulates and domesticated cattle, sheep, and goats browse the leaves and twigs (Pelton 1953). Despite the high number of organisms that use this shrub, no biotic agents are known to damage the plant severely enough or remove enough biomass that their action directly results in the restriction or death of rhizome-stem base clusters and in the subsequent reduction of western snowberry colonies.

Western snowberry appears to have adequate mechanisms to resist insect and fungus attacks, and the shrub appears to be quite resistant to browsing attacks because of its comparative unpalatability and active vegetative reproduction (Pelton 1953). In an analysis of browse survey data collected by North Dakota Game and Fish Department personnel over a 19 year period, Volesky (1982) found that western snowberry stems received low incidence of heavy hedging (>40%) except in one year that had considerable growing season water stress. McCarty (1967) reported that although young sucker stems were consumed following mowing treatments and vegetative sprouts were livestock feed in degenerate pastures heavily infested with western

snowberry, the shrub was not commonly utilized by livestock. Banister (1991) observed that cows will not eat much snowberry until pasture utilization reaches 65% to 70% during spring and 50% during fall; at these high utilization levels, pasture recovery requires two growing seasons of rest.

Grasses are superior competitors for belowground resources and can suppress western snowberry encroachment (Kochy 1999, Kochy and Wilson 2000, Peltzer and Kochy 2001). Because of these competitive abilities, grasses are the sought-after agent organisms that can be manipulated to successfully manage western snowberry colonies biologically. Coordinating grazing periods with appropriate grass growth stages can promote grass growth, improve the health status of grass plants, and increase grass herbage production by stimulating both beneficial activity of soil organisms and vegetative reproduction by tillering and by enhancing biological and ecological processes in grassland ecosystems (Manske 2000a). Strengthening the competitiveness of grass plants reduces the quantity of belowground resources available for western snowberry; the reduction of resources retards or reverses the shrub's encroachment into grasslands.

The degree of competitiveness from grasses is not constant under all types of management practices. The positive or negative response of grasses to defoliation depends on the amount of leaf material removed and the growth stage of the plant. Removing too much leaf area or grazing too early or too late in the seasonal development of the plant diminishes the plant's competitive abilities and permits greater quantities of belowground resources to become available for western snowberry colonies. These conditions facilitate the enlargement and spread of western snowberry colonies on pastures managed by traditional grazing practices, on land managed by overgrazing practices (Pelton 1953), and on idle land managed with no defoliation (Smith 1985).

Grass plants evolved 20 million years ago with early herbivores that are now extinct. During this time, grasses developed biological processes that help the plants withstand and recover from defoliation

(Manske 2000a). This complex of processes (McNaughton 1979, 1983, Briske 1991, Briske and Richards 1995), called defoliation resistance mechanisms, accelerates both the growth rate of the grazed plant and its development of foliage and roots. Two biological processes of primary concern to grassland managers are the increased beneficial activity of soil organisms (Coleman et al. 1983) and the stimulation of vegetative reproduction by secondary tiller development from axillary buds (Briske and Richards 1995). Grazing that removes a small amount of leaf area from the grass plant between the third-leaf stage and flowering stage can trigger these beneficial responses (Manske 1999).

There is a mutually beneficial relationship between the grass plant's root system and soil organisms. The narrow zone of soil around the roots of perennial grassland plants, the rhizosphere, contains bacteria, protozoa, nematodes, mites, springtails, and endomycorrhizal fungi (Elliot 1978, Anderson et al. 1981, Harley and Smith 1983, Curl and Truelove 1986, Whipps 1990, Campbell and Greaves 1990). The grass plant's roots release carbon compounds (Campbell and Greaves 1990), including sugars, to these rhizosphere organisms, and the organisms release mineral nitrogen that the plant's roots absorb (Ingham et al. 1985, Clarholm 1985, Biondini et al. 1988, Frederick and Klein 1994, Frank and Groffman 1998). The endomycorrhizal fungi also provide phosphorus, other mineral nutrients, and water that the plant needs for growth (Moorman and Reeves 1979, Harley and Smith 1983, Allen and Allen 1990, Koide 1993, Marschner and Dell 1994, Smith and Read 1997). Activity of the soil microorganisms increases with the availability of carbon compounds in the rhizosphere (Curl and Truelove 1986, Whipps 1990), and the elevated microorganism activity results in an increase in nitrogen available to the grass plant (Coleman et al. 1983, Klein et al. 1988, Burrows and Pflieger 2002, Rillig et al. 2002, Bird et al. 2002, Driver et al. 2005).

Grazing lead tillers between the third-leaf stage and the flowering stage can increase the quantity of carbon compounds the defoliated plant releases into the rhizosphere (Hamilton III and Frank 2001). The increase in nitrogen produced by elevated rates of microorganism activity allows the plant to accelerate growth and recover more quickly from defoliation. This beneficial activity does not seem to occur when grazing is conducted during the middle and late growth stages of the grass plant.

Grazing grass plants prior to the third-leaf stage negatively affects grass growth (Manske 2000b). Early seasonal growth of grass plants depends on carbohydrates stored in the roots, rhizomes, and stem bases (Trlica 1977), and prematurely grazed plants are unable to replenish adequate amounts of carbohydrates to support active growth (Coyne et al. 1995, Manske 1999). Starting grazing after the third-leaf stage and before the flowering stage allows plants to establish sufficient leaf area to produce adequate photosynthetic assimilates to meet leaf growth requirements and allows all leaf bud primordia in the apical meristem to develop into leaf buds (Manske 1999).

Management strategies that defer grazing until after the flowering stage were intended to enhance sexual reproduction and increase the quantity of seeds produced. However, deferred grazing does not improve grass plant density (Sarvis 1941, Manske et al. 1988). Most young grass plants in grassland ecosystems start not as seedlings but as vegetative tillers that grow from axillary buds on the crowns of an established plant. These vegetative tillers make up the majority of the plant population because they have a competitive advantage over seedlings. Tillers initially draw support from the root systems of parent tillers, while seedlings rely on their own less-developed structures.

Tiller development from axillary buds is regulated by lead tillers (Briske and Richards 1995) through a process called lead tiller dominance. The lead tillers produce an inhibitory hormone that prevents the growth hormone from activating growth within axillary buds (Briske and Richards 1995). Grazing that removes a small amount of young leaf tissue from the aboveground portion of lead tillers after the three-leaf stage and before the flowering stage reduces the amount of the inhibitory hormone in the plant (Briske and Richards 1994). With that inhibitory hormone reduced, the growth hormones stimulate vegetative reproduction (Murphy and Briske 1992, Briske and Richards 1994), and secondary tillers develop from the previous year's axillary buds (Langer 1972).

If no defoliation occurs before the flowering stage, as on a deferred grazing strategy, the lead tiller inhibits vegetative tiller development until the inhibitory hormone production naturally declines during the flowering stage. This hormone reduction permits one axillary bud to grow and develop into a secondary tiller, which in turn produces inhibitory hormones that prevent growth of the other six to eight axillary crown buds (Mueller and Richards 1986).

These dormant axillary buds are never activated and become senescent with the lead tiller. No evidence has been found to suggest that grazing the lead tiller after it has reached the flowering stage has beneficial stimulatory effects on vegetative tiller development (Manske 2000a).

All grass species in the Northern Plains have strong lead tiller dominance except Kentucky bluegrass and meadow bromegrass, which have low levels of inhibitory hormones and relatively higher levels of tiller development. Plants with these growth characteristics have greater demands for water than grasses with strong lead tillers and cease growth processes during minor water deficiency periods.

Grasses with strong lead tillers produce one set of lead tillers and one set of secondary tillers. Proper grazing management can increase the number of secondary tillers that develop, but the growing season length does not permit the development of a third set of tillers. The number of sets of tillers determines the number of times each pasture in a rotation system can be grazed. Two sets of tillers permit two rotation grazing periods. Rotation systems that graze each pasture more than two times are not coordinated with grass plant growth and do not meet grass plants' biological requirements (Manske 2000a).

The twice-over rotation system was designed to meet the biological requirements of the plants and to coordinate two grazing periods with grass growth stages. This coordinated defoliation stimulates biological and ecological processes within grass plants and the ecosystem so that beneficial changes to plant growth, soil organisms, and biogeochemical cycles in the ecosystem result (Manske 2000a).

A 3- to 6-pasture rotation system is used on native rangeland from early June until mid October, with each pasture grazed for two periods. Each native range pasture is grazed for 7 to 17 days during the first period, the 45-day interval from 1 June to 15 July. The length of the first period on each pasture is the same percentage of 45 days as the percentage of the total season's grazeable forage each pasture contributes (Manske 2000a).

During the first period, grasses are between the third-leaf and flowering stages, the stages of plant development at which grazing produces beneficial effects by stimulating the defoliation resistance mechanisms that increase tillering from axillary buds and enhance activity of rhizosphere organisms. Increased vegetative reproduction by tillering

contributes to the development of greater plant basal cover and to the production of greater grass herbage weight; increased activity of the soil organisms in the rhizosphere supplies the plant with greater quantities of nutrients to support additional growth (Manske 2000a).

During the second period, after mid July and before mid October, each pasture is grazed for double the number of days it was grazed during the first period. Removing livestock from native rangeland pastures in mid October, during the early fall, allows native grasses to store nutrients that will maintain plant processes over the winter and to retain the fall vegetative growth that will become next season's lead tillers (Manske 2003). This practice ensures healthy plants in the spring and greater herbage production during the next growing season (Manske 2000a).

Grazing effects on grass

Grazing effects are often simplistically perceived to be just the removal of leaf material from grass plants. However, defoliation by grazing produces complex effects on grass plants. Different grazing management treatments cause diverse changes in plant growth, plant density, herbage biomass produced, and soil organism activity on grassland ecosystems.

The effects from different grazing management treatments on vegetative tillering and soil rhizosphere organism activity were investigated on an area of mixed grass prairie near Dickinson, North Dakota, USA, in 2002 (Gorder, Manske, and Stroh 2004). Tiller density and rhizosphere volume of western wheatgrass plants were used to evaluate the different effects from four grazing management treatments on stimulation of the vegetative tillering process and of the soil organism activity in the rhizosphere, respectively. The four management treatments were 1) 4.5-month twice-over rotation system, 2) 4.5-month seasonlong, 3) 6.0-month seasonlong, and 4) long-term nongrazed control. Livestock on the 4.5-month twice-over rotation management treatment grazed each of three pastures for two periods from early June until mid October. Livestock on the 4.5-month seasonlong management treatment grazed one pasture from early June until mid October. Livestock on the 6.0-month seasonlong management treatment grazed one pasture from mid May until mid November. The long-term nongrazed management treatment had not been grazed, mowed, or burned for more than 30 years before the initiation of these research treatments (Gorder, Manske, and Stroh 2004). Two replicated plant and soil samples

were collected monthly from silty range sites on each of the four defoliation treatments. Plastic PVC pipe 3 inches (7.62 cm) in diameter and 4 inches (10.16 cm) long was forced into sample site soil, and the soil-plant cores were excavated intact. The matrix soil was separated from the rhizospheres of western wheatgrass plants. The tillers of each plant were categorized as lead, secondary, or fall types, and the densities per square meter were determined. The length and diameter of the rhizosphere around each root of every plant were measured with a vernier caliper, and volume was determined (Gorder, Manske, and Stroh 2004).

Total tiller density on the 4.5-month twice-over rotation treatment was greater than that on the 4.5-month seasonlong and 6.0-month seasonlong treatments during June, August, and September and greater than that on the long-term nongrazed treatment during June (table 1, figure 1). Total rhizosphere volume per cubic meter of soil on the 4.5-month twice-over rotation treatment was greater than that on the 4.5-month seasonlong and 6.0-month seasonlong treatments during July, August, and September and greater than that on the nongrazed treatment during August and September (table 2, figure 2) (Gorder, Manske, and Stroh 2004).

Stimulation of vegetative reproduction from the twice-over rotation grazing treatment during the previous year increased western wheatgrass tiller density. Most of the increased tillers carried over through the winter and the result was greater tiller density on that treatment than on the other treatments in June of the study year. The tiller stimulation that resulted from the twice-over rotation grazing treatment during the year of the study increased the western wheatgrass tiller density so that during the entire latter portion of the growing season the density was greater on that biologically effective treatment than on the other grazing treatments.

The activity of symbiotic soil organisms, as indicated by the volume of the rhizosphere, increased on the twice-over rotation system following defoliation during the stimulation grazing period, which occurred on the sample area from early July to mid July during the year of the study. The rhizosphere volume per plant increased on the twice-over rotation treatment following the stimulation grazing period, and the total rhizosphere volume in the soil increased following the stimulation period and remained greater during the entire latter portion of the growing season.

The twice-over rotation system matches defoliation periods with grass phenological stages of growth, stimulating grass defoliation resistance mechanisms that meet the biological requirements of plants and enhance the biogeochemical processes in grassland ecosystems. Stimulation of these biological and ecological mechanisms increases the vegetative tillering process and the rhizosphere organism activity. Traditional management practices that are designed for other priorities than to meet plant requirements or enhance ecosystem processes impede the function of defoliation resistance mechanisms. Inhibition of these mechanisms reduces the development of grass vegetative tillers and the activity of rhizosphere organisms (Gorder, Manske, and Stroh 2004).

Grazing effects on western snowberry

The effects of grazing treatments on western snowberry plants in the mixed grass prairie were studied in southcentral North Dakota, USA, at the North Dakota State University Central Grasslands Research and Extension Center (Sturn 1987, Kirby et al. 1988). Study sites were selected based on similar criteria prior to the implementation of the grazing treatments. Shrub stem density, shrub canopy cover, and current year shrub biomass production data were collected along the same permanently marked transects in 1982 and again in 1986. Precipitation rates were favorable for plant growth during the five-year study period, with average annual precipitation at 118.4% of the long-term mean of 17.9 inches (45.6 cm). The idle control treatment had been last grazed in 1979. The seasonlong and short duration grazing treatments were started in 1982, and the twice-over rotation grazing treatment was started in 1983 (Sturn 1987, Kirby et al. 1988).

The initial shrub stem densities were not similar on all treatments (table 3) and western snowberry response was not the same on the different grazing treatments. The densities of sucker and young stems decreased on the control and twice-over rotation treatments and increased on the short duration treatment; the densities of sucker stems significantly increased on the seasonlong treatment between 1982 and 1986. The short duration treatment had significantly greater sucker stem densities in 1986 than the control and twice-over rotation treatments. The densities of mature stems increased on the control and short duration treatments and decreased on the seasonlong treatment between 1982 and 1986. The short duration treatment had significantly greater mature stem densities in 1986 than the seasonlong treatment. The densities of total

stems increased on the seasonlong and short duration treatments and decreased on the control and twice-over rotation treatments between 1982 and 1986. The short duration treatment had significantly greater total stem densities in 1986 than the control treatment.

Shrub percent canopy cover (table 3) increased on the short duration treatment and decreased significantly on the control, seasonlong, and twice-over rotation treatments between 1982 and 1986. The short duration treatment had significantly greater percent canopy cover in 1986 than the seasonlong and twice-over rotation treatments.

Shrub current year twig and leaf production (table 3) increased significantly between 1982 and 1986 on the short duration treatment. The short duration treatment had significantly greater shrub production in 1986 than the seasonlong treatment. The seasonlong treatment had significantly greater shrub production in 1986 than the twice-over rotation treatment.

After five years of management on the idle control treatment, western snowberry communities had decreased sucker and young stem densities and increased mature stem densities that resulted in decreased total stem densities, significantly decreased percent canopy cover, and only slightly increased shrub twig and leaf production.

After five years of management on the seasonlong treatment, western snowberry communities had significantly increased sucker stem densities and decreased mature stem densities that resulted in increased total stem densities and increased shrub twig and leaf production, but because young stems have less canopy than old stems, there was a significant reduction in percent canopy cover.

After five years of management on the short duration treatment, western snowberry communities had increased sucker stem densities and increased mature stem densities that resulted in increased total stem densities, increased percent canopy cover, and significantly increased shrub twig and leaf biomass production.

After five years on the twice-over rotation management treatment, western snowberry communities had decreased young stem densities and no change in mature and decadent stem densities; the result was decreased total stem densities, significantly decreased percent canopy cover, and only slightly increased shrub twig and leaf production.

Management Implications

Livestock grazing has only a relatively small direct effect on aerial stems of western snowberry and the size and densities of the colonies. However, the effects from grazing management practices on the adjacent grassland community can regulate the rate at which the western snowberry colonies increase and spread.

Grazing management practices that do not meet grass biological requirements or enhance ecosystem processes impede vegetative tillering and activity levels of rhizosphere organisms; as a result, the competitive abilities of grass plants are weakened. The degree to which biological and ecological processes are inhibited by antagonistic grazing practices will be reflected inversely by the rate of western snowberry invasion.

Grazing management practices that meet the biological requirements of plants and enhance the biogeochemical processes in grassland ecosystems increase the amount of vegetative tillering and rhizosphere organism activity. The result is a healthy, dense, productive grass population that is highly competitive for belowground resources and creates the strongest possible biological barrier to western snowberry encroachment.

Acknowledgment

I am grateful to Amy M. Kraus for assistance in preparation of this manuscript. I am grateful to Sheri Schneider for assistance in production of this manuscript and for development of the tables and figures.

Table 1. Total tiller density of western wheatgrass per square meter.

Grazing Management	June	July	August	September	Growing Season
4.5-m Twice-over rotation	2412.09a	1206.04a	1973.53a	1425.32a	1754.25a
4.5-m Seasonlong	548.20b	657.84a	767.48b	657.84b	657.84b
6.0-m Seasonlong	767.48b	548.20a	822.30b	767.48b	726.37b
Nongrazed	548.20b	548.20a	877.12ab	1206.04a	794.89b

Data from Gorder, Manske, and Stroh 2004

Means in the same column and followed by the same letter are not significantly different ($P < 0.05$).

Table 2. Rhizosphere volume (cm^3) per cubic meter of soil.

Grazing Management	June	July	August	September	Growing Season
4.5-m Twice-over rotation	3214.75a	3867.54a	7183.27a	6586.06a	5212.91a
4.5-m Seasonlong	1800.93a	692.21b	1963.02b	1802.97b	1564.78bc
6.0-m Seasonlong	1695.21a	1087.08b	1128.08b	658.29c	1142.17c
Nongrazed	1725.24a	2804.61a	2391.97b	2438.47b	2340.07b

Data from Gorder, Manske, and Stroh 2004

Means in the same column and followed by the same letter are not significantly different ($P < 0.05$).

Table 3. Western snowberry response to grazing treatments after five years.

Treatments	Idle Control	Seasonlong	Short Duration	Twice-over Rotation
Years				
Sucker and young stem density (stems/m ²)				
1982	34b	14a	43b	32b
1986	26b	27b	49a	28b
% change/5 yr	-23.5%	92.9%*	14.0%	-12.5%
Mature stem density (stems/m ²)				
1982	22a	18ab	19ab	15b
1986	25a	12c	21ab	15bc
% change/5 yr	13.6%	-33.3%	10.5%	0.0%
Decadent stem density (stems/m ²)				
1982	6b	5b	11a	5b
1986	4b	3b	9a	5b
% change/5 yr	-33.3%	-40.0%	-18.2%	0.0%
Total stem density (stems/m ²)				
1982	62ab	37c	73a	52b
1986	55b	42c	79a	48bc
% change/5 yr	-11.3%	13.5%	8.2%	-7.7%
Shrub canopy cover (%)				
1982	59a	41b	40b	39b
1986	46a	25b	46a	25b
% change/5 yr	-22.0%*	-39.0%*	15.0%	-35.9%*
Shrub twig and leaf biomass production (lbs/ac)				
1982	1917.8a	1257.7bc	1516.4ab	1034.7c
1986	1989.2ab	1703.7b	2337.0a	1168.5c
% change/5 yr	3.7%	35.5%	54.1%*	12.9%

Data from Sturn 1987 and Kirby et al. 1988

Means in the same row and followed by the same letter are not significantly different (P<0.05).

*Percent change after five years is significantly different (P<0.05).

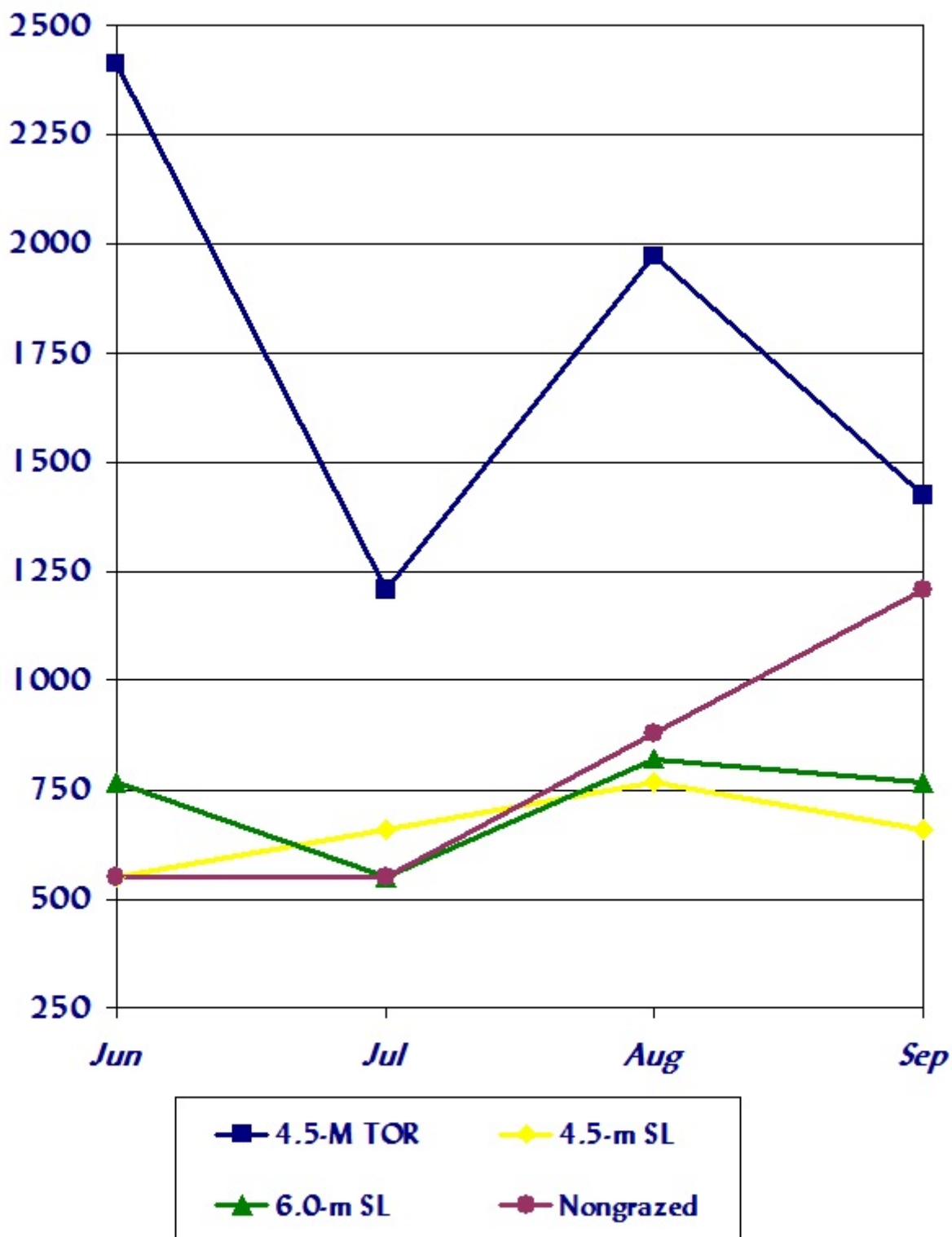


Figure 1. Total Tiller Density of western wheatgrass per square meter, data from Gorder, Manske, and Stroh 2004.

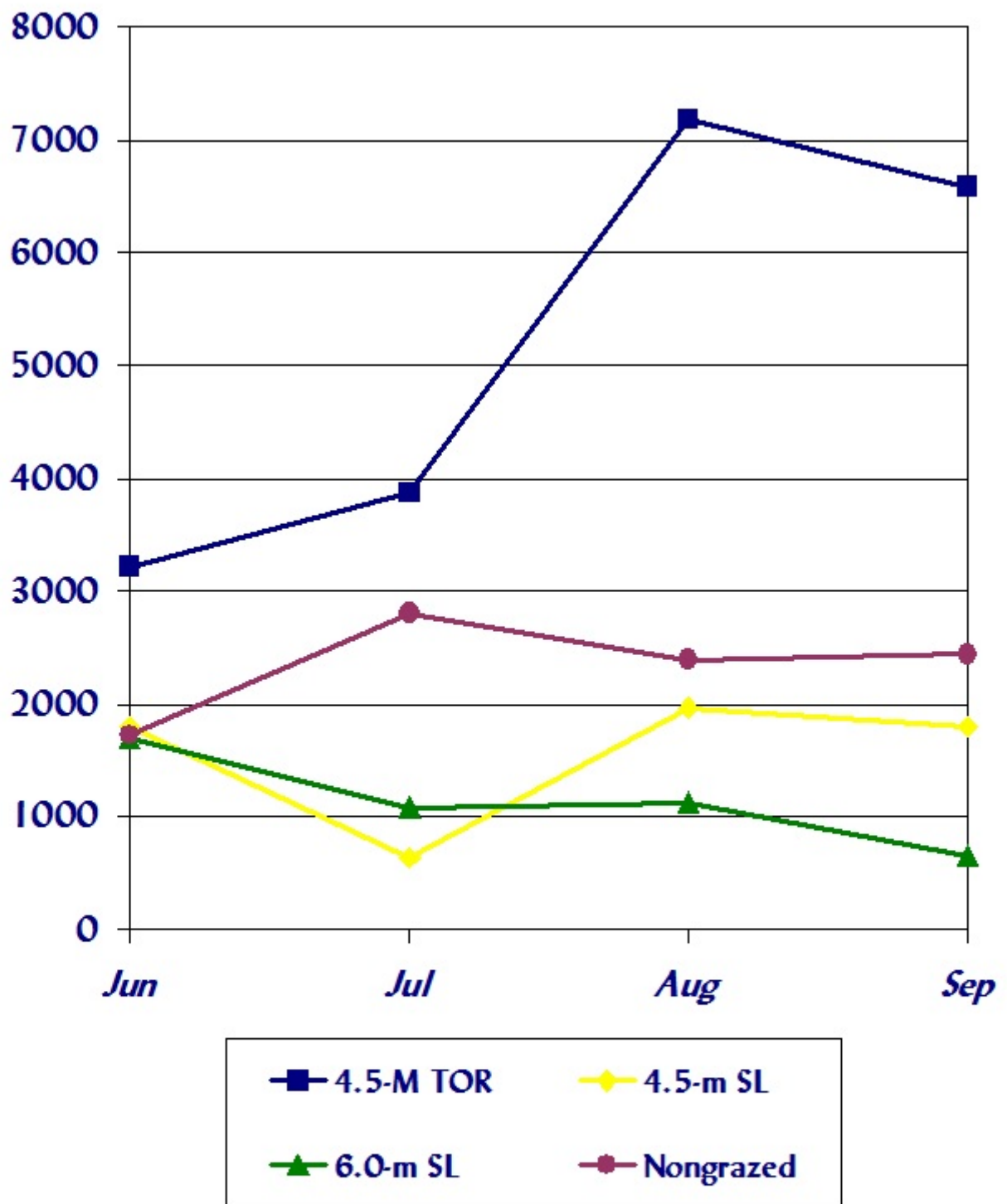


Figure 2. Rhizosphere volume (cm³) per cubic meter of soil, data from Gorder, Manske, and Stroh 2004.

Literature Cited

- Allen, E.B., and M.F. Allen. 1990.** The mediation of competition by mycorrhizae in successional and patchy environments. p. 307-389. in J.B. Grace and D. Tilman (eds.). Perspectives on plant competition. Academic Press Inc., San Diego, CA.
- Anderson, R.V., D.C. Coleman, C.V. Cole, and E.T. Elliott. 1981.** Effect of nematodes *Acroboloides sp.* and *Mesodiplogaster lheritieri* on substrate utilization and nitrogen and phosphorus mineralization. Ecology 62:549-555.
- Banister, R. 1991.** Snowberry. Rangelands 13:33-34.
- Biondini, M., D.A. Klein, and E.F. Redente. 1988.** Carbon and nitrogen losses through root exudation by *Agropyron cristatum*, *A. smithii*, and *Bouteloua gracilis*. Soil Biology and Biochemistry 20:477-482.
- Bird, S.B., J.E. Herrick, M.M. Wander, and S.F. Wright. 2002.** Spatial heterogeneity of aggregate stability and soil carbon in semi-arid rangeland. Environmental Pollution 116:445-455.
- Briske, D.D. 1991.** Developmental morphology and physiology of grasses. p. 85-108. in R.K. Heitschmidt and J.W. Stuth (eds.). Grazing management: an ecological perspective. Timber Press, Portland, OR.
- Briske, D.D., and J.H. Richards. 1994.** Physiological responses of individual plants to grazing: current status and ecological significance. p. 147-176. in M. Vavra, W.A. Laycock, and R.D. Pieper (eds.). Ecological implications of livestock herbivory in the west. Society for Range Management, Denver, CO.
- Briske, D.D., and J.H. Richards. 1995.** Plant response to defoliation: a physiological morphological, and demographic evaluation. p. 635-710. in D.J. Bedunah and R.E. Sosebee (eds.). Wildland plants: physiological ecology and developmental morphology. Society for Range Management, Denver, CO.
- Burrows, R.L., and F.L. Pflieger. 2002.** Arbuscular mycorrhizal fungi respond to increasing plant diversity. Canadian Journal of Botany 80:120-130.
- Campbell, R., and M.P. Greaves. 1990.** Anatomy and community structure of the rhizosphere. p. 11-34. in J.M. Lynch (ed.). The rhizosphere. John Wiley and Sons, New York, NY.
- Clarholm, M. 1985.** Interactions of bacteria, protozoa, and plants leading to mineralization of soil nitrogen. Soil Biology and Biochemistry 17:181-187.
- Coleman, D.C., C.P.P. Reid, and C.V. Cole. 1983.** Biological strategies of nutrient cycling in soil ecosystems. Advances in Ecological Research 13:1-55.
- Coyne, P.I., M.J. Trlica, and C.E. Owensby. 1995.** Carbon and nitrogen dynamics in range plants. p. 59-167. in D.J. Bedunah and R.E. Sosebee (eds.). Wildland plants: physiological ecology and developmental morphology. Society for Range Management, Denver, CO.
- Curl, E.A., and B. Truelove. 1986.** The rhizosphere. Springer-Verlag, New York, NY.
- Driver, J.D., W.E. Holben, and M.C. Rillig. 2005.** Characterization of glomalin as a hyphal wall component of arbuscular mycorrhizal fungi. Soil Biology and Biochemistry 37:101-106.
- Elliott, E.T. 1978.** Carbon, nitrogen and phosphorus transformations in gnotobiotic soil microcosms. M.S. Thesis. Colorado State University, Ft. Collins, CO.
- Frank, D.A., and P.M. Groffman. 1998.** Ungulate vs. landscape control of soil C and N processes in grasslands of Yellowstone National Park. Ecology 79:2229-2241.
- Frederick, B.A., and D.A. Klein. 1994.** Nitrogen effects on rhizosphere processes of range grasses from different successional seres. Plant and Soil 161:241-250.

- Gorder, M.M., L.L. Manske, and T.L. Stroh. 2004.** Grazing treatment effects on vegetative tillering and soil rhizospheres of western wheatgrass. NDSU Dickinson Research Extension Center. Range Research Report DREC 04-1056. Dickinson, ND. 13p.
- Hamilton, III, E.W., and D.A. Frank. 2001.** Can plants stimulate soil microbes and their own nutrient supply? Evidence from a grazing tolerant grass. *Ecology* 82:2397-2402.
- Harley, J.L., and S.E. Smith. 1983.** Mycorrhizal symbiosis. Academic Press, New York, NY.
- Ingham, R.E., J.A. Trofymow, E.R. Ingham, and D.C. Coleman. 1985.** Interactions of bacteria, fungi, and the nematode grazers: effects of nutrient cycling and plant growth. *Ecological Monographs* 55:119-140.
- Klein, D.A., B.A. Frederick, M. Biondini, and M.J. Trlica. 1988.** Rhizosphere microorganism effects on soluble amino acids, sugars, and organic acids in the root zone of *Agropyron cristatum*, *A. smithii*, and *Bouteloua gracilis*. *Plant and Soil* 110:19-25.
- Kirby, D.R., G.M. Sturn, and T.A. Ransom-Nelson. 1988.** Effects of grazing on western snowberry communities in North Dakota. *Prairie Naturalist* 20:161-169.
- Kochy, M. 1999.** Grass-tree interactions in western Canada. Ph.D. Dissertation. University of Regina. Regina, Saskatchewan, Canada.
- Kochy, M., and S.D. Wilson. 2000.** Competitive effects of shrubs and grasses in prairie. *Oikos* 91:385-395.
- Koide, R.T. 1993.** Physiology of the mycorrhizal plant. p. 33-54. *in* D.S. Ingram, and P.H. Williams (eds.). *Mycorrhiza synthesis*. Academic Press, London, UK.
- Langer, R.H.M. 1972.** How grasses grow. Edward Arnold, London, Great Britain.
- Manske, L.L., W.T. Barker, and M.E. Biondini. 1988.** Effects of grazing management treatments on grassland plant communities and prairie grouse habitat. USDA Forest Service. General Technical Report RM-159. p. 58-72.
- Manske, L.L. 1999.** Can native prairie be sustained under livestock grazing? p. 99-108. *in* J. Thorpe, T.A. Steeves, and M. Gollop (eds.). *Proceedings of the Fifth Prairie Conservation and Endangered Species Conference*. Provincial Museum of Alberta. Natural History Occasional Paper No. 24. Edmonton, Alberta, Canada.
- Manske, L.L. 2000a.** Management of Northern Great Plains prairie based on biological requirements of the plants. NDSU Dickinson Research Extension Center. Range Science Report DREC 00-1028. Dickinson, ND. 12p.
- Manske, L.L. 2000b.** Grazing before grass is ready. NDSU Dickinson Research Extension Center. Range Management Report DREC 00-1032. Dickinson, ND. 6p.
- Manske, L.L. 2003.** Effects of fall grazing on grass-leaf height. NDSU Dickinson Research Extension Center. Range Management Report DREC 03-1031b. Dickinson, ND. 7p.
- Marschner, H., and B. Dell. 1994.** Nutrient uptake in mycorrhizal symbiosis. *Plant and Soil* 159:89-102.
- McCarty, M.K. 1967.** Control of western snowberry in Nebraska. *Weeds* 15:130-133.
- McNaughton, S.J. 1979.** Grazing as an optimization process: grass-ungulate relationships in the Serengeti. *American Naturalist* 113:691-703.
- McNaughton, S.J. 1983.** Compensatory plant growth as a response to herbivory. *Oikos* 40:329-336.
- Moorman, T., and F.B. Reeves. 1979.** The role of endomycorrhizae in revegetation practices in the semi-arid west. II. A bioassay to determine the effect of land disturbance on endomycorrhizal populations. *American Journal of Botany* 66:14-18.
- Mueller, R.J., and J.H. Richards. 1986.** Morphological analysis of tillering in *Agropyron spicatum* and *Agropyron desertorum*. *Annals of Botany* 58:911-921.

- Murphy, J.S., and D.D. Briske. 1992.** Regulation of tillering by apical dominance: chronology, interpretive value, and current perspectives. *Journal of Range Management* 45:419-429.
- Pelton, J. 1953.** Studies on the life-history of *Symphoricarpos occidentalis* Hook., in Minnesota. *Ecological Monographs* 23:17-39.
- Peltzer, D.A., and M. Kochy. 2001.** Competitive effects of grasses and woody plants in mixed grass prairie. *Journal of Ecology* 89:519-527.
- Rillig, M.C., S.F. Wright, and V.T. Eviner. 2002.** The role of arbuscular mycorrhizal fungi and glomalin in soil aggregation: comparing effects of five plant species. *Plant and Soil* 238:325-333.
- Sarvis, J.T. 1941.** Grazing investigations on the Northern Great Plains. North Dakota Agricultural Experiment Station. Bulletin 308. Fargo, ND.
- Smith, K.A. 1985.** Canada thistle response to prescribed burning (North Dakota). *Restoration and Management Notes* 3:87.
- Smith, S.E., and D.J. Read. 1997.** Mycorrhizal symbiosis. Academic Press, San Diego, CA.
- Sturn, G.M. 1987.** Response of western snowberry (*Symphoricarpos occidentalis* Hook.) dominated communities to grazing in south central North Dakota. M.S. Thesis. North Dakota State University. Fargo, ND.
- Trlica, M.J. 1977.** Distribution and utilization of carbohydrate reserves in range plants. p. 73-97. in R.E. Sosebee (ed.). Range plant physiology. Range Science Series No. 4. Society for Range Management. Denver, CO.
- Volesky, J.D. 1982.** Big game browse study evaluation. M.S. Thesis. North Dakota State University. Fargo, ND.
- Whipps, J.M. 1990.** Carbon economy. p. 59-97. in J.M. Lynch (ed.). The rhizosphere. John Wiley and Sons, New York, NY.