

Evaluation of Processes that Inhibit Encroachment of Woody Species into Native Rangelands of the Northern Plains



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Encroachment of woody species into native rangelands of the Northern Plains is a greater problem now than it was prior to the Homestead Act of 1862. The occurrence of this phenomenon on the landscape indicates that the ecological processes that had been inhibiting encroachment of woody species into native prairie have been changed after 1862 and are no longer functioning at the same level of effectiveness as before 1862. An understanding of the cause or causes for this regression in the ecological processes will assist in finding solutions to the problem of woody species encroachment into rangelands of the Northern Plains.

During the 150 years after the implementation of the Homestead Act, fire management and grazing management of native prairie of the Northern Plains have had major changes. Fire management: pre 1862, natural caused and human caused grassland fires were limited in size only by physical landscape barriers and had irregular return intervals, post 1862, natural caused fires have been suppressed as quickly as possible and human prescribed grassland fires have been greatly restricted in size, place, and time. Grazing management: pre 1862, free roaming bison herds grazed open range, post 1862, domesticated livestock grazed restricted size pastures with defined boundaries.

Many grassland ecologists have observed that the occurrence of fire was the force that prevented intrusion of shrubs and trees into grasslands (Weaver 1954; Humphrey 1962; Daubenmire 1974; Stoddart, Smith, and Box 1975; Wright and Bailey 1982), and, the obvious corollary, that suppression of fire has facilitated the invasion of woody shrubs and trees into grasslands (Humphrey 1962; Stoddart, Smith, and Box 1975; Wright and Bailey 1982). This observational concept is almost universally accepted among modern grassland ecologists. However, the processes of how fire prevents woody species encroachment into prairie has not been clearly explained. The relationships between fire management and grassland ecosystem processes requires additional evaluation.

Grazing management is generally not accepted as a force that could prevent intrusion of shrubs and trees into grasslands. However, most currently used grazing management concepts are archaic and still focus just on the aboveground

grassland components; many theoretical grassland ecologists view grazing of domesticated livestock as a detrimental activity on rangelands and that prairie ecosystems could be managed with fire alone. Grassland ecosystem science is in the early stages of determining the biological requirements of both above and belowground components and the activation of ecological processes. How woody species encroachment relates to the defoliation resistance mechanisms, the ecosystem biogeochemical processes, and the grass resource competitiveness have not been clearly explained. The relationships between grazing management and grassland ecosystem processes requires additional evaluation.

Procedures

The ecological processes that inhibit encroachment of woody species into native prairie have changed since 1862. These changes in the ecological processes are a result of the changes in fire management or the changes in grazing management that have occurred since the implementation of the Homestead Act of 1862. The effects of fire management and the effects of grazing management on ecological processes will be evaluated and the reduction in the effectiveness of the ecological processes to inhibit wood species encroachment since 1862 will attempt to be correlated with the changes in fire management or the changes in grazing management.

The relationships of fire management on the inhibitory effects of ecological processes on woody species encroachment into prairie will be evaluated by a literature review of growth development and sexual and vegetative regeneration characteristics of fifty three of the major woody species that have invaded Northern Plains rangelands.

The relationships of grazing management on the inhibitory effects of ecological processes on woody species encroachment into prairie will be evaluated by a literature review of the defoliation resistance mechanisms, the ecosystem biogeochemical processes, and the grass resource competitiveness in Northern Plains native prairie ecosystems.

Results and Discussion: Fire Management

The growth development and sexual and vegetative regeneration characteristics of fifty three of the major invasive woody species of the Northern Plains (table 1) were evaluated to identify the relationships of fire management on the inhibitory effects of ecological processes on woody species encroachment into prairie.

Characteristics of Woody Species

Common juniper, *Juniperus communis* L. is a member of the cypress family, Cupressaceae, and is a native, long lived perennial (to 170 years), evergreen, gymnosperm, shrub that is intolerant of shade. Aerial growth has numerous branching stems that form dense clumps usually less than 5 feet (1.5 m) tall. Some stems are decumbent and spreading on the ground with the tip ascending up forming mats 7-13 feet (2-4 m) across. Regeneration is by weak vegetative and sexual reproduction. Vegetative growth is from decumbent stems that touch soil and develop adventitious roots and then develop aerial stems resulting in the ability of plant parts to survive separated from the main plant and to expand the colony. Sexual reproduction is from male and female strobili (cones) that are mostly dioecious and grow on different plants, develop during May to June, and are pollinated by wind. The fleshy female berrylike cones mature during the second growing season in August to October. The seeds have poor germination rates. Fire usually consumes the entire plant because the resinous foliage is highly flammable. Some plants could survive partial burns or patch burns. The root crown is without adventitious buds and does not sprout after damage to aerial stems. This summary information on growth development and regeneration of common juniper was based on the works of Stevens 1963, Great Plains Flora Association 1986, Mozingo 1987, Tirmenstein 1999a, and Larson and Johnson 2007.

Creeping juniper, *Juniperus horizontalis* Moench., is a member of the cypress family, Cupressaceae, and is a native, long lived perennial (to 140 years), slow growing, evergreen, gymnosperm shrub. Aerial growth has numerous prostrate stems with long, trailing or creeping branches forming mats 10-20 feet (3-5 m) across with several short erect stems less than 10 inches (30 cm) tall. The root system is shallow with several major and minor roots from the prostrate stems that are mostly 5-14 inches (13-35 cm) deep. Most ecotypes have a large treesized taproot at the center of the plant; a few ecotypes are without a main taproot. Regeneration is

by weak vegetative and sexual reproduction. Vegetative growth is from prostrate stems that touch soil and develop adventitious roots and then develop aerial stems resulting in the ability of plant parts to survive separated from the main plant and to expand the colony. Sexual reproduction is from male and female strobili (cones) that are mostly dioecious and grow on different plants, develop during May to June, and are pollinated by wind. The fleshy female berrylike cones mature during the second growing season in August to September. Seed production is usually poor, seed germination rate is very low, and seedling survival is rare. Fire usually consumes the entire plant including the large taproot because the resinous foliage is highly combustible. Some partially unburned plants could survive after a low severity fire. This summary information on growth development and regeneration of creeping juniper was based on the works of Stevens 1963, Great Plains Flora Association 1986, Gucker 2006, and Larson and Johnson 2007.

Rocky Mountain juniper, *Juniper scopulorum* Sarg., is a member of the cypress family, Cupressaceae, and is a native, long lived perennial (to 250-300 years), evergreen, gymnosperm, large shrub or medium sized tree. Aerial growth has one main upright trunk to 12 inches (3 dm) in diameter with numerous spreading and ascending branches forming a stubby round or broadly pyramidal crown to 33 feet (10 m) tall. The root system is a taproot with shallow lateral roots. Regeneration is by sexual reproduction. The root crown does not have adventitious buds. Sexual reproduction is from male and female strobili (cones) that are mostly dioecious and growing on different plants, develop during April to June, and are pollinated by wind. The fleshy female berrylike cones mature during the second growing season in September to October. Fire usually kills the entire plant. A few old trees can survive low severity fire or patch burns. The root crown does not sprout after damage to aerial stems. This summary information on growth development and regeneration of Rocky Mountain juniper was based on the works of Stevens 1963, Great Plains Flora Association 1986, Scher 2002, Stevens 2003, Larson and Johnson 2007, and Stubbendieck et al. 2011.

Ponderosa pine, *Pinus ponderosa* Lawson, is a member of the pine family, Pinaceae, and is a native, long lived perennial (to 300-600 years), fast growing, evergreen, conifer tree that is intolerant of shade. Aerial growth is a single straight trunk up to 2-4 feet (0.6-1.3 m) in dbh with numerous spreading branches growing from whorls that form a pyramidal crown in young trees and a broad rounded crown in

older trees that can grow over 100 feet (30-35 m) tall. Lower branches are usually self pruned. Leaves are long needles in bundles of two. The root system is deep and spreading resulting in wind firm trees. Regeneration is by sexual reproduction. The root crown does not have adventitious buds. Sexual reproduction is from male and female unisexual cones that are monoecious developing at separate locations of the same tree. Outcross pollination by wind occurs during April to June. The female cones mature during the second growing season in August to September releasing winged seeds that are mostly wind dispersed. Seedlings are relatively shade intolerant and require open areas for establishment. The typical low rainfall during late summer and early fall of the Northern Plains causes high mortality of seedlings and young trees. The thick bark of mature trees is relatively resistant to ground fires. Some seedlings can survive low intensity fires. However, high intensity ground fires and crown fires kill most of the trees. The root crown does not produce sprouts after damage to aerial stems. This summary information on growth development and regeneration of ponderosa pine was based on the works of Stevens 1963, Great Plains Flora Association 1986, Howard 2003a, Larson and Johnson 2007, Stubbendieck et al. 2011, and Row et al. 2012a.

American elm, *Ulmus americana* L., is a member of the elm family, Ulmaceae, and is a native, long lived perennial (to 175-200 years), fast growing, deciduous, cool season tree. Aerial growth is a single straight trunk to 48-60 inches (122-152 cm) in dbh that fork about 10-20 feet (3-6 m) above ground with several erect limbs gradually curving outwards to form a wide spreading crown to 100 or more feet (30 m) tall. Root system has a deep taproot and widespread lateral roots within 3-4 feet (1-1.2 m) of the soil surface. Regeneration is by vegetative and sexual reproduction. Vegetative growth is from sprouts developed from the stem base or from roots of damaged trees. Sexual reproduction is from perfect, bisexual, small, nonshowy flowers that emerge from buds during early May ahead of the leaves. Outcross pollination is by wind. Fruits are flat winged samaras that mature during May-early June and dispersed by wind. Fire easily causes damage to aerial parts. Low and moderately severe fires top kill saplings and young trees, and can cause complete tissue death in mature trees when the cambium is exposed to 140° F (60° C) temperatures. After damage by fire or cutting, vigorous sprouts develop from the stem base, shallow roots, and stump. Sprouts rarely develop from damaged large trees older than 150 years. This summary information on growth development and regeneration

of American elm was based on the works of Stevens 1963, Great Plains Flora Association 1986, Coladonato 1992, and Johnson and Larson 2007.

Bur oak, *Quercus macrocarpa* Michx., is a member of the oak (beech) family, Fagaceae, and is a native, long lived perennial (to 300-400 years), slow growing, deciduous, cool season tree in favorable sites and a dwarfed shrub in harsh sites that is drought tolerant. Aerial growth is a single massive trunk with large stout horizontal branches in the lower crown and ascending branches in the upper crown forming a rounded crown to 82 feet (25 m) tall in favorable sites. In harsh sites, the scrub oak form has crooked gnarled branches and grows to 15 feet (4.6 m) tall. The root system has extensive, wide spreading lateral roots and a deep taproot. Regeneration is by vegetative and sexual reproduction. Vegetative growth is sprouts or sobols developed from the root crown and shallow roots of damaged trees. Sexual reproduction is from monoecious imperfect unisexual flowers borne in separate male and female catkins that emerge on the same plant during late April-mid June. Outcross pollination is by wind. The fruit is a large acorn that matures in one growing season, dropping from the tree during August through November. Fire top kills sapling and young trees activating vigorous sprouts from adventitious buds on the root crown. Fire typically does not damage mature trees because of the insulating thick bark. Repeated top kill by fire or by heavy browsing causes the development of oak "grubs" at the soil surface capable of producing numerous sprouts that can develop into thickets of stunted shrubs. This summary information on growth development and regeneration of bur oak was based on the works of Stevens 1963, Great Plains Flora Association 1986, Johnson and Larson 2007, Gucker 2011, and Row et al. 2012b.

Green ash, *Fraxinus pennsylvanica* Marsh., is a member of the olive family, Oleaceae, and is a native, perennial, fast growing, deciduous, cool season medium sized tree that is tolerant of flooding, intolerant of shading, and is frost avoidant. Aerial growth is a single large straight trunk up to 1.6 feet (0.5 m) in dbh with several slender spreading branches that form an open, irregular crown to 50 feet (15 m) tall. The root system is extensive and shallow descending to 5-10 feet (1.5-3 m) deep. The lateral roots are long with few branches. Regeneration is by vegetative and sexual reproduction. Vegetative growth is by sprouts from the root crown and stem base. Damage to aerial parts activates dormant (epicormic) buds. Sexual reproduction is by dioecious, imperfect, unisexual flowers that emerge

on separate male and female trees during May before the leaves. Pollination is by wind. The fruit is a winged samara that matures during August-September. Fire kills seeds and seedlings. Damage to the trunk of young and mature trees by fire, drought, flooding, or logging activate vegetative basal sprouts. This summary information on growth development and regeneration of green ash was based on the works of Stevens 1963, Great Plains Flora Association 1986, Dickerson 2002, Gucker 2005, and Johnson and Larson 2007.

Balsam poplar, *Populus balsamifera* L., is a member of the willow family, Salicaceae, and is a native, perennial, fast growing, deciduous, cool season tree. Aerial growth is a single straight stem with a few ascending branches in the upper 2/3 of the trunk forming a broad open crown to 33-100 feet (10-30 m) tall. The root system is an extensive shallow lateral root network. Regeneration is by vegetative and sexual reproduction. Vegetative growth is sprouts from stems, stumps, buried branches, and suckers, or sobols, from shallow lateral roots. Dense stands (groves or bluffs) expand by suckers (sobols) from subsoil lateral roots 0.4 inch (1 cm) in diameter at 0.8 inch (2 cm) below the soil surface and can contain single or multiple genetic clones. Sexual reproduction is from dioecious, imperfect, unisexual flowers borne in separate male and female drooping catkins that emerge on different plants during May. Seeds have tufts of long hairs easily blown by the wind. Seeds have a high germination rate. Fire can top kill stems, but rarely can fire consume entire stands with one burn; multiple fires are usually required to kill aerial stems of old stands. Most shallow lateral roots in moist soil survive severe fires. Top kill or severe damage to aerial stems stimulates vigorous root sucker growth greatly increasing stem density at explosive rates. This summary information on growth development and regeneration of balsam poplar was based on the works of Stevens 1963, Great Plains Flora Association 1986, Harris 1990, and Larson and Johnson 2007.

Plains cottonwood, *Populus deltoides* Bartr. ex Marsh. ssp *monilifera* (Ait.) Eckernwalder, is a member of the willow family, Salicaceae, and is a native, short lived perennial (about 90 years), quick growing, deciduous, cool season hardwood tree that is drought tolerant, moderately tolerant of water logged soil and short term flooding, and shade intolerant. Aerial growth is a single large trunk with 5-80 inch (12-200 cm) in dbh that divides near the base into large ascending branches that curve outward to form a broad rounded crown to 10-100 feet (3-30 m) tall. The root system is relatively deep at about 8

feet (2.5 m) for young trees and about 16 feet (5 m) for mature trees. Exposed lateral roots develop the typical thick bark of the trunk. Regeneration is by vegetative and sexual reproduction. Vegetative growth is by sprouts from the root crowns and stumps, and by adventitious suckers from the roots. The sucker growth arises from hormonally suppressed buds embedded in the periderm of intact roots after death or injury of aerial parts. Sprouts can also develop from broken limbs and crown breakage. Sexual reproduction is from dioecious, imperfect, unisexual flowers borne in separate male and female drooping catkins that emerge on different trees during late April-May. Seeds have tufts of long hairs easily blown by wind. Germination occurs within 1-2 weeks on moist exposed soil in full sunlight. Fire caused top kill or severe damage to aerial parts, and drought caused branch die back activate vegetative sprout development. The number of sprouts per tree are few and the mortality rates are usually high with only about 10% survival. This summary information on growth development and regeneration of plains cottonwood was based on the works of Stevens 1963, Great Plains Flora Association 1986, Taylor 2001, NRCS Staff 2002a, and Larson and Johnson 2007.

Quaking aspen, *Populus tremuloides* Michx., is a member of the willow family, Salicaceae, and is a native, short lived perennial (50-60 years), rapid growing, deciduous, cool season, small to medium sized tree that is intolerant of shade, waterlogged soil, and long term flooding. Aerial growth is a single erect trunk that is usually less than 16 inches (40 cm) in dbh with horizontal to shallowly ascending branches in the upper half of the trunk forming a narrow spherically round crown usually less than 50 feet (15 m) tall. The extensive clonal root system can survive for 1000's of years is relatively shallow with a widespreading lateral root network branching into dense fine roots extending outwardly over 100 feet (30 m) with vertical sinker roots growing downward to 9-10 feet (2.7-3 m) deep. Numerous sobols (shoots) arise from the shallow lateral roots forming dense clonal stands (grooves or bluffs) that cover a few acres in size. Regeneration is by vegetative and sexual reproduction. Vegetative growth is suckers (sobols) originating from the meristem of lateral roots that have greater than 0.5 inch (1.3 cm) in diameter and less than 5 inches (13 cm) from the soil surface. Sexual reproduction is from dioecious, imperfect, unisexual, flowers borne on separate male and female drooping catkins that emerge on different plants during May-June. The fruits mature during June-July. Seeds have tufts of hairs that are easily blown by the wind. Seedlings have low survival rates in dry areas and in shaded

areas. The potential for sucker (sobel) growth is enormous after top kill. The extensive lateral roots of clonal stands have thousands of buds hormonally suppressed by apical dominance. Top kill of stems by fire, wind breakage, girdling, lumber harvest, or chemical defoliation stop the apical control and stimulate vigorous sprout growth. This summary information on growth development and regeneration of quaking aspen was based on the works of Stevens 1963, Great Plains Flora Association 1986, Howard 1996, Nesom 2003a, Larson and Johnson 2007, and Stubbendieck et al. 2011.

Peachleaf willow, *Salix amygdaloides* Anders., is a member of the willow family, Salicaceae, and is a native, short lived perennial, deciduous, cool season, small to medium sized tree, or sometimes in the short grass prairie, a thicket forming shrub. Aerial growth is usually a single main trunk often leaning with spreading branches and drooping branchlets and twigs forming a gnarled and irregular crown to 39 feet (12 m) tall. The root system has spreading multibranching roots that descend down to the depth of the water table. Regeneration is by vegetative and sexual reproduction. Vegetative growth is primarily sprouts from the root crown. Sprouts (suckers) do not grow from the roots. Broken branches or decumbent stems that touch soil can develop adventitious roots, then develop aerial stems, and continue development as an individual plant independent from the main plant. Several adventitious buds that are located on the trunk (bole) just above or just below ground level can also produce vegetative sprout growth. Sexual reproduction is mostly from dioecious, imperfect, unisexual, flowers borne on separate male organs and female catkins that emerge on different trees during May. The fruits mature during June. Seeds have tufts of hairs that are easily blown by the wind. Seeds must germinate within 12-24 hours on moist bare soil. Established seedlings are rare. Fire can top kill or severely damage the trunk, stimulating sprout growth from the root crown. Severe fire on dry soil can kill the root crown preventing sprout growth. This summary information on growth development and regeneration of peachleaf willow was based on the works of Stevens 1963, Great Plains Flora Association 1986, Stevens and Dozier 2003a, Larson and Johnson 2007, and Fryer 2012.

Beaked willow, *Salix bebbiana* Sarg., is a member of the willow family, Salicaceae, and is a native, short lived perennial, fast growing, deciduous, cool season, large shrub or small multistemmed tree. Aerial growth has numerous stems arising at wide angles from a large root crown; stems with much

branching form a rounded crown 10-15 feet (3-4.5 m) tall. This is one of the willows that form diamond deformations of the stem caused by fungal attack at the junction of the branch. The root system is shallow and dense. Regeneration is by vegetative and sexual reproduction. Vegetative growth is primarily sprouts from the root crown and stem base following damage to the aerial stems. Broken branches and stems, and decumbent stems that touch soil can develop adventitious roots and then develop aerial stems resulting in the ability of plant parts to survive separated from the main plant and to expand the colony. Sexual reproduction is from dioecious, imperfect, unisexual flowers borne on separate male and female catkins that emerge on different plants during May. Pollination is by bees. Seeds are viable for only a few days and require moist soil in full sunlight. Fire can top kill plants and stimulate vigorous sprouting. Severe fire that removes the organic layer can kill the root crown. This summary information on growth development and regeneration of beaked willow was based on the works of Stevens 1963, Great Plains Flora Association 1986, Tesky 1992, Favorite 2003, Larson and Johnson 2007, and Stubbendieck et al. 2011.

Coyote willow, narrowleaf willow, *Salix exigua* Nutt., is a member of the willow family, Salicaceae, and is a native, short lived perennial (10-20 years), winter deciduous, cool season shrub that is drought resistant, tolerant of flooding, and very tolerant of frost. Aerial growth has numerous erect shoots usually 6.5-20 feet (2-6 m) tall arising from lateral root networks forming large clonal colonies that can cover 1000 square feet (325 m²). The extensive root system is woody and spreading. The lateral roots have shoot buds that produce long rows of aerial stems. Regeneration is by vegetative and sexual reproduction. Vegetative growth is primarily sprouts from lateral roots, root crowns, and stem bases. Bent stems that make contact with moist soil can produce adventitious roots and then develop aerial stems, and are capable of surviving separated from the main plant. Sexual reproduction is from dioecious, imperfect, unisexual flowers borne on separate male and female catkins that emerge on different plants during May-June. Pollination is by insect, primarily bees. Seeds are dispersed by wind and water, and must germinate within 24 hours. Seedlings have a high mortality rate. Fire can top kill plants and stimulate vigorous sprouting. Severe fire that removes the organic layer can kill the root crown, at least some of the lateral roots are protected by mineral soil. This summary information on growth development and regeneration of coyote willow was based on the works of Stevens 1963, Great Plains

Flora Association 1986, Stevens et al. 2003, Anderson 2006, Larson and Johnson 2007, and Stubbendieck et al. 2011.

Sandbar willow, *Salix interior* Rowlee, is a member of the willow family, Salicaceae, and is a native, perennial, deciduous, cool season shrub. Aerial growth has numerous erect shoots usually less than 16 feet (5 m) tall arising from rhizome networks forming large dense clonal thickets. The extensive root system includes networks of rhizomes that can spread aggressively. Regeneration is by vegetative and sexual reproduction. Vegetative growth is primarily sprouts from rhizomes. Sexual reproduction is from dioecious, imperfect, unisexual flowers borne on separate male and female catkins that emerge on different plants during late May-early June. Fruits are capsules that mature during June-early July. Fire can top kill plants and stimulate vigorous rhizome sprouts. This summary information on growth development and regeneration of sandbar willow was based on the works of Stevens 1963, NRC Staff 2002b, and Larson and Johnson 2007.

Prairie willow, *Salix humilis* Marsh., is a member of the willow family, Salicaceae, and is a native, perennial, deciduous, cool season, upland shrub. Aerial growth has numerous, short, erect shoots usually less than 10 feet (3 m) tall that form clonal colonies. The root system is extensive. Regeneration is by vegetative and sexual reproduction. Vegetative growth is primarily sprouts from root crowns and stem bases. Sexual reproduction is from dioecious, imperfect, unisexual flowers borne on separate male and female catkins that emerge on different plants during May before the leaves. Fruits are capsules that mature during May-early June. Seeds have silky hairs at the base that are easily blown by wind. Fire can top kill plants and stimulate sprouting. This summary information on growth development and regeneration of prairie willow was based on the works of Stevens 1963, Great Plains Flora Association 1986, and Stevens and Dozier 2003b.

American hazelnut, *Corylus americana* Walt., is a member of the birch family, Betulaceae, and is a native, perennial, deciduous, cool season shrub that is shade tolerant. Aerial growth has a few straight main stems with numerous spreading ascending branches forming a crown 3-7 feet (0.9-2 m) tall; stems arise from rhizome networks forming dense colonial thickets. The root system is extensive, branching profusely into very fine lateral roots in the top 6 inches (15 cm) of soil with numerous small vertical roots. An extensive rhizome network

interconnects the clonal stem bases. Regeneration is by vegetative and sexual reproduction. Vegetative growth is primarily sprouts from rhizomes. Sexual reproduction is by monoecious imperfect, unisexual, tiny, inconspicuous flowers that were formed the previous summer and emerge the next spring before the leaves during May with male and female organs at separate locations on the same plant. The fruit is an acornlike nut that matures during the late summer-early fall. Low to moderate severity spring and summer fires easily top kill the plants and stimulate sprouting from the rhizomes. This summary information on growth development and regeneration of American hazelnut was based on the works of Stevens 1963, Great Plains Flora Association 1986, Coladonato 1993, and Nesom 2007.

Beaked hazelnut, *Corylus cornuta* Marsh., is a member of the birch family, Betulaceae, and is a native, perennial, deciduous, cool season shrub that is moderately shade tolerant. Aerial growth is multiple ascending stems 3-7 feet (1-2 m) tall arising from rhizome networks forming dense colonial thickets with 3,000 to 60,000 stems per acre (7400 to 148,000 stems per hectare). The root system has a taproot that descends down greater than 2 feet (0.6 m) deep with extensive dense lateral roots intertwined with the rhizome system mostly within the top 8 inches (20 cm) of soil. An extensive rhizome network interconnects the clonal stem bases. Regeneration is by vegetative and sexual reproduction. Vegetative growth is sprouts from root crowns and from the aggressive rhizomes. Bent stems that make contact with soil can produce adventitious roots and then develop aerial stems resulting with the capability to survive separated from the main plant. Sexual reproduction is mostly by monoecious imperfect, unisexual flowers that emerge before the leaves during late May with the male and female organs located on separate twigs of the same plant. Pollination is by wind. The fruit is an acornlike nut that mature during August-September and is dispersed by mammals and birds. The seed has a short one year life span. Seedling establishment is sporadic and rare. Fire can top kill the plants and stimulate sprouting from the root crown and the extensive rhizomes. This summary information on growth development and regeneration of beaked hazelnut was based on the works of Stevens 1963, Great Plains Flora Association 1986, Nesom 2006a, Fryer 2007, and Larson and Johnson 2007.

Kinnikinnick, bearberry, *Arctostaphylos uva-ursi* (L.) Spreng., is a member of the heath family, Ericaceae, and is a native, long lived perennial, evergreen, cool season shrub that is

tolerant of cold and partial shade. Aerial growth has numerous woody prostrate creeping flexible stems or stolons arising from a single root crown; erect branches growing upward along the horizontal stems and the upward turned terminal stem ends reach a height of 6 inches (15 cm); the extensive horizontal stems form a dense mat 3-7 feet (1-2 m) across. The root system is extensive with some roots growing down to 36-72 inches (91-183 cm) deep, and with additional short feeding roots developing at the nodes of the upright branches. Regeneration is by vegetative and sexual reproduction. Vegetative growth is sprouts from latent buds on the horizontal stems and from dormant (epicormic) buds on the stem bases and root crowns. Stems severed from the main plant can develop a deep root system and survive as an individual plant. Buried stems form nodules and produce adventitious roots and then develop aerial stems and expand the colony. Sexual reproduction is from perfect bisexual flowers with both male and female reproductive organs that emerge during May-June. The fruit, which is berrylike drupe, matures during July-October and usually persists on the plant through winter. Only a very small number of seeds germinate. Fire damages the aerial parts with portions top killed. Sprouts develop from the stem bases, root crowns, and surviving segments of the horizontal stems. This summary information on growth development and regeneration of kinnikinnick was based on the works of Stevens 1963, Great Plains Flora Association 1986, Crane 1991, NRCS Staff 2006, Larson and Johnson 2007, and Stubbendieck et al. 2011.

Juneberry, Saskatoon serviceberry, *Amelanchier alnifolia* Nutt., is a member of the rose family, Rosaceae, and is a native, short lived perennial (6-20 years), deciduous, cool season shrub or small tree. Aerial growth is single or clustered erect stems spreading to erect branches forming a rounded crown 3-26 feet (1-8 m) tall; stems arise from an aggressive network of rhizomes; increasing stem numbers develop colonies that can form into dense thickets. The root system is extensive including a mass of roots extending from the root crowns that develop below each aerial stem. An extensive rhizome network of shallow and deep vertical and horizontal rhizomes and aboveground stolons interconnect the root crowns. Regeneration is by vegetative and sexual reproduction. Vegetative growth is sprouts from buds on the root crowns, stolons, and aggressive rhizomes. Sexual reproduction is from perfect bisexual showy flowers with both male and female organs on an upright raceme that emerge during early May. The fruit is a sweet berrylike pome that matures during June.

Seeds are spread by birds and mammals. However, establishment of seedlings is rare. Fire can top kill aerial stems and activate sprout growth from buds on root crowns and rhizomes. Stem cover usually increases following fire. Severe fire may kill some of the shallow rhizomes, however, the deep horizontal and vertical rhizomes usually survive. This summary information on growth development and regeneration of Juneberry was based on the works of Stevens 1963, Great Plains Flora Association 1986, Fryer 1997, Nesom 2006b, Larson and Johnson 2007, and Stubbendieck et al. 2011.

Northern roundleaf hawthorn, *Crataegus chrysoarpa* Ashe, is a member of the rose family, Rosaceae, and is a native, perennial, deciduous, cool season shrub or small tree that is tolerant of drought, wind, wet soils, and atmospheric pollution. Aerial growth has several stout flexible stems arising in a cluster from a stem base; the stems are branched forming a rounded crown 3-13 feet (1-4 m) tall; branches have spines 1-3 inches (2-7 cm) long; increasing stem numbers develop into dense thickets. The root system is shallow and diffuse, widely spreading. Regeneration is by vegetative and sexual reproduction. Vegetative growth is sprouts from the stem base and suckers from the shallow lateral roots. Sexual reproduction is from perfect bisexual showy flowers with both male and female organs that emerge during late May-June. The fruit is a pome that matures during late August. The aerial parts are flammable and easily top kill by fire which activates sprout growth from the stem bases, and sucker growth from the shallow lateral roots. This summary information on growth development and regeneration of northern roundleaf hawthorn was based on the works of Stevens 1963, Great Plains Flora Association 1986, and Larson and Johnson 2007.

Shubby cinquefoil, *Dasiphora floribunda* (Pursh) Kartesz, (*Potentilla fruticosa* L.), is a member of the rose family, Rosaceae, and is a native, long lived perennial (25-36 years), deciduous, cool season, low mat to erect shrub that is winter hardy and cold tolerant. Aerial growth has multiple stems arising from a stem base; these stems are erect or prostrate with numerous branches forming a low mat to erect crown 1-6.5 feet (0.3-2 m) tall. The root system has numerous thin woody roots widely spreading at shallow to moderate deep depths. Regeneration is by vegetative and sexual reproduction. Vegetative growth is sprouts from the root crown. The decumbent stems that touch soil can develop adventitious roots and then develop aerial stems that can develop into a separate plant if severed from the main plant. Sexual reproduction is from

perfect bisexual showy flowers with both male and female organs; flowers on old growth emerge during June and flowers on new growth emerge during August. Seeds are achenes that mature during June-September and are dispersed by wind. Top kill by fire activates vigorous sprouting from the root crown. Aerial stems are susceptible to top kill by fire because the fibrous bark is extremely flammable resulting in flash burns of high intensity. Spring burns on moist soil cause less damage than summer and fall burns. Fires on dry soil can damage the root crown. This summary information on growth development and regeneration of shrubby cinquefoil was based on the works of Stevens 1963, Great Plains Flora Association 1986, Anderson 2001, Larson and Johnson 2007, and Stubbendieck et al. 2011.

Wild plum, *Prunus americana* Marsh., is a member of the rose family, Rosaceae, and is a native, short lived perennial (about 20 years), deciduous, cool season shrub to small tree that is shade tolerant. Aerial growth has single to multiple stout crooked stems, or trunks, arising from a stem base; numerous stiff spreading lateral branches form a wide flat topped irregular crown 3-30 feet (1-10 m) tall; most branchlets have stout thorns. The root system has spreading roots, most of which remain shallow, with some vertical roots descending to 6 feet (1.8 m) depths; lateral roots extend outward to 11 feet (3.4 m) long. Regeneration is by vegetative and sexual reproduction. Vegetative growth is shoots from the root crowns and suckers from the shallow lateral roots. Aggressive root and aerial stem growth forms long lived dense thickets. Sexual reproduction is from perfect bisexual fragrant showy flowers with both male and female organs that emerge during May before the leaves. Pollination is by bees. The fruit is a drupe that ripens during mid-late summer. The seed is inside a hard woody stone that matures during September-mid October. Fire top kills stems and activates vigorous sprout and sucker growth; stem density is greater two years post fire than that prefire. Pruning and browsing increases fruit production. This summary information on growth development and regeneration of wild plum was based on the works of Stevens 1963, Great Plains Flora Association 1986, Stevens and Kaiser 2003, Johnson and Larson 2007, and Fryer 2010.

Pin cherry, *Prunus pensylvanica* L., is a member of the rose family, Rosaceae, and is a native, short lived perennial (20-40 years), deciduous, cool season shrub to small tree that is shade intolerant. Aerial growth has a short straight stem, or trunk, arising from a stem base; widely spreading branches form a narrow round topped crown usually 5-15 feet

(1.5-4.5 m) tall and spreading to 5-10 feet (1.5-3 m) wide. The root system is shallow usually less than 14-24 inches (36-61 cm) deep with many lateral branches than can grow rapidly. Regeneration is by vegetative and sexual reproduction. Vegetative growth is sprouts from the stem base and suckers from the shallow lateral roots. Aggressive root and aerial stem growth forms clonal thickets that can cover up to 153 square feet (14.3 m²). Sexual reproduction is from perfect bisexual showy flowers with both male and female organs that emerge during mid May. Pollination is by insects. The fruit is a drupe that ripens during July-August. The seed is inside a hard woody stone. Seed distribution is by birds and small mammals. Seeds can remain viable a long time in the seed bank. Seedling survival is usually low. Fire can top kill aerial parts and activate the great potential for growth of sprouts from stem bases and suckers from lateral roots. Fire does not kill seeds in the seed bank and stimulates rapid germination following a burn. This summary information on growth development and regeneration of pin cherry was based on the works of Stevens 1963, Great Plains Flora Association 1986, Anderson 2004b, and Larson and Johnson 2007.

Sand cherry, *Prunus pumila* L., is a member of the rose family, Rosaceae, and is a native, perennial, deciduous, cool season shrub that is drought tolerant. Aerial growth has several creeping stems that radiate outward from a stem base 10-15 feet (3-4.5 m) long; spreading vertical branches ascend from the horizontal stems and seldom grow to 12-15 inches (30-38 cm) tall. The root system is fibrous with extensive spreading lateral roots. Most of the root biomass remains within the top 10 inches (25 cm) of soil, with some vertical roots descending to 8-12 feet (2.4-3.7 m) deep. An abundant rhizome system exists with equal distribution at shallow and deep soil layers; the rhizome network interconnects the stem bases. Regeneration is by vegetative and sexual reproduction. Vegetative growth is by sprouts from the root crowns and rhizomes and by suckers from the shallow lateral roots. Sexual reproduction is from perfect bisexual small showy flowers with both male and female organs that emerge during May-early June. Self pollination is possible; cross pollination is by insects. The fruit is a drupe that ripens during late July-September. The seed is inside a hard woody stone. Seed distribution is by birds and small mammals. Low and moderate severity fire top kill aerial parts and activate shoot growth from the root crowns, rhizomes, and lateral roots. Some shallow roots and rhizomes can be killed by fire on dry soil, however, the deep roots and rhizomes are well insulated from the heat. This summary information

on growth development and regeneration of sand cherry was based on the works of Stevens 1963, Great Plains Flora Association 1986, NCRS Staff 2002c, Taylor 2006, and Larson and Johnson 2007.

Chokecherry, *Prunus virginiana* L., is a member of the rose family, Rosaceae, and is a native, perennial, deciduous, cool season shrub or small tree that is intolerant of shade, poor drainage, frequent flooding, and high clay soils. Aerial growth has numerous slender stems arising from a stem base; the stem bases are interconnected by a rhizome network; stems branch near the base with the main branches upright and spreading forming a highly variable crown 3-20 feet (1-6 m) tall. The root system is extensive and deep; a complex network of rhizomes with 0.4-0.8 inch (1-2 cm) diameters have separate root systems established at intervals; the vertical roots descend to more than 6 feet (1.8 m) deep, and the lateral roots extend greater than 35 feet (10.7 m) outward from the rhizome connection. Aggressive soboliferous rhizome and aerial stem development forms extensive thickets. Regeneration is by vegetative and sexual reproduction. Vegetative growth is primarily sprouts from aggressive rhizomes. Sexual reproduction is from perfect bisexual fragrant showy flowers with both male and female organs arranged on drooping racemes that emerge during May-early June. The fruit is a drupe that ripens during July-September. The seed is inside a hard woody stone. Seed distribution is by birds and small mammals. Seed germination rate improves after passing through an animals digestive tract. Fire top kills aerial stems and foliage activating rapid and prolific sprout growth from the rhizomes and shoot growth from adventitious buds on the root crowns. Seed germination rate improves with the heat treatment from a burn. This summary information on growth development and regeneration of chokecherry was based on the works of Stevens 1963, Great Plains Flora Association 1986, Johnson 2000, Stubbendieck et al. 2003, Crowder et al. 2004, Johnson and Larson 2007, and Stubbendieck et al. 2011.

Prickly wild rose, *Rosa acicularis* Lindl., is a member of the rose family, Rosaceae, and is a native, perennial, deciduous, shrub that is moderately shade tolerant. Aerial growth has numerous stout erect stems widely branched 1-3 feet (6-10 dm) tall arising from stem bases interconnected by rhizomes; stems and branches are densely covered with straight, slender, unequal sized prickles. The root system is extensive with many fine lateral roots within the top 8 inches (20 cm) of soil and with deep vertical roots extending down to 55 inches (14 dm) deep. A widespread rhizome system exists 8-12 inches (20-30

cm) below the soil surface. Clones of 8 to 11 aerial stems linked by horizontal rhizomes can cover 12-24 square yards (10-20 m²) of land. These rose clones can live for hundreds of years. Regeneration is by vegetative and sexual reproduction. Vegetative growth is primarily sprouts from the rhizomes. Sexual reproduction is from perfect bisexual fragrant showy flowers with both male and female organs that emerge during May-July. The fruit is a hip that is usually retained on the plant through winter. The seeds are achenes and distributed by birds and small mammals. Fire top kills aerial stems and activates sprout growth from the rhizomes that are protected from heat by soil. This summary information on growth development and regeneration of prickly wild rose was based on the works of Stevens 1963, Great Plains Flora Association 1986, Crane 1990, and Johnson and Larson 2007.

Prairie wild rose, *Rosa arkansana* Porter, is a member of the rose family, Rosaceae, and is a native, perennial, deciduous shrub or subshrub. Aerial growth is stout erect flexible widely branching herbaceous to slightly woody stems that regrow annually from stout horizontal roots. The stems grow to 4-20 inches (1-5 dm) tall and die back partly or completely to near the stem base from drought or freezing. Stems are densely covered with small bristly prickles. The new stems are nonwoody and the old stems deposit lignin around the cell walls. The root system has very stout deep vertical roots that descend to 10-12 feet (3-3.7 m) below the soil surface, and has stout widespreading horizontal roots near the soil surface. Regeneration is by vegetative and sexual reproduction. Vegetative growth is sprouts from the root crowns and stout horizontal roots. Sexual reproduction is from perfect bisexual fragrant showy flowers with both male and female organs that emerge during May-August. Pollination is by insects. The fruit is a hip that is usually retained on the plant through winter. The seeds are achenes and distributed birds and mammals. Seeds can survive in the seed bank several years and usually have low germination rates. Fire top kills aerial stems and activates sprout growth from the root crowns and stout horizontal roots. This summary information on growth development and regeneration of prairie wild rose was based on the works of Stevens 1963, Great Plains Flora Association 1986, Stubbendieck et al. 2003, Hauser 2006a, and Johnson and Larson 2007.

Smooth wild rose, *Rosa blanda* Ait., is a member of the rose family, Rosaceae, and is a native, perennial, deciduous shrub. Aerial growth has numerous erect woody stems 3-7 feet (0.5-1.5 m) tall; stems are widely branched above and with no prickles

except for a few near the base. The root system has stout roots; aggressive root and aerial stem growth form clonal colonies. Regeneration is by vegetative and sexual reproduction. Vegetative growth is sprouts from the root crowns and stout horizontal roots. Sexual reproduction is from perfect bisexual fragrant showy flowers with both male and female organs that emerge during late May-June. Pollination is by insects. The fruit is a hip. The seeds are achenes. Fire top kills aerial stems and activates sprout growth from the root crowns and stout horizontal roots. This summary information on growth development and regeneration of smooth wild rose was based on the works of Stevens 1963, Great Plains Flora Association 1986, and Johnson and Larson 2007.

Western wild rose, Woods rose, *Rosa woodsii* Lindl., is a member of the rose family, Rosaceae, and is a native, long lived perennial, deciduous shrub. Aerial growth has numerous erect, stout woody stems 3-10 feet (1-3 m) tall; stems are branched above; stems and branches are usually covered with straight thorns. The root system is relatively shallow with branching fibrous roots; several vertical roots descend to 4-6 feet (1.2-1.8 m) below the soil surface, a system of rhizomes interconnect the stem bases and are capable of aggressive growth forming dense nearly impenetrable thickets. Regeneration is by vegetative and sexual reproduction. Vegetative growth is sprouts from the root crowns and rhizome system. Stems that bend and touch soil can develop adventitious roots and then develop aerial stems and are capable of surviving as independent plants. Sexual reproduction is from perfect bisexual fragrant showy flowers with both male and female organs that emerge during May-July. Pollination is by insects. The fruit is a hip that remains on the plant after the leaves have fallen. The seeds are achenes and distribution is by birds and mammals. Seeds can survive in the seed bank several years, however, there is little seedling growth and establishment. Fire top kills aerial stems and activates sprout growth from the root crowns and rhizomes. This summary information on growth development and regeneration of western wild rose was based on the works of Stevens 1963, Great Plains Flora Association 1986, Mozingo 1987, Hauser 2006b, Larson and Johnson 2007, Stubbendieck et al. 2011, and Pavek and Skinner 2013.

White spiraea, *Spiraea alba* Du Roi, is a member of the rose family, Rosaceae, and is a native, perennial, deciduous, woody shrub. Aerial growth has numerous erect fine stems with many branches 2-4 feet (6-12 dm) tall. The root system includes the

development of rhizomes that can spread and form clonal colonies. Regeneration is by vegetative and sexual reproduction. Vegetative growth is sprouts from the root crowns and rhizomes. Sexual reproduction is from perfect bisexual fragrant flowers with both male and female organs that emerge during June-July. Seeds mature during August-September. Fire top kills aerial stems and activates sprout growth from the root crowns and rhizomes. This summary information on growth development and regeneration of white spiraea was based on the works of Stevens 1963, and Great Plains Flora Association 1986.

Leadplant, *Amorpha canescens* Pursh, is a member of the legume (bean) family, Fabaceae, and is a native, perennial, deciduous, warm season shrub or subshrub that is drought tolerant and winter hardy. Aerial growth has one to several erect or ascending stems with spreading branches 1-3 feet (3-9 dm) tall. Stems arise from a woody stem base singly or clustered; young stems are not woody, and old stems are woody and persistent. The root system has a taproot and has branched vertical roots that can descend down to 7-20 feet (2-5 m) deep; branched horizontal roots extend 4-5 feet (1-1.5 m) away from the root crown; some secondary lateral roots extend outward for 16.5 feet (5 m). Roots develop nodules for symbiotic rhizobia bacteria that can fix soil air nitrogen. A rhizome system interconnects a few to several root crowns and can form clonal colonies. Regeneration is by vegetative and sexual reproduction. Vegetative growth is sprouts from the root crowns and rhizome system. Sexual reproduction is from a compound cluster of one petaled perfect bisexual flowers with both male and female organs that emerge during July. Flowers are obligate outcrossers and are pollinated by bees, beetles, and other insects. Enormous numbers of flowers and seeds are produced per plant. Fruit is an indehiscent legume pod with one small seed that matures during August-September. Seedlings do not compete well with grasses. Fire top kills aerial stems and activates sprout growth from the root crowns and rhizomes. Clonal colonies expand in size, and stem densities greatly increase post fire. This summary information on growth development and regeneration of leadplant was based on the works of Stevens 1963, Great Plains Flora Association 1986, Johnson and Larson 2007, Stubbendieck et al. 2011, Fryer 2011, and Casey 2011.

False indigo, *Amorpha fruticosa* L., is a member of the legume (bean) family, Fabaceae, and is a native, perennial, deciduous shrub. Aerial growth has clustered stems arising from a stem base; stems with branches above form a bushy crown 3-10 feet

(1-3 m) tall. The root system has extensive spreading lateral roots that interconnect the stem bases and can form sizeable clonal colonies. Roots develop nodules for symbiotic rhizobia bacteria that can fix soil air nitrogen. Regeneration is by vegetative and sexual reproduction. Vegetative growth is sprouts from the root crowns and lateral root system. Sexual reproduction is from a cluster of one petaled perfect bisexual scented flowers with both male and female organs that emerge during late June-July. Pollination is by insects. Fruit is a legume pod with one small seed that matures during August. Fire top kills aerial stems and activates sprout growth from the root crowns and the lateral roots. This summary information on growth development and regeneration of false indigo was based on the works of Stevens 1963, Great Plains Flora Association 1986, Moore 2006, and Larson and Johnson 2007.

Dwarf wild indigo, *Amorpha nana* Nutt., is a member of the legume (bean) family, Fabaceae, and is a native, perennial, deciduous shrub. Aerial growth has erect to ascending stems with branches above forming a crown 8-16 inches (2-4 dm) tall. The root system has extensive spreading lateral roots and has development of a rhizome system. Regeneration is by vegetative and sexual reproduction. Vegetative growth is sprouts from the root crowns, lateral roots, and rhizomes. Sexual reproduction is from solitary racemes with dense one petaled perfect bisexual flowers with both male and female organs that emerge during late June-July. Fruit is a legume pod with one small seed. Fire top kills aerial stems and activates sprout growth from the root crowns, lateral roots, and rhizomes. This summary information on growth development and regeneration of dwarf wild indigo was based on the works of Stevens 1963, Great Plains Flora Association 1986, and Johnson and Larson 2007.

Wild licorice, *Glycyrrhiza lepidota* Pursh, is a member of the legume (bean) family, Fabaceae, and is a native, perennial plant. Aerial growth has annual erect herbaceous stems 1-3.5 feet (3-10 dm) tall arising from deep, extensive woody rhizome systems. Older stems deposit lignin in cell walls resulting in stiff fibrous structure but does not form true wood. Stems die back to ground level in fall. The root system has deep extensive fleshy roots and has a deep woody rhizome system with many branches extending several feet; the rhizome systems have a tremendous capacity to produce sprouts that can form large clonal colonies. Regeneration is by vegetative and sexual reproduction. Vegetative growth is sprouts from the extensive deep woody rhizome system. Sexual reproduction is from racemes with numerous perfect

bisexual flowers with both male and female organs that emerge during July-August. Fruit is a legume pod with 3-5 seeds; the pod is covered with burlike hooked prickles that help distribution by animals. Large quantities of seeds are produced with low germination rates. Fire top kills aerial stems and activates sprout growth from the deep woody rhizome system. This summary information on growth development and regeneration of wild licorice was based on the works of Stevens 1963, Great Plains Flora Association 1986, Esser 1994a, Stubbendieck et al. 2003, Johnson and Larson 2007, and Wynia ND.

Silverberry, wolfwillow, *Elaeagnus commutata* Bernh., is a member of the oleaster family, Elaeagnaceae, and is a native, long lived perennial, deciduous shrub that is shade intolerant, somewhat drought resistant, and requires soil disturbance that removes grass competition to become established. Aerial growth has erect woody stems 3.3-13 feet (1-4 m) tall, with compact branches and no thorns; single stems arise from a stem base connected by an extensive rhizome system. The root system has several vertical and lateral roots spreading from each stem base. These branched roots develop nodules for symbiotic rhizobia bacteria that can fix soil air nitrogen. A complex branched rhizome system interconnects numerous stem bases, each with one aerial stem, forming loose clonal colonies. Occasionally, rhizomes will grow above soil level and become stolons. Regeneration is by vegetative and sexual reproduction. Vegetative growth are single sprouts from a rhizome branch end. Sexual reproduction is mostly from perfect bisexual scented flowers with both male and female organs that emerge during mid June. Pollination is by insects. Fruit is drupelike. Seed is dispersed by birds. Fire top kills or seriously damages aerial stems and activates sprout growth from the rhizomes and sometimes from the stem bases. Stem density increases, however, cover is usually decreased for several years post fire. This summary information on growth development and regeneration of silverberry was based on the works of Stevens 1963, Great Plains Flora Association 1986, Esser 1994b, and Nesom 2006c.

Buffaloberry, *Shepherdia argentea* (Pursh) Nutt., is a member of the oleaster family, Elaeagnaceae, and is a native, perennial (7-32 years), deciduous, cool season large shrub that is drought hardy, winter hardy, and shade intolerant. Aerial growth has numerous erect stems 7-17 feet (2-5 m) tall with irregular spreading to ascending branches. Older twig ends have opposite pairs of sharp thorns. Stem bases are connected by a complex network of rhizomes that can form dense impenetrable clonal

thickets. The root system has several vertical and lateral roots at each stem base. These branched roots develop nodules for symbiotic rhizobia bacteria that can fix soil air nitrogen. Most roots occur within the top 4 feet (1.2 m) of soil, with a maximum depth to 5.8 feet (1.8 m) deep, and with the longest lateral root extending 22 feet (6.7 m) outward. An extensive system of rhizomes interconnect numerous stem bases forming unisexual clonal thickets. The longest rhizome connecting two stem bases was 20 feet (6 m) long. Regeneration is by vegetative and sexual reproduction. Vegetative growth is sprouts from a rhizomes and from adventitious buds on the root crowns. Sexual reproduction is from dioecious imperfect unisexual petalless flowers with separate male and female organs on different clonal plants emerging during late April-May before the leaves. Pollination is by insects, primarily bees. Fruit is drupelike and has one seed that matures during August-September and remains on the plant until spring or until eaten and dispersed by birds. Fire top kills or seriously damages aerial stems and activates sprout growth from rhizomes and root crowns. Stem density increases, however, cover is usually decreased for several years post fire. This summary information on growth development and regeneration of buffaloberry was based on the works of Stevens 1963, Great Plains Flora Association 1986, Esser 1995, Knudson 2006, Johnson and Larson 2007, and Stubbendieck et al. 2011.

Fragrant sumac, *Rhus aromatica* Ait., is a member of the cashew (sumac) family, Anacardiaceae, and is a native, perennial, deciduous with winter dormancy, cool season shrub. Fragrant sumac is a highly variable species with three recognized varieties and is primarily distributed throughout North America east of the US Rocky Mountains. Skunkbush is a closely related highly variable species with six recognized varieties and is primarily distributed throughout North America west of the Mississippi River. The ranges of these two similar species overlap in the Great Plains of the United States and Canada and it is extremely difficult to differentiate between these two plants in the field. For fragrant sumac, aerial growth has numerous stems arising from stem bases; the stems have many slender ascending branches forming an irregular crown 3-7 feet (1-2 m) tall. The three lobed leaves have a disagreeable odor when bruised. The root system is shallow and extensive. A rhizome system interconnects the stem bases forming clonal thickets. Regeneration is by vegetative and sexual reproduction. Vegetative growth is sprouts from the rhizomes, lateral roots, and root crowns. Stems that are bent and touch soil can develop adventitious

roots; aerial sprouts can then develop from the resulting new stem bases. Sexual reproduction is mostly from polygamodioecious imperfect unisexual flowers with separate male and female organs on different clonal plants emerging during late May. A few perfect bisexual flowers may be found on the same plants. Pollination is by insects, primarily bees. The fruit is a one seeded drupe that matures during September and persists on the plant until eaten and dispersed by birds and small mammals. Fire top kills aerial stems and activates vigorous sprout growth from the rhizomes that are deep enough to be protected by soil. Sprouts also develop from surviving lateral roots and the root crowns. This summary information on growth development and regeneration of fragrant sumac was based on the works of Great Plains Flora Association 1986, Nesom 2003b, Taylor 2004, Larson and Johnson 2007, and Stubbendieck et al. 2011.

Skunkbush, *Rhus trilobata* Nutt., is a member of the cashew (sumac) family, Anacardiaceae, and is a native, perennial, deciduous, cool season shrub that is intolerant of flooding and high water tables. Skunkbush is a highly variable species with six recognized varieties and is primarily distributed throughout North America west of the Mississippi River. Fragrant sumac is a closely related highly variable species with three recognized varieties and is primarily distributed throughout North America east of the US Rocky Mountains. The ranges of these two similar species overlap in the Great Plains of the United States and Canada and it is extremely difficult to differentiate between these two plants in the field. For skunkbush, aerial growth has numerous stems arising from stem bases; the stems have many irregular spreading branches forming a dense rounded crown 2-6.5 feet (0.6-2 m) tall and with a wider diameter. The three lobed leaves have a disagreeable odor when bruised. The root system has a taproot and has deep extensively branched fibrous roots. A shallow spreading woody rhizome system interconnects the numerous stem bases forming patches of clonal thickets 20-30 feet (6-9 m) across. Individual rhizomes can live for more than 30 years. Regeneration is by vegetative and sexual reproduction. Vegetative growth is sprouts from the rhizomes and root crowns. Sexual reproduction is mostly from polygamodioecious imperfect unisexual flowers with separate male and female organs located on different plants that emerge during late May-June. Pollination is presumably by small mammals. The fruit is a one seeded drupe that matures by October and persists on the plant until eaten and dispersed by birds and small mammals. Individual plants have low seed production. Seeds have poor germination rates

and seedling establishment is rare. Fire top kills aerial stems and activates vigorous sprout growth from the rhizomes, with some sprout development from adventitious buds on the roots crowns. This summary information on growth development and regeneration of skunkbush was based on the works of Stevens 1963, Great Plains Flora Association 1986, Mozingo 1987, Nesom 2003c, Anderson 2004c, and Larson and Johnson 2007.

Western snowberry, wolfberry, buckbrush, *Symphoricarpos occidentalis* Hook., is a member of the honeysuckle family, Caprifoliaceae, and is a native, perennial, deciduous, cool season shrub. Aerial growth has few to several erect flexible stems arising from a woody stem base 1-3 feet (0.3-1 m) tall. Branches develop on the top half of the main stem. Starting the second growing season, one new branch develops from the previous years branch, and a single new branch develops each consecutive growing season. The age of each stem can be determined by the number of branches on that stem. Leaves, flowers, and fruits develop only on current years branches. The root system has vertical roots at each stem base that descend 5 feet (1.5 m) deep, with lateral roots extending 30 inches (76 cm) outward. Several rhizomes develop from each stem base that are about 14 inches (36 cm) deep and extend about 3 feet (1 m) outward with little or no branches; one to several new stems develop at the rhizome ends during spring, followed by the development of a new stem base at that site. The distance between stem bases is about the effective distance of apical hormone control of meristematic buds. The rhizomes between stem bases have opposite paired buds at about 1 inch (2.5 cm) increments, with each bud having the potential to develop into a sprout after apical hormonal control is disrupted. Regeneration is by vegetative and sexual reproduction. Vegetative growth is sprouts from the rhizomes and stem bases. Aggressive development by rhizome and stem bases form dense low colonies that are 3-700 feet (1-200 m) in diameter. Sexual reproduction is from racemes developing from the ends of branches and from the axils of leaves with dense clusters of perfect bisexual flowers with both male and female organs that emerge during late June-August. Pollination is by insects. Fruit is a two nutlet drupe that matures during August-September and is persistent on the plant until eaten and dispersed by birds and small mammals. Seedling establishment is rare. Fire easily top kills aerial stems and activates vigorous sprout growth from the opposite paired buds on rhizomes and from the buds on stem bases. Mowing that cuts off the top half of the stems and heavy browsing removes the apical hormonal control and also activates sprout growth from the rhizomes

and stem bases. This summary information on growth development and regeneration of western snowberry was based on the works of Stevens 1963, Great Plains Flora Association 1986, Stubbendieck et al. 2003, Manske 2006a, Hauser 2007, Johnson and Larson 2007, and Stubbendieck et al. 2011.

Fourwing saltbush, *Atriplex canescens* (Pursh) Nutt., is a member of the goosefoot family, Chenopodiaceae, and is a native, long lived perennial (29-100 years), variable from deciduous to evergreen, rapidly evolving, warm season shrub that is resistant to salt, cold, and drought conditions. Aerial growth has several stout, erect, rigid, brittle stems heavily branched forming a round crown to 10 feet (3 m) tall; lateral branches have spines. The root system has a taproot that extends down to 20 feet (6 m) deep and has numerous small lateral feeder roots. Most ecotypes have rhizomes and some ecotypes do not have rhizomes. The populations with rhizomes form large dense colonies. Regeneration is by vegetative and sexual reproduction. Vegetative growth is sprouts from the root crowns, stem bases, branches, and rhizomes. Some ecotypes do not sprout from the root crowns and rhizomes. Sexual reproduction is mostly from dioecious, imperfect, unisexual flowers that emerge during June-August with male and female organs on separate plants. Pollination is by wind. The four wings develop with the fruit from two small bracts that enclose the female reproductive organ. Fruits are achenes with four wings that mature during fall. Seedling establishment is usually good on disturbed arid lands. Fire can top kill plants and stimulate vigorous sprouting from root crowns and rhizomes. Browsing activates sprout growth from stem bases and from branches. This summary information on growth development and regeneration of fourwing saltbush was based on the works of Great Plains Flora Association 1986, Mozingo 1987, Howard 2003b, Johnson and Larson 2007, Stubbendieck et al. 2011, and Ogle et al. 2012a.

Moundscale saltsage, *Atriplex gardneri* (Moq.) Dietr., (*Atriplex nuttallii*), is a member of the goosefoot family, Chenopodiaceae, and is a native, perennial, suffruticosa (somewhat woody) warm season subshrub that is drought tolerant. Aerial growth has many herbaceous stems not over 20 inches (50 cm) tall arising from a decumbent woody stem base forming a large dense spreading tuft or sometimes a nearly prostrate mat. The root system has vertical roots that descent 2-4.5 feet (0.6-1.4 m) deep and has lateral roots that spread 5-7 feet (1.5-2.1 m) outward. Regeneration is by vegetative and sexual reproduction. Vegetative growth is sprouts from the woody stem bases, root crowns, and from

shallow lateral roots. Sexual reproduction is from typically dioecious, imperfect, unisexual flowers with male and female organs on separate plants. Seed production is abundant and may remain on the plants for two years. The long lived seeds are wind dispersed. Plant chemical composition contains high ash minerals causing low flammability and slow burn resulting in a high tolerance of fire with little tissue death. When top kill from fire occurs, prolific sprouting is activated on the stem bases, root crowns, and lateral roots. This summary information on growth development and regeneration of moundscale saltsage was based on the works of Stevens 1963, Great Plains Flora Association 1986, Reed 1993, and Stubbendieck et al. 2011.

Winterfat, *Krascheninnikovia lanata* (Pursh) Meeuse & Smit, (*Eurotia lanata*), is a member of the goosefoot family, Chenopodiaceae, and is a native, long lived perennial (to 136 years), cool season subshrub that is tolerant of cold and saline conditions, and intolerant of shade, acidic soils, and flooding. Aerial growth has numerous erect annual secondary herbaceous stems 1-2 feet (0.3-0.6 m) tall arising from a central woody stem base that develops from a woody root crown. Two sets of leaves are produced each growing season. Spring buds produce large succulent leaves with sparse hairs; during midsummer, the spring leaves die and are gradually replaced by smaller compact leaves densely covered with hairs. By early August, almost all photosynthesis and transpiration has ceased. The small leaf foliage is retained through the winter and contains greater than 10% crude protein. The root system has a deep taproot that descends to 25 feet (7.6 m) in depth and has numerous branching lateral roots that remain within the top 3.3 feet (1 m) of soil extending 4.8 feet (1.5 m) outward. Regeneration is by vegetative and sexual reproduction. Vegetative growth is by sprouts from adventitious buds on the root crown and by aerial stem growth from perennating buds on the central woody stem base located at or just above the ground surface. Sexual reproduction is mostly from monoecious, imperfect, unisexual, inconspicuous flowers that emerge during June with separate male and female organs on the same plant. The fruit, which is an utricle, ripen during August. Seeds are produced only during wet growing seasons, dispersed short distances by wind, and have high germination rates in moist soil, however, establishment of seedlings is difficult. Moderate browsing activates sprouts from buds on the central stem base. Damage or top kill by fire activates sprouts from buds on the root crown. Severe fires can kill parts or all of the stem base and root crown. This summary information on growth

development and regeneration of winterfat was based on the works of Stevens 1963, Great Plains Flora Association 1986, Mozingo 1987, Carey 1995, Johnson and Larson 2007, Stubbendieck et al. 2011, and Ogle et al. 2012b.

Greasewood, *Sarcobatus vermiculatus* (Hook.) Torr., is a member of the goosefoot family, Chenopodiaceae, and is a native, long lived perennial, rapid growing, deciduous, warm season shrub that is tolerant of drought, sodic soils, saline soils, high water table, and prolonged flooding, and is a phreatophyte. Aerial growth has multiple rigidly stout brittle stems arising from a large root crown; the stems have many spreading branches that form a large clonal clump with an irregular to rounded crown 1-10 feet (0.3-3 m) tall; the ends of the small branches taper to sharp thorns. The root system has numerous taproots with branches that can penetrate to the edge of the ground water table down to 20-57 feet (6-17 m) below the surface, and has numerous dense shallow lateral roots that extend many yards (meters) beyond the canopy. Regeneration is by vegetative and sexual reproduction. Vegetative growth is from sprouts developing from adventitious buds on the root crown and on the shallow lateral roots. Sexual reproduction is mostly from monoecious, imperfect, unisexual, nonshowy flowers with separate male and female organs on the same plant that emerge during July-August. These separate male and female flowers on the same plant are dichogamous and mature at different times to prevent selffertilization. Pollination is by wind. The fruit is an achene and matures during late summer. Seed production is usually low. The seeds have long wings and are dispersed by wind. Seed germination rate is usually high. Low to moderate severity fire can cause top kill and activate sprout development from buds on the root crown and on the shallow lateral roots. Severe fire on dry soil can damage or kill the root crown and some of the shallow lateral roots. This summary information on growth development and regeneration of greasewood was based on the works of Stevens 1963, Great Plains Flora Association 1986, Mozingo 1987, Anderson 2004a, Benson et al. 2007, Johnson and Larson 2007, and Stubbendieck et al. 2011.

Green sage, tarragon, *Artemisia dracunculus* L., is a member of the aster (sunflower) family, Asteraceae, and is a native, perennial, deciduous, warm season subshrub-shrub that is drought tolerant and intolerant of shading. Aerial growth has unbranched reddish stems arising from thick horizontal rhizomes; stems are single until tip is removed by browsing, after which stem clusters form that are 1.5-3 feet (4.5-9.1 m) tall. The root system

has large quantities of adventitious roots that contain cork formed within the xylem tissue that can descend to 7 feet (2.1 m) in depth; thick rhizomes develop horizontally below the soil surface. Symbiotic associations with mycorrhiza fungi develop on the roots. Regeneration is by vegetative and sexual reproduction. Vegetative growth is sprouts from rhizomes. Sexual reproduction is from numerous inconspicuous flowers clustered on small heads that emerge during August-September. Pollination is by wind. Seed is a small achene. Fire top kills aerial stems; the rhizomes are protected by the soil, sprouts from rhizomes develop following fire. This summary information on growth development and regeneration of green sage was based on the works of Stevens 1963, Great Plains Flora Association 1986, Stubbendieck et al. 2003, Groen 2005a, Hurteau 2006a, and Johnson and Larson 2007.

Fringed sage, *Artemisia frigida* Willd., is a member of the aster (sunflower) family, Asteraceae, and is a native, perennial, deciduous, warm season shrub or subshrub that is drought resistant. Aerial growth has solitary to numerous (after tip of solitary stem has been browsed), erect, herbaceous, annual flowering stems 3-16 inches (7.6-40 cm) tall arising from a tough, woody crown base; stems and leaves are tomentose, covered with dense soft gray silky hairs. The root system has a taproot 0.4 inches (10 mm) in diameter that can descend to 5.3 feet (1.6 m) in depth. Many vertical roots originate from the root crown and descend vertically or obliquely to the depth of the taproot. Many horizontal lateral roots remain within the top 35 inches (89 cm) of soil, produce numerous branches, and can extend 10 inches (25 cm) outward. Symbiotic associations with mycorrhiza fungi develop on the roots. The woody crown base produces numerous branched short rhizomes; numerous aerial shoots can develop from the rhizomes forming a dense tuft or mat. Regeneration is by vegetative and sexual reproduction. Vegetative growth is sprouts from the crown base and rhizomes. Sexual reproduction is from numerous inconspicuous tiny flowers clustered on small greenish heads that emerge during July-August. Pollination is by wind. The seed is a small achene. No seeds are produced during dry growing seasons; under favorable moisture, less than half of the plants produce seed. Fire top kills aerial stems; sprouts from the crown bases and rhizomes develop from less than 50% of the plants post fire. Plant size, crown cover, and density have sometimes been reduced for a few growing seasons post fire. This summary information on growth development and regeneration of fringed sage was based on the works of Stevens 1963, Great Plains Flora Association

1986, Stubbendieck et al. 2003, McWilliams 2003b, Stevens 2006, Johnson and Larson 2007, Stubbendieck et al. 2011, and Shultz 2012.

White sage, *Artemisia ludoviciana* Nutt., is a member of the aster (sunflower) family, Asteraceae, and is a native, perennial, deciduous, warm season subshrub-shrub. Aerial growth has solitary to numerous, erect, herbaceous stems 0.5-3 feet (15-91 cm) tall arising from thick, woody rhizomes; the portions of the rhizome with an aerial stem develop into a thick stem base; stems and leaves are mostly tomentose, covered with soft white fuzzy hairs. Stems die back to the rhizome during winter. The root system has extensive fibrous vertical roots than can descend to 27.5 inches (70 cm) deep. Horizontal lateral roots branch and become intertwined forming a firm mesh in the upper 2 inches (5 cm) of soil. The coarse woody rhizomes remain between 1-5.5 inches (2.5-14 cm) deep forming a dense network that can reach 6.5-10 feet (2-3 m) in diameter; clonal plants with aggressive rhizomes can extend further and develop colonies with 50 foot (15 m) diameters. The colonies develop thicker stem densities with age. Regeneration is by vegetative and sexual reproduction. Vegetative growth is sprouts from rhizomes and older stem bases. Sexual reproduction is from numerous inconspicuous flowers clustered on small heads that emerge during August-September. Pollination is by wind. The seed is a small achene. Fire top kills aerial stems; sprouts develop from rhizomes and older stem bases. This summary information on growth development and regeneration of white sage was based on the works of Stevens 1963, Great Plains Flora Association 1986, Stubbendieck et al. 2003, Anderson 2005, Stevens and Roberts 2006, Johnson and Larson 2007, and Stubbendieck et al. 2011.

Sand sagebrush, *Artemisia filifolia* Torr., is a member of the aster (sunflower) family, Asteraceae, and is a native, perennial, deciduous, warm season shrub. Aerial growth has a main stem arising from a stem base; numerous fine branches form an irregular to rounded crown 1.5-3 feet (0.5-1 m) tall. The root system has a taproot and extensive lateral roots that can stabilize the plant in deep sand. Regeneration is by vegetative and sexual reproduction. Vegetative growth is sprouts from the stem base. Sexual reproduction is from numerous inconspicuous flowers clustered on small heads that emerge during August-October. Pollination is by wind. The seed is a small achene. Fire top kills aerial stems; sprouts from the stem base develop post fire. This summary information on growth development and regeneration of sand sagebrush was based on the works of Great

Plains Flora Association 1986, Stubbendieck et al. 2003, McWilliams 2003a, Johnson and Larson 2007, Stubbendieck et al. 2011, and Shultz 2012.

Plains silver sagebrush, *Artemisia cana* Pursh, is a member of the aster (sunflower) family, Asteraceae, and is a native, long lived perennial, late deciduous with a few leaves remaining through winter, warm season shrub that is flood tolerant. Aerial growth has several decumbent to ascending twisted stems arising from a large stem base; stems have numerous twisted branches forming an irregular rounded crown 1.3-3.3 feet (0.4-1 m) tall, and with a width about the same size. Current years twigs and leaves are tomentose, covered with dense white hairs that have a silvery reflectance in sunlight. The root system has a deep taproot that can descend to 7-10 feet (2-4 m) deep, and has extensive lateral roots. Stout shallow rhizomes extend outward to 3.4 feet (1 m) from the stem base; the rhizomes have numerous buds with the potential to produce about 52 sprouts. Regeneration is by vegetative and sexual reproduction. Vegetative growth is sprouts from vertical stem bases and from horizontal rhizomes. A rhizome network interconnects the stem bases; aggressive development can form large clonal colonies. Segments of decumbent stems that touch soil can develop adventitious roots followed by the development of aerial sprouts that can result in a greatly enlarged colony. Sexual reproduction is from numerous small inconspicuous yellowish flowers clustered on small heads that emerge during August-September. The plants strong odor sometimes reaches irritating levels. Outcross pollination is by wind. The fruit is single seeded; the seed is a small achene that is dispersed by wind and can be transported great distances along with drifting snow. Plants produce large quantities of seed that have high germination rates, however, seedling establishment and survival are low. Fire, mowing, and browsing damage the aerial stems that removes the hormone controlled apical dominance and causes activation of sprout growth from buds on the stem bases, rhizomes, and roots. This summary information on growth development and regeneration of plains silver sagebrush was based on the works of Stevens 1963, Great Plains Flora Association 1986, Mozingo 1987, Howard 2002, Manske 2006b, Johnson and Larson 2007, Stubbendieck et al. 2011, and Shultz 2012.

Wyoming big sagebrush, *Artemisia tridentata* Nutt. subsp. *wyomingensis* Beetle & Young, is a member of the aster (sunflower) family, Asteraceae, and is a native, long lived perennial (usually 26-57 years, up to 150 years), semideciduous, warm season shrub that is drought

tolerant and is not fire resistant. Aerial growth has several twisted stems arising from a stem base; stems have numerous stout branches forming uneven rounded crowns 18-30 inches (46-76 cm) tall. The stems grow in irregular shapes because the annual rings of wood laid down are not uniform around the center of the stem. Two types of leaves are produced each year. Large leaves that have high rates of photosynthesis develop during spring and are active during late May to early June. Most new stem growth occurs during the first two weeks of June. The large leaves die and drop off by late June and are replaced by small dense leaves that arise from the axils of the large spring leaves. Activity in the small leaves stops at the beginning of the cold season. Many of the mature small leaves remain on the plant throughout the winter. The next spring, the few living small leaves remaining on the stems resume some activity until new large spring leaves appear. The root system has one or more well developed taproots that can descend 3.3-13 feet (1-4 m) deep, and has numerous extensive lateral roots that spread radially outward to 5 feet (1.5 m), grow near the soil surface, and can absorb the moisture from light rainfall events. Symbiotic associations with mycorrhizae fungi develop on the roots. Regeneration is by sexual reproduction; big sagebrush does not root sprout after fire. Sexual reproduction is from numerous small inconspicuous perfect flowers that emerge during August-September. Outcross pollination is by wind. Seeds are small achenes. Seedlings have low competitiveness with grasses and can only establish in areas without grass cover. Fire and mechanical brush beating cause severe damage to aerial stems and can completely kill the plant; widespread treatments can nearly eliminate the shrub from an area for many years. This summary information on growth development and regeneration of Wyoming big sagebrush was based on the works of Stevens 1963, Great Plains Flora Association 1986, Mozingo 1987, Howard 1999, Tilley et al. 2005, Johnson and Larson 2007, Stubbendieck et al. 2011, and Shultz 2012.

Rubber rabbitbrush, *Ericameria nauseosa* (Pallas ex Pursh) Nesom & Baird, (*Chrysothamnus nauseosus*), is a member of the aster (sunflower) family, Asteraceae, and is a native, perennial, deciduous with die back of annual aerial stems, warm season shrub. Aerial growth has a short stout woody trunk arising from a stem base; numerous straight, limber, ascending to spreading, annual stems with few branches develop from the woody trunk forming a large rounded broom shaped crown 1-5 feet (0.3-1.5 m) tall and 1-3.3 feet (0.3-1 m) wide. The root system has a deep taproot and has extensive lateral roots. Regeneration is by vegetative and sexual

reproduction. Vegetative growth is primarily sprouts from epicormic (dormant) buds on the main woody trunk or perennial stem and some sprouts develop from adventitious buds on the root crown. Sexual reproduction is from small perfect flowers with both male and female organs in numerous yellow heads in rounded to flattopped clusters that emerge during late July-August. The seed is a small light achene with pappus of fine tufts of hair which aid in dispersal by wind. Foliage and annual stems have a high resin content, are highly flammable, and readily consumed by fire, causing top kill. The main woody trunk is typically unharmed, activating rapid to very rapid sprout growth, resulting in larger robust plants soon after a fire. This summary information on growth development and regeneration of rubber rabbitbrush was based on the works of Stevens 1963, Great Plains Flora Association 1986, Mozingo 1987, Tirmenstein 1999b, Johnson and Larson 2007, Scheinost et al. 2010, and Stubbendieck et al. 2011.

Yellow (green) rabbitbrush, *Chrysothamnus viscidiflorus* (Hook.) Nutt., is a member of the aster (sunflower) family, Asteraceae, and is a native, short lived perennial (12-13 years), deciduous with die back of annual aerial flower stalks, warm season shrub that is drought resistant. Aerial growth has several spreading woody stems arising from a stem base; the woody stems have many brittle, erect, annual flower stalks with many branches that form a compact irregular rounded crown 8-40 inches (20-102 cm) tall. The root system has a taproot that can descend to 1.9 feet (0.6 m) deep, and has extensive lateral roots. Regeneration is by vegetative and sexual reproduction. Vegetative growth is sprouts from epicormic (dormant) buds located below the soil surface on the stem base and from perennating buds on the woody stems. Sexual reproduction is from small flowers clustered in heads that are borne in compact terminal cymes that emerge during August-September. The seed is a small achene dispersed long distances by wind. Seedling mortality is high. Foliage and annual stalks have a high resin content, are highly flammable, and readily consumed by fire, causing top kill. The main woody stem is usually not harmed, activating sprout growth from buds on the main woody stem and from the stem base. This summary information on growth development and regeneration of yellow (green) rabbitbrush was based on the works of Great Plains Flora Association 1986, Mozingo 1987, Tirmenstein 1999c, Stubbendieck et al. 2011, and Tilley and St. John 2012.

Broom snakeweed, *Gutierrezia sarothrae* (Pursh) Britt. & Rusby, is a member of the aster (sunflower) family, Asteraceae, and is a native, short

lived perennial (20 years), deciduous with partial die back of annual aerial flower stalks, warm season shrub or subshrub that is drought tolerant and has a high water use efficiency. Aerial growth has a single to several woody decumbent spreading stems at ground level arising from a stem base; the woody stems produce numerous erect fine annual branched stalks that rebranch forming a dense crown 8-28 inches (20-70 cm) tall. The root system has a stout deep woody taproot and has numerous extensive long lateral roots. The lateral roots that grow close to the soil surface can capture moisture from light rainfall events. Regeneration is by vegetative and sexual reproduction. Vegetative growth is sprouts from adventitious buds on the root crown and from perennating buds on the woody decumbent stems. Sexual reproduction is from small flowers clustered in heads that are borne in compact terminal corymbs that emerge during August-October. Pollination is by insects. Seed is an achene dispersed by wind. Aerial parts are highly combustible and are top killed by fire. Sprouts develop from adventitious buds on the root crown and from perennating buds on the woody decumbent stems. This summary information on growth development and regeneration of broom snakeweed was based on the works of Stevens 1963, Great Plains Flora Association 1986, Mozingo 1987, Tirmenstein 1999d, Stubbendieck et al. 2003, Hurteau 2006b, Johnson and Larson 2007, and Stubbendieck et al. 2011.

Great Plains yucca, *Yucca glauca* Nutt., is a member of the agava family, Agavaceae, and is a native, perennial, evergreen monocot, warm season shrub. Aerial growth has a very stout, short woody stem that arises from a stem base; the stem can branch and develop one to a few crowns of spirally arranged densely clustered rosette of radiating alternate leaves that are stiff, strongly fibrous, bayonet shaped, with a sharp tip and thready margins. The main stem increases in height as new leaf whorls appear at the center. The root system has a stout taproot that can descend to 20 feet (6 m) in depth and has extensive lateral roots that can extend outwardly for 20-30 feet (6-9 m). An extensive network of rhizomes form a mat 4-24 inches (10-60 cm) below the soil surface that interconnect numerous stem bases; each stem base has one or two large diameter rhizomes. Regeneration is by vegetative and sexual reproduction. Vegetative growth are branches and lateral shoots (ramets) from older main stems that each can develop a full rosette of leaves. New stout stems form from rhizomes and start as a small rosette of leaves. Sexual reproduction is from 15 to 50 perfect drooping showy flowers attached to a raceme 3-5 feet (1-1.5 m) tall that extends well above the

leaves and emerges during June-July. Pollination is by a symbiotic hawk moth. Fruits are capsules maturing during August-September. Seeds are flat and have a small marginal wing. Fire top kills aerial leaves and may damage aerial stems; sprouts develop from surviving portions of the stem and from the rhizomes that were protected by soil. Fire greatly reduces seed viability. This summary information on growth development and regeneration of great plains yucca was based on the works of Stevens 1963, Great Plains Flora Association 1986, Stubbendieck et al. 2003, Groan 2005b, and Johnson and Larson 2007.

Mechanisms of Fire

Presumably, in order for fire to prevent encroachment of woody plants into grasslands, fire would need to prevent woody plant seed production, seedling establishment, and be able to totally destroy established woody plants. The mechanisms by which fire prevents woody plants from encroaching into rangeland was evaluated by describing growth development and sexual and vegetative regeneration characteristics of fifty three of the major woody species that have encroached into native prairie of the Northern Plains (table 1). The growth form of these invasive woody species included 9 (17.0%) trees, 6 (11.3%) small trees or large shrubs, 31 (58.5%) shrubs, and 7 (13.2%) subshrubs. Two woody species with tree growth forms also had reduced shrub growth forms on harsh environments (table 2).

None of the woody species that have invaded into the prairie flora of the Northern Plains originated there. These invasive woody species had affinities to one or two other North American floras; 34.0% of the woody species came from the northern flora, 28.3% of the woody species came from the eastern flora, 37.7% of the woody species came from the western flora, and 7.5% of the woody species came from the Great Basin flora (table 2) (Zaczkowski 1972, Mozingo 1987).

All of the invasive woody species, 53 (100%), regenerate by sexual reproduction and produce seeds (table 3). Most of the woody species produce seeds that have low germination rates, seedlings that have low competitiveness with grass sod, and seedlings that mostly have low to rare establishment rates. Woody plant seedling establishment into grassland ecosystems generally requires some type of preceding activity that disrupts the continuity of the grassland structure providing open bare moist soil spots with full sunlight that are then available for transported woody plant seeds to land and develop. Without the coincidental damage

to grassland structure, woody plant seedlings would not become established into rangeland. Grassland fires have a tendency to increase the number and size of open soil spots for one or two growing seasons rather than reduce the bare soil spots.

Prevention of woody species encroachment into rangeland with fire would require complete destruction of each plant that had been able to become established. However, total plant kill caused by fire occurs only in five, 9.4%, of the woody species (table 3); four of the species are evergreen conifers, two are trees and two are shrubs; the two shrubs are usually totally consumed by fire because they contain flammable resins; only one, 1.9%, deciduous shrub, big sagebrush, has total plant kill from fire. The vast majority, 48 (90.6%), of the invasive woody species are not totally killed by fire, however, these plants do receive enough injury from fire that results in top kill of the aboveground stems and foliage (table 3). Top kill of the woody species is a temporary condition for variable lengths of time depending on the recovery mechanisms of the different species. Three (5.7%) woody tree species have thick trunk bark that insulates the cambium tissue from heat damage preventing top kill of mature plants from light to moderate severe fires; two of these trees are deciduous and one is a conifer (table 3).

Five (9.4%) woody species lack vegetative buds and do not produce vegetative sprouts following fire (table 4); four of these are coniferous species and one is a deciduous shrub. The partial damage or top kill caused by fire activates sprout growth from vegetative buds located on surviving plant parts of 48 (90.6%) of the invasive woody species (table 3). Vegetative buds can be located on the root crowns, the stem bases, the rhizomes, the stolons, the lateral roots, or on the trunk of woody species. Eight (15.1%) of the woody species have vegetative buds at only one location, twenty seven (50.9%) have vegetative buds at two locations, eleven (20.8%) have vegetative buds at three locations, and two (3.8%) have vegetative buds at four different locations (table 4). Vegetative buds are located on the root crowns of 56.6% of the species, on the stem bases of 37.7% of the species, on the rhizomes of 43.4% of the species, on the stolons of 5.7% of the species, on the lateral roots of 34.0% of the species, and on the trunk of 17.0 % of the woody species (table 4). In addition, thirteen (24.5%) of the woody species have the ability to develop adventitious roots on aerial stems that have by some mechanism been bent down with part of the stem touching soil (table 4).

Five woody species, common juniper,

creeping juniper, Rocky Mountain juniper, ponderosa pine, and big sagebrush, are usually destroyed with total plant kill by fire. The other 48 woody species are deciduous trees and shrubs and are only temporarily set back with partial damage or top kill of the aerial stems by fire; these woody species recover and replace the damaged parts with sprout growth from vegetative buds.

Fire had been a recurrent environmental factor on the prairies of the Northern Plains prior to 1862. Fire damages, kills, or consumes the aboveground parts of grasses, forbs, shrubs, and trees. The severity of the effects of fire on plant species varies with the amount of soil water, the quantity of fine fuel, and the seasonal period and frequency of the burns. The historical fire return interval has been estimated to have been 3 to 4 years for tall grass prairie, 5 to 10 years for moist mixed grass prairie, and around 25 years for dry mixed grass prairie (including the northern short grass prairie) (Wright and Bailey 1982, Bragg 1995). The seasonal period when fires occurred was interpreted from a review of extensive historical grassland fire information by Higgins (1986). He found that 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 plausible practice was burning the mixed grass prairie during late summer and fall and the tall grass prairie during spring. Lightning-set fires occurred during summer and early fall, with 73% occurring during July and August (Higgins 1986). The Northern Plains prairie has probably had considerably more late season fires, occurring after mid July, than spring or early summer fires.

Short fire return intervals and complete burns would prevent trees and some shrubs from maturing to seed producing age. Long fire return intervals and partial or incomplete burns would permit trees and shrubs to develop for a long enough time to mature and be able to produce seeds. Prevention of woody species seeds from being dispersed onto Northern Plains prairies would require fire restriction of annual seed production of each woody species growing in an area that was greater than the distance of seed distribution. Fire can not prevent woody species seed production and seed dispersal into prairie of the Northern Plains.

Forty eight (90.6%) of the major woody species that have become established on grasslands are not totally killed by fire and all of these species can produce vegetative sprouts after fire has caused severe damage or top kill to the aboveground parts.

Woody species that have become established in grassland communities and that can reproduce by vegetative sprouts can not be eliminated from that plant community by fire alone; however, frequent complete burns can temporarily reduce the woody species in size; moreover, many of these woody species greatly increase in stem density two or three years post fire. Interestingly, the aerial parts of woody species that can reproduce by vegetative sprouts have relatively short life spans of around 20 to 100 years, however, the belowground parts that are protected by soil usually have very long life spans of hundreds to thousands of years.

Only five (9.4%) of the major woody species that have become established on Northern Plains grasslands can be totally killed by fire and these 5 species, 4 conifers and 1 deciduous shrub, do not produce vegetative sprouts after the aboveground parts are severely damaged or killed by fire. The only way these five woody species can survive fire is through partial burns or patch fires. Interestingly, the aerial parts of these five woody species that can not reproduce by vegetative sprouts have extremely long life spans, common juniper has a life span to 170 years, creeping juniper has a life span to 140 years, Rocky Mountain juniper has a life span to 250 or 300 years, ponderosa pine has a life span to 300 or 600 years, and big sagebrush has a life span to 150 years.

This study was unable to identify any mechanisms by which fire could assuredly prevent woody species encroachment into rangelands of the Northern Plains. The historical concept that fire prevents woody species encroachment into grassland communities appears to have been based on short term observations that misinterpreted top kill of woody species as total plant kill. Even today, most modern quantitative studies on the effects of fire are based only on short term aboveground plant data. Fire was a recurrent environmental factor on the prairies of the Northern Plains prior to 1862, however, fire has no mechanisms to provide sufficient force that could prevent intrusion of shrubs and trees into grasslands. Now, post Homestead Act, fire, like drought, is a nonessential environmental factor on grassland communities of the Northern Plains.

Table 1. Invasive woody plant species of the Northern Plains prairie.	
Cypress Family	Cupressaceae
Common juniper	<i>Juniperus communis</i> L.
Creeping juniper	<i>Juniperus horizontalis</i> Moench.
Rocky Mountain juniper	<i>Juniper scopulorum</i> Sarg.
Pine Family	Pinaceae
Ponderosa pine	<i>Pinus ponderosa</i> Lawson
Elm Family	Ulmaceae
American elm	<i>Ulmus americana</i> L.
Oak (Beech) Family	Fagaceae
Bur oak	<i>Quercus macrocarpa</i> Michx.
Olive Family	Oleaceae
Green ash	<i>Fraxinus pennsylvanica</i> Marsh.
Willow Family	Salicaceae
Balsam poplar	<i>Populus balsamifera</i> L.
Plains cottonwood	<i>Populus deltoides</i> Bartr. ex Marsh.
Quaking aspen	<i>Populus tremuloides</i> Michx.
Peachleaf willow	<i>Salix amygdaloides</i> Anders.
Beaked willow	<i>Salix bebbiana</i> Sarg.
Coyote willow	<i>Salix exigua</i> Nutt.
Sandbar willow	<i>Salix interior</i> Rowlee
Prairie willow	<i>Salix humilis</i> Marsh.
Birch Family	Betulaceae
American hazelnut	<i>Corylus americana</i> Walt.
Beaked hazelnut	<i>Corylus cornuta</i> Marsh.
Heath Family	Ericaceae
Kinnikinnick	<i>Arctostaphylos uva-ursi</i> (L.) Spreng.

Table 1(cont.). Invasive woody plant species of the Northern Plains prairie.	
Rose Family	Rosaceae
Juneberry	<i>Amelanchier alnifolia</i> Nutt.
Northern hawthorn	<i>Crataegus chrysocarpa</i> Ashe.
Shrubby cinquefoil	<i>Dasiphora floribunda</i> (Pursh) Kartesz
Wild plum	<i>Prunus americana</i> Marsh.
Pin cherry	<i>Prunus pensylvanica</i> L.
Sand cherry	<i>Prunus pumila</i> L.
Chokecherry	<i>Prunus virginiana</i> L.
Prickley wild rose	<i>Rosa acicularis</i> Lindl.
Prairie wild rose	<i>Rosa arkansana</i> Porter.
Smooth wild rose	<i>Rosa blanda</i> Ait.
Western wild rose	<i>Rosa woodsii</i> Lindl.
White spiraea	<i>Spiraea alba</i> Du Roi
Legume (Bean) Family	Fabaceae
Leadplant	<i>Amorpha canescens</i> Pursh
False indigo	<i>Amorpha fruticosa</i> L.
Dwarf wild indigo	<i>Amorpha nana</i> Nutt.
Wild licorice	<i>Glycyrrhiza lepidota</i> Pursh
Oleaster Family	Elaeagnaceae
Silverberry	<i>Elaeagnus commutata</i> Bernh.
Buffaloberry	<i>Shepherdia argentea</i> (Pursh) Nutt.
Cashew (Sumac) Family	Anacardiaceae
Fragrant sumac	<i>Rhus aromatica</i> Ait.
Skunkbush	<i>Rhus trilobata</i> Nutt.
Honeysuckle Family	Caprifoliaceae
Western snowberry	<i>Symphoricarpos occidentalis</i> Hook.

Table 1(cont.). Invasive woody plant species of the Northern Plains prairie.	
Goosefoot Family	Chenopodiaceae
Fourwing saltbush	<i>Atriplex canescens</i> (Pursh) Nutt.
Moundscale saltsage	<i>Atriplex gardneri</i> (Moq.) Dietr.
Winterfat	<i>Krascheninnikovia lanata</i> (Pursh) Meeuse & Smit.
Greasewood	<i>Sarcobatus vermiculatus</i> (Hook.) Torr.
Aster (Sunflower) Family	Asteraceae
Green sage	<i>Artemisia dracunculus</i> L.
Fringed sage	<i>Artemisia frigida</i> Willd.
White sage	<i>Artemisia ludoviciana</i> Nutt.
Sand sagebrush	<i>Artemisia filifolia</i> Torr.
Silver sagebrush	<i>Artemisia cana</i> Pursh
Big sagebrush	<i>Artemisia tridentata</i> Nutt.
Rubber rabbitbrush	<i>Ericameria nauseosa</i> (Pallas ex Pursh) Nesom & Baird.
Yellow rabbitbrush	<i>Chrysothamnus viscidiflorus</i> (Hook.) Nutt.
Broom snakeweed	<i>Gutierrezia sarothrae</i> (Pursh) Britt. & Rusby
Agave Family	Agavaceae
Great Plains yucca	<i>Yucca glauca</i> Nutt.

Table 2. Growth form and North American flora affinity of woody plants that encroach into Rangelands of the Northern Plains.

Woody Plants	Growth Form				Flora Affinity			
	Tree	Sm Tree Lg Shrub	Shrub	Sub Shrub	North	East	West	Great Basin
Common juniper			X		X			
Creeping juniper			X		X			
Rocky Mtn juniper	X						X	
Ponderosa pine	X						X	
American elm	X					X		
Bur oak	X		X			X		
Green ash	X					X		
Balsam poplar	X				X			
Plains cottonwood	X					X		
Quaking aspen	X				X			
Peachleaf willow	X		X		X			
Beaked willow		X			X			
Coyote willow			X				X	
Sandbar willow			X		X			
Prairie willow			X			X		
American hazelnut			X		X	X		
Beaked hazelnut			X		X	X		
Kinnikinnick			X		X			
Juneberry		X			X		X	
Northern hawthorn		X			X			
Shrubby cinquefoil			X		X			
Wild plum		X				X		
Pin cherry		X			X			
Sand cherry			X			X		
Chokecherry		X			X			
Prickly wild rose			X		X			
Prairie wild rose			X				X	

Table 2 (cont.). Growth form and North American flora affinity of woody plants that encroach into Rangelands of the Northern Plains.								
Woody Plants	Growth Form				Flora Affinity			
	Tree	Sm Tree Lg Shrub	Shrub	Sub Shrub	North	East	West	Great Basin
Smooth wild rose			X			X		
Western wild rose			X				X	
White spiraea			X			X		
Leadplant			X			X		
False indigo			X			X		
Dwarf wild indigo			X			X		
Wild licorice				X			X	
Silverberry			X		X			
Buffaloberry			X				X	
Fragrant sumac			X			X		
Skunkbush			X				X	
Western snowberry			X		X		X	
Fourwing saltbush			X					X
Moundscale saltsage				X			X	
Winterfat				X			X	
Greasewood			X					X
Green sage				X			X	
Fringed sage				X			X	
White sage				X			X	
Sand sagebrush			X				X	
Silver sagebrush			X				X	
Big sagebrush			X				X	
Rubber rabbitbrush			X					X
Yellow rabbitbrush			X					X
Broom snakeweed				X			X	
Great Plains yucca			X				X	
Totals #	9	6	31	7	18	15	20	4
Percentage %	17.0	11.3	58.5	13.2	34.0	28.3	37.7	7.5

Table 3. Fire effects and Regeneration type of woody plants that encroach into Rangelands of the Northern Plains.						
Woody Plants	Fire Effects				Regeneration Types	
	Total Plant Kill	Top Kill	Trunk Little Damage	Activates Vegetative Buds	Vegetative	Sexual
Common juniper	X				X	X
Creeping juniper	X				X	X
Rocky Mtn juniper	X					X
Ponderosa pine	X		X			X
American elm		X		X	X	X
Bur oak		X	X	X	X	X
Green ash		X	X	X	X	X
Balsam poplar		X		X	X	X
Plains cottonwood		X		X	X	X
Quaking aspen		X		X	X	X
Peachleaf willow		X		X	X	X
Beaked willow		X		X	X	X
Coyote willow		X		X	X	X
Sandbar willow		X		X	X	X
Prairie willow		X		X	X	X
American hazelnut		X		X	X	X
Beaked hazelnut		X		X	X	X
Kinnikinnick		X		X	X	X
Juneberry		X		X	X	X
Northern hawthorn		X		X	X	X
Shrubby cinquefoil		X		X	X	X
Wild plum		X		X	X	X
Pin cherry		X		X	X	X
Sand cherry		X		X	X	X
Chokecherry		X		X	X	X
Prickley wild rose		X		X	X	X
Prairie wild rose		X		X	X	X

Table 3 (cont.). Fire effects and Regeneration type of woody plants that encroach into Rangelands of the Northern Plains.						
Woody Plants	Fire Effects				Regeneration Types	
	Total Plant Kill	Top Kill	Trunk Little Damage	Activates Vegetative Buds	Vegetative	Sexual
Smooth wild rose		X		X	X	X
Western wild rose		X		X	X	X
White spiraea		X		X	X	X
Leadplant		X		X	X	X
False indigo		X		X	X	X
Dwarf wild indigo		X		X	X	X
Wild licorice		X		X	X	X
Silverberry		X		X	X	X
Buffaloberry		X		X	X	X
Fragrant sumac		X		X	X	X
Skunkbush		X		X	X	X
Western snowberry		X		X	X	X
Fourwing saltbush		X		X	X	X
Moundscale saltsage		X		X	X	X
Winterfat		X		X	X	X
Greasewood		X		X	X	X
Green sage		X		X	X	X
Fringed sage		X		X	X	X
White sage		X		X	X	X
Sand sagebrush		X		X	X	X
Silver sagebrush		X		X	X	X
Big sagebrush	X					X
Rubber rabbitbrush		X		X	X	X
Yellow rabbitbrush		X		X	X	X
Broom snakeweed		X		X	X	X
Great Plains yucca		X		X	X	X
Totals #	5	48	3	48	50	53
Percentage %	9.4	90.6	5.7	90.6	94.3	100.0

Table 4. Vegetative bud location of woody plants that encroach into Rangelands of the Northern Plains.								
Woody Plants	Vegetative Bud Location							
	Root Crown	Stem Base	Rhizome	Stolon	Lateral Roots	Trunk	Bent Stem to Soil	No buds Present
Common juniper							X	X
Creeping juniper							X	X
Rocky Mtn juniper								X
Ponderosa pine								X
American elm		X			X			
Bur oak	X				X	X		
Green ash	X	X						
Balsam poplar		X			X	X	X	
Plains cottonwood	X				X	X	X	
Quaking aspen					X			
Peachleaf willow	X					X	X	
Beaked willow	X	X					X	
Coyote willow	X	X			X		X	
Sandbar willow			X					
Prairie willow	X	X						
American hazelnut	X		X				X	
Beaked hazelnut			X					
Kinnikinnick	X	X		X		X	X	
Juneberry	X		X	X				
Northern hawthorn		X			X			
Shrubby cinquefoil	X						X	
Wild plum	X				X			
Pin cherry		X			X			
Sand cherry	X		X		X			
Chokecherry	X		X					
Prickly wild rose			X					
Prairie wild rose	X				X			

Table 4 (cont.). Vegetative bud location of woody plants that encroach into Rangelands of the Northern Plains.								
Woody Plants	Vegetative Bud Location							
	Root Crown	Stem Base	Rhizome	Stolon	Lateral Roots	Trunk	Bent Stem to Soil	No buds Present
Smooth wild rose	X				X			
Western wild rose	X		X				X	
White spiraea	X		X					
Leadplant	X		X					
False indigo	X				X			
Dwarf wild indigo	X		X		X			
Wild licorice			X					
Silverberry		X	X	X				
Buffaloberry	X		X					
Fragrant sumac	X		X		X		X	
Skunkbush	X		X					
Western snowberry		X	X					
Fourwing saltbush	X	X	X			X		
Moundscale saltsage	X	X			X			
Winterfat	X	X						
Greasewood	X				X			
Green sage			X					
Fringed sage		X	X					
White sage		X	X					
Sand sagebrush		X						
Silver sagebrush		X	X		X		X	
Big sagebrush								X
Rubber rabbitbrush	X					X		
Yellow rabbitbrush		X				X		
Broom snakeweed	X					X		
Great Plains yucca		X	X					
Totals #	30	20	23	3	18	9	13	5
Percentage %	56.6	37.7	43.4	5.7	34.0	17.0	24.5	9.4

Results and Discussion: Grazing Management

The defoliation resistance mechanisms, the ecosystem biogeochemical processes, and the grass resource competitiveness in native prairie ecosystems were evaluated to identify the relationships of grazing management on the inhibitory effects of ecological processes on woody species encroachment into prairie.

Ecosystem Mechanisms and Processes

Rangelands are complex ecosystems consisting of numerous biotic (living) and abiotic (nonliving) components. The biotic components are the grass plants, soil organisms, and grazing graminivores that have biological and physiological requirements. The abiotic components include radiant energy from sunlight and the essential major elements of carbon, hydrogen, nitrogen, and oxygen with separate but closely linked biogeochemical cycles that transform the elements between organic forms and inorganic forms, and with numerous biological, chemical, and atmospheric pathways that transfer the major essential elements into and out of the ecosystem. The minor essential elements consist of seven macrominerals and ten microminerals that are required by most living organisms. The minor elements have biogeochemical cycles or parts of cycles that transform the elements between organic and inorganic forms while they are within an ecosystem. There are numerous pathways that transfer minor essential elements out of an ecosystem. However, there are no readily available natural pathways that can transfer minor essential elements into an ecosystem. After a macromineral or a micromineral has been depleted from a rangeland ecosystem, that soil is deficient of that minor essential element. Rangeland ecosystems are functioning units of coacting biotic organisms interacting with the abiotic components and the environmental factors.

Grass plants, soil organisms, and graminivores have developed complex symbiotic relationships. The grazing graminivores depend on grass plants for nutritious forage. Grass plants depend on rhizosphere organisms for mineralization of essential elements, primarily nitrogen, from the soil organic matter. The main sources of soil organic matter are grazing animal waste and dead plant material. Rhizosphere organisms depend on grass plants for energy in the form of short carbon chains. Grass plants exude short carbon chain energy through the roots into the rhizosphere following partial defoliation of the aboveground leaf material by grazing graminivores. Grass plants produce

double the leaf biomass than is needed by the plant to provide nutritious leaf forage to the grazing graminivores.

Grass Tiller Growth

Grass plants use the essential elements in the inorganic form to synthesize vital organic compounds of carbohydrates, proteins, and nucleic acids for growth. Grass tillers consist of shoots and roots. The shoot is the stem and leaves, and comprises repeated structural units called phytomers (Beard 1973, Dahl 1995). A phytomer consists of a leaf, with a blade and a sheath separated by a collar; a node, the location of leaf attachment to the stem; an internode, the stem between two nodes; and an axillary bud, meristematic tissue capable of developing into a new tiller (Hyder 1974, Dahl and Hyder 1977). Each tiller shoot generally produces 6 to 8 phytomers per growing season (Langer 1972, Dahl 1995). The crown of a grass tiller is the lower portion of a shoot and has two or more nodes (Dahl 1995). Fibrous roots grow from crown nodes that are located below ground. The internodes of the crown nodes associated with roots, crown tillers, and rhizome tillers do not elongate (Dahl 1995).

Phytomers develop from leaf primordia that form on alternating sides of the apical meristem (Evans and Grover 1940, Langer 1972, Beard 1973, Dahl 1995). Almost all of the phytomer cells are produced in the apical meristem while the leaf primordia is a minute bud (Langer 1972). The oldest cells of a leaf are at the tip, and the youngest cells are at the base (Langer 1972, Dahl 1995). Several leaf primordia are at various stages of development at any one time. The oldest leaf is outermost, while younger leaves grow up through existing leaf sheaths (Rechenthin 1956, Beard 1973). Growth of the leaf results through cell enlargement and elongation (Esau 1960, Dahl 1995). A few new cells are produced by intercalary meristem located at the base of the blade, the base of the sheath, and the base of the internode (Esau 1960). Cell expansion occurs in the region protected by the sheaths of older leaves. When the cells emerge and are exposed to light, expansion ceases and photosynthesis and transpiration begin (Langer 1972). Once a leaf blade is fully expanded, no further growth of that blade is possible (Dahl 1995).

Individual leaves of grass tillers are relatively short lived. Young middle-aged leaves are in their prime when the rate of apparent photosynthesis is maximum and the leaves begin exporting assimilates to other parts (Langer 1972).

At this point, the leaf has its greatest dry weight. Leaf senescence, or aging, begins shortly after middle age. Senescence begins at the tip, the oldest part of the leaf, and spreads downward. As senescence progresses, apparent photosynthesis and movement of assimilates from the leaf to the other parts of the plant decrease (Langer 1972). The rate of senescence occurs at about the same rate as leaf appearance but is influenced by environmental conditions. During senescence, cell constituents are mobilized and redistributed to other parts of the plant (Beard 1973). This process causes weight of the leaf to decrease (Leopold and Kriedemann 1975). The percentage of dryness in a leaf blade is an indication of the degree of senescence.

Longevity of grass tillers usually extend two growing seasons (Langer 1956, Butler and Briske 1988, Manske 2009a). Production of new leaf primordia continues until the status of the apical meristem changes from vegetative to reproductive. Sexual reproductive growth begins during the second growing season after the lead tiller has attained a certain minimum amount of vegetative development (Dahl 1995). Initiation of the reproductive growth stage is triggered by photoperiod (Roberts 1939, Leopold and Kriedemann 1975, Dahl 1995) but can be slightly modified by temperature and precipitation (McMillan 1957, Leopold and Kriedemann 1975, Dahl and Hyder 1977). Most secondary vegetative tillers initiate growth during the first growing season, overwinter, resume growth during the second subsequent growing season, become florally induced, and proceed with development of sexual reproductive structures (Briske and Richards 1995). When the florally induced grass lead tiller is between the third new leaf stage and three and a half new leaf stage, the apical meristem ceases to produce leaf primordia and begins to produce flower primordia (Frank 1996, Frank et al. 1997). Previously formed leaf buds continue to grow and develop (Esau 1960, Langer 1972). Most native cool season grasses reach the three and a half new leaf stage around early June, and most native warm season grasses reach the three and a half new leaf stage around mid June (Manske 1999a).

The flower bud primordia develop into the inflorescence, with the apical dome becoming the terminal spikelet. The first external evidence of flower stalk development is swelling of the enclosing sheath known as the “boot” stage. During the head emergence phenophase, 4 or 5 of the upper internodes, along with the attached leaf sheaths, elongate very rapidly by intercalary meristem cell development and the inflorescence reaches near

maximum height. The flower (anthesis) phenophase occurs when the feathery stigmas (female parts) spread out and the anthers (male parts) are exposed (Langer 1972). The life cycle of a tiller with the apical meristem status changed to reproductive terminates during that growing season (Briske and Richards 1995).

Recruitment of new grass plants developed from seedlings is negligible in healthy grassland ecosystems. The frequency of true seedlings is extremely 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 vegetative tillers, and when resources are readily available to the growing seedling. Vegetative tiller growth is the dominant form of reproduction in semiarid and mesic grasslands (Belsky 1992, Chapman and Peat 1992, Briske and Richards 1995, Chapman 1996, Manske 1999a) not sexual reproduction and the development of seedlings.

Vegetative secondary tillers develop from lead tillers by the process of tillering. A vegetative tiller is a shoot derived from growth of an axillary bud (Dahl 1995) and is a complete unit with roots, stem, and leaves. All young tillers are dependent on the lead tiller for carbohydrates until they have developed their own root systems and mature leaves (Dahl 1995). After secondary tillers become independent, they remain in vascular connection with other tillers of the grass plant (Moser 1977, Dahl and Hyder 1977, Dahl 1995). There are two types of tillering: crown tillers and rhizome tillers. Grass plants can produce both crown tillers and rhizome tillers. Generally, one tiller growth type is produced by a grass species more than the other tiller type. However, the expressivity of tiller type can be influenced by several growth factors and environmental conditions, and can be manipulated by defoliation management (Manske 2011b).

Meristematic activity in axillary buds and the subsequent development of vegetative tillers is regulated by auxin, a growth-inhibiting hormone produced in the apical meristem and young developing leaves of lead tillers (Briske and Richards 1995). The physiological process by which the lead tiller exerts hormonal control over axillary bud growth is lead tiller (apical) dominance (Briske and Richards 1995). Tiller growth from axillary buds is inhibited indirectly by auxin, as the inhibiting hormone does not enter the axillary buds (Briske and Richards 1995). Auxin interferes with the metabolic

function of cytokinin, a growth hormone (Briske and Richards 1995). Partial defoliation of young leaf material from grass tillers at phenological growth between the three and a half new leaf stage and the flower (anthesis) stage can stimulate vegetative growth of secondary tillers from axillary buds. Defoliation temporarily reduces the production of the blockage hormone, auxin (Briske and Richards 1994). This abrupt reduction of plant auxin in the lead tiller allows for cytokinin synthesis or utilization in multiple axillary buds, stimulating the development of vegetative tillers (Murphy and Briske 1992, Briske and Richards 1994). Several axillary buds develop into secondary tillers following partial defoliation of lead tillers at vegetative stages of phenological growth. Apparently, none of the developing secondary tillers have growth far enough advanced to take complete hormonal control over the other developing axillary buds (Manske 1996a).

Growth of several secondary tillers from axillary buds requires an abundant supply of carbon and nitrogen. The source of the carbon is not from stored carbohydrates, but from increased photosynthetic capacity of remaining mature leaves and rejuvenated portions of older leaves not completely senescent (Ryle and Powell 1975, Richards and Caldwell 1985, Briske and Richards 1995, Coyne et al. 1995). The quantity of leaf area required to provide adequate quantities of carbon is 66% to 75% of the predefoliation leaf area. The source of nitrogen for growth of secondary tillers from axillary buds is not from stored nitrogen but is the mineral nitrogen in the rhizosphere that the microorganisms had converted from soil organic nitrogen (Millard et al. 1990, Ourry et al. 1990). A threshold quantity of 100 pounds per acre (112 kg/ha) of mineral nitrogen needs to be available to the partially defoliated grass tillers in order for full activation of the vegetative tiller production processes (Manske 2009a, 2010b, 2011d).

If no defoliation occurs before the flower (anthesis) stage, the lead tiller continues to hormonally inhibit secondary tiller development from axillary buds. Production of the inhibitory hormone, auxin, declines gradually as the lead tiller reaches the flower stage. The natural reduction of auxin in the lead tiller usually permits only one secondary tiller to develop from the potential of 5 to 8 buds. This developing secondary tiller produces auxin in the apical meristem and young developing leaves that hormonally suppresses development of additional axillary buds.

The longer axillary buds remain hormonally inhibited, the less likely they are to form tillers (Mueller and Richards 1986). The age of the meristematic tissue of the axillary buds that produce secondary tillers is the same age as the meristematic tissue that produce the lead tillers and, most likely, both the lead tiller and secondary tiller meristematic tissue was produced during the previous growing season. Axillary buds survive as long as the lead tiller remains alive. The lead tiller terminates life by senescence during the same growing season that the apical meristem changes from vegetative to reproductive status, and all unstimulated axillary buds terminate with the lead tiller.

Fall tillers are produced by cool-season grasses during the winter hardening process that starts around mid August. Warm-season grasses produce fall tiller buds that remain at or below ground level until the next growing season. The age of the meristematic tissue that produces fall tillers and fall tiller buds is one generation younger than the meristem that produced the lead tillers and secondary tillers. Secondary tillers with apical meristem remaining in the vegetative status, fall tillers, and fall tiller buds become the lead tillers and vegetative tillers during the subsequent growing season.

Longevity of grass plants in grassland ecosystems is dependent on development of tillers through vegetative production from axillary buds. Grass plant longevity of major northern species managed with traditional grazing practices is known to endure at least for 27 to 43 years (Briske and Richards 1995). Grass plant longevity would be expected to be greatly extended when biologically effective grazing management specifically designed to stimulate the vegetative tiller production mechanisms is implemented.

Rhizosphere Organisms

The rhizosphere is the narrow zone of soil around active roots of perennial grassland plants and is comprised of bacteria, protozoa, nematodes, springtails, mites, endomycorrhizal fungi (Elliot 1978, Anderson et al. 1981, Harley and Smith 1983, Curl and Truelove 1986, Whipps 1990, Campbell and Greaves 1990) and ectomycorrhizal fungi (Caesar-TonThat et al. 2001b, Manske and Caesar-TonThat 2003, Manske 2007). The activity of rhizosphere organisms increases along the trophic hierarchy, starting with the bacteria. This microflora trophic level lacks chlorophyll and has low carbon (energy) content. Bacteria are microscopic single celled saprophytic organisms that consume large quantities

of soil organic matter and are one of the primary producers of the rhizosphere. Increases in biomass and activity of the bacteria elevates the concentration of carbon dioxide (CO₂) resulting in stimulation of activity in the other rhizosphere organisms. Protozoa are single-celled microorganisms that are mainly small amoeba and feed primarily on bacteria. Nematodes are a diverse group of small nonsegmented worms. Most nematodes feed primarily on bacteria or fungi, some feed on protozoa, and some eat other nematodes. Springtails are the most abundant insect in grassland soils and they travel among rhizosphere structures. Minute springtails ingest considerable quantities of soil organic matter in order to eat fungi and bacteria. Mites are small eight-legged arachnids that travel among rhizosphere structures and feed on fungi, nematodes, small insects, and other mites. Mites help distribute fungus spores and bacteria through the soil by carrying them on their exoskeleton. Endomycorrhizal fungi are the other primary producers of the rhizosphere and are achlorophyllous saprophytes that live on dead organic matter and can not fix carbon because they lack chlorophyll. The bacteria and fungi are the microflora saprotrophic organisms at the bottom of the food chain and makeup the greatest biomass of the rhizosphere. Both bacteria and fungi contain high proportions of nitrogen in relation to their carbon content. The rhizosphere organisms of the microfauna trophic levels graze on bacteria or fungi and ingest greater quantities of nitrogen than they need for a balanced diet based on energy (carbon); the excess nitrogen is excreted as ammonium (NH₄). The primary symbiotic function of the endomycorrhizal fungi is to nitrify the ammonium (NH₄) excreted by rhizosphere organisms and convert it into nitrate (NO₃), which is a form of mineral nitrogen usable by grass plants. The elevated rhizosphere organism activity caused by the increase in available carbon compounds results in a greater quantity of organic nitrogen converted into mineral nitrogen (Coleman et al. 1983, Klein et al. 1988, Burrows and Pflieger 2002, Rillig et al. 2002, Bird et al. 2002, Driver et al. 2005).

Along with the improvement of ecosystem biogeochemical processes and the resulting increase in available mineral nitrogen, the increase of mycorrhizal fungi biomass and activity benefits other grassland ecosystem functions. Endomycorrhizal fungi develop arbuscules, vesicles, and hyphae within root tissue of the host plant (Harley and Smith 1983) and secrete adhesive polysaccharides that bond soil particles around grass roots forming the structural environment for rhizosphere organisms, and the adhesive polysaccharides bind soil into aggregates

resulting in increased soil pore spaces, increased water holding capacity, and increased rooting depth. Endomycorrhizal fungi also move phosphorus, other mineral nutrients, and water to the plant roots for absorption (Moorman and Reeves 1979, Harley and Smith 1983, Allen and Allen 1990, Box and Hammond 1990, Marschner 1992, Koide 1993, Marschner and Dell 1994, Smith and Read 1997).

Ectomycorrhizal fungi develop a sheath around the root with hyphae that do not enter the tissue of the host plant (Harley and Smith 1983) and secrete large amounts of adhesive polysaccharides forming water-stable aggregates in soil that are water permeable but not water soluble, and the increased soil aggregation improves soil quality, increases soil oxygenation, increases water infiltration, and decreases erodibility (Caesar-TonThat and Cochran 2000, Caesar-TonThat et al. 2001a, Caesar-TonThat et al. 2001b, Caesar-TonThat 2002, Manske and Caesar-TonThat 2003, Manske 2007).

Defoliation Resistance Mechanisms

The complex of mechanisms and processes connected with the extensive interactions of the biotic and abiotic ecosystem components collectively became the defoliation resistance mechanisms and biogeochemical processes (Manske 2011b). If any of the numerous processes do not function at potential level, the ecosystem does not produce at potential level. Management of rangeland ecosystems must meet the biological and physiological requirements of the biotic components and stimulate the biogeochemical processes that cycle the abiotic components.

Activation of the three primary defoliation resistance mechanisms requires proper timing of partial defoliation. The effects of defoliation are not simply the removal of herbage from grass plants (Langer 1963, 1972): foliage removal disrupts plant growth and photosynthesis, and defoliation also changes physiological processes in all parts of the plant; alters the plant community microclimate by changing light transmission, moisture relations, and temperature; and changes the soil environment, thereby affecting soil organism activity (Manske 2000a). Grass plants developed the defoliation resistance mechanisms in response to grazing during the period of coevolution with graminivores (McNaughton 1979, 1983; Coleman et al. 1983; Briske 1991; Briske and Richards 1995; Manske 1999a, 2011b). The defoliation resistance mechanisms help grass tillers withstand and recover from partial defoliation by grazing. The three main

resistance mechanisms are: compensatory internal physiological processes, internal vegetative production of secondary tillers from axillary buds, and external symbiotic rhizosphere organism activity (McNaughton 1979, 1983; Coleman et al. 1983; Ingham et al. 1985; Mueller and Richards 1986; Richards et al. 1988; Briske 1991; Murphy and Briske 1992; Briske and Richards 1994, 1995; Manske 1999a, 2011b).

The defoliation resistance mechanisms are a complex assemblage of biogeochemical and physiological processes that involve intricate interactions among rhizosphere microorganisms, grass plants, and large grazing graminivores. Activation of these mechanisms provides important biological and physiological processes permitting native grasses to produce greater herbage biomass and to increase basal cover; these mechanisms also enable grass plants to replace lost leaf material, to restore disrupted physiological processes, and to vegetatively produce secondary tillers from axillary buds after partial defoliation by grazing. The defoliation resistance mechanisms function at variable levels of activation depending on the quantity of available mineral nitrogen in grassland ecosystem soil. When mineral nitrogen is available at 100 lbs/ac (112 kg/ha) or greater, the defoliation resistance mechanisms function at full activation (Manske 2011e). When mineral nitrogen is available at less than 100 lbs/ac (112 kg/ha), defoliation resistance mechanisms function at levels less than full activation (Manske 2009a, 2011d). In addition, the water (precipitation) use efficiency processes decrease in grass plants growing in ecosystems with less than 100 lbs/ac (112 kg/ha) available mineral nitrogen causing herbage biomass production to be reduced by 49.6% (Wight and Black 1972, 1979).

The quantity of available mineral nitrogen in grassland ecosystems is dependent on the rate of mineralization of soil organic nitrogen by rhizosphere organisms (Coleman et al. 1983). The larger the rhizosphere volume and microorganism biomass the greater the quantity of soil mineral nitrogen converted (Gorder, Manske, and Stroh 2004). Rhizosphere volume and microorganism biomass are limited by access to simple carbohydrate energy (Curl and Truelove 1986). Healthy grass plants capture and fix carbon during photosynthesis and produce carbohydrates in quantities greater than the amount needed for tiller growth and development (Coyne et al. 1995). Partial defoliation of grass tillers at vegetative phenological growth stages by large grazing graminivores causes greater quantities of exudates containing simple carbohydrates to be

released from the grass tillers through the roots into the rhizosphere (Hamilton and Frank 2001). With the increase in availability of carbon compounds in the rhizosphere, the biomass and activity of the microorganisms increases (Anderson et al. 1981, Curl and Truelove 1986, Whipps 1990). The increase in rhizosphere organism biomass and activity results in greater rates of mineralization of soil organic nitrogen converting greater quantities of available mineral nitrogen (Coleman et al. 1983, Klein et al. 1988, Burrows and Pflieger 2002, Rillig et al. 2002, Bird et al. 2002, Driver et al. 2005). Mineral nitrogen available in quantities of 100 lbs/ac (112 kg/ha) or greater allow defoliated grass tillers full activation of the defoliation resistance mechanisms (Manske 2009a, 2011d, 2011e). Full activation of the compensatory internal physiological processes within grass plants accelerates growth rates of replacement leaves and shoots, increases photosynthetic capacity of remaining mature leaves, increases allocation of carbon and nitrogen, improves water (precipitation) use efficiency, and increases restoration of biological and physiological processes enabling rapid and complete recovery of partially defoliated grass tillers. Full activation of the asexual internal processes of vegetative production increases secondary tiller development from axillary buds and increases initiated tiller density during the grazing season. Full activation of the external symbiotic rhizosphere organism activity increases mineralization of mineral nitrogen, increases ecosystem biogeochemical cycling of essential elements, and improves belowground resource uptake competitiveness (Wight and Black 1972, 1979; McNaughton 1979, 1983; Coleman et al. 1983; Ingham et al. 1985; Mueller and Richards 1986; Richards et al. 1988; Briske 1991; Murphy and Briske 1992; Briske and Richards 1994, 1995; Manske 1999a, 2011b; Kochy and Wilson 2000).

Biogeochemical Processes

Biogeochemical processes are processes performed by soil microorganisms that renew the nutrient flow activities in ecosystem soils of renewable natural resources. Biogeochemical processes transform stored essential elements from organic forms into plant usable inorganic forms. Biogeochemical processes capture replacement quantities of lost or removed major essential elements of carbon, hydrogen, nitrogen, and oxygen with assistance from active live plants and transform the replacement essential elements into storage as organic forms for later use. Biogeochemical processes decompose complex unusable organic material into compounds and then into reusable essential elements. The quantity of biogeochemical processes conducted

in renewable natural resource ecosystems determines the degree of ecosystem renewal and is dependant on the rhizosphere volume and soil microorganism biomass.

An evolutionary survival mechanism of grass plants in response to partial defoliation and the loss of leaf area as forage to grazing graminivores is the production of double the quantity of leaf biomass than needed for normal plant growth and maintenance (Crider 1955, Coyne et al. 1995). All of the aboveground herbage biomass produced by perennial grasses in a growing season represents about 33% of the total biomass produced. About 67% of the annual perennial grass biomass is produced belowground. About 50% of the aboveground biomass is expendable by the plant. About half of the expendable leaf material is removed as senescent leaves that are broken from the plant and fall to the ground as litter, or removed as leaf material consumed by wildlife or consumed and destroyed by grasshoppers and other insects. About half of the expendable leaf material, or 25% of the aboveground biomass is consumed by grazing livestock (Manske 2012b).

Perennial grass leaf material consists of digestible nutrients and nondigestible structural components. About 15% of the nutrients contained in the consumed leaf material is extracted by stocker heifers and steers and retained for growth. About 30% of the nutrients contained in the consumed leaf material is extracted by lactating cows, with a portion retained by the cow for production, and the remainder of the extracted nutrients passed to her calf for growth (Russelle 1992, Gibson 2009).

All of the nondigestible dry matter and most of the nutrients consumed by grazing graminivores are deposited on the ground as manure in a couple of days. Most of the nutrients consumed and used by graminivores for maintenance are returned to the ecosystem in the feces and urine. None of the herbage biomass dry matter produced during a growing season is removed by graminivores from the rangeland ecosystem. All of the essential elements contained in the belowground biomass and contained in the nonconsumed aboveground biomass stay in the ecosystem. Nearly all of the essential elements used in the annual production of herbage biomass and soil organism biomass are retained and recycled in the ecosystem. Recycling of retained ecosystem organic matter by soil microorganisms decomposes complex unusable material into compounds and then into reusable essential elements.

Some essential elements are lost or removed from the ecosystem as output. If the rangeland ecosystem is burned, almost all of the essential elements in the aboveground herbage are volatilized, and if the soil is dry, some of the belowground essential elements are also lost (Russelle 1992). The metabolic process of respiration in soil organisms, plants, livestock, wildlife, and grasshoppers results in a lose of some essential elements as carbon dioxide, water vapor, and heat energy. Some essential elements are removed from the ecosystem as weight biomass produced by wildlife and grasshoppers. The essential elements transferred from grass plants to grazing livestock and used for animal growth are removed from the ecosystem (Gibson 2009).

The small proportion of the ecosystem essential elements that are lost or removed annually need to be replenished by capturing input essential elements from the surrounding environment through ecosystem processes. The biogeochemical processes associated with active live plants and soil microorganisms can capture replacement quantities for the lost major essential elements of carbon, hydrogen, nitrogen, and oxygen.

Atmospheric carbon dioxide (CO₂) is the ecosystem input source for carbon. Atmospheric carbon dioxide which composes about 0.03% of the gasses in the atmosphere, exists at concentrations of around 370 to 385 mg/kg and is not limiting on rangelands. The carbon dioxide is fixed with hydrogen from soil water during the plant process of photosynthesis which converts energy from sunlight into chemical energy and assimilates simple carbohydrates. Capturing energy by fixing carbon has a relatively low impact on the plant organisms that posses chlorophyll and has low biological costs to the ecosystem resources (Manske 2011b).

Soil water (H₂O) is infiltrated precipitation water and is the ecosystem input source for hydrogen. Soil water is absorbed through the roots and distributed throughout the plant within the xylem vascular tissue. When the rate of water absorption by the roots is less than the rate of water loss from transpiration through stomata openings, plant tissue develops water stress (Brown 1995). Plant water stress limits growth. In western North Dakota, the perennial plant growing season months have a long-term periodicity rate of water deficiency conditions at 32.7%, for a mean of 2.0 months with water deficiency per growing season (Manske et al. 2010).

Wet deposition of nitrogen oxides (NO, N₂O) following lightning discharges is the ecosystem

input source for nitrogen (Manske 2009b). The source of nitrogen for plant growth is mineral nitrogen (NO_3 , NH_4) converted from soil organic nitrogen by rhizosphere organisms. Low quantities of available soil mineral nitrogen below 100 lbs/ac (112 kg/ha) is the major limiting factor of herbage growth on rangelands (Wight and Black 1979) and limits productivity more often than low water on rangeland ecosystems (Tilman 1990). However, rangeland soils are not deficient of nitrogen. Most of the nitrogen is immobilized in the soil as organic nitrogen. Untilled rangeland soils contain about 3 to 8 tons of organic nitrogen per acre (Manske 2011a). Soil organic nitrogen must be mineralized by rhizosphere organisms to become plant usable mineral nitrogen. The quantity of rhizosphere organisms is the limiting factor in rangeland ecosystems low in mineral nitrogen. Biomass and activity of organisms in the rhizosphere are limited by access to energy from simple carbohydrates which can be exudated from grass leaf tillers with partial defoliation by grazing graminivores when grass tillers are at vegetative growth stages. Transforming nitrogen from organic nitrogen to mineral nitrogen and back to organic nitrogen is complex and has a great impact on many organisms at multiple trophic levels and has high biological costs on the ecosystem resources (Manske 2011a, 2011b).

Carbon dioxide, water, and nitrogen oxides are the ecosystem input sources for oxygen. Atmospheric oxygen composes about 28% of the gasses in the atmosphere. The oxygen cycle between the biotic and abiotic components of the ecosystem is closely linked to the carbon cycle and the water, or hydrological, cycle. Oxygen is vital for all organisms that carry out aerobic respiration. Oxygen is not limiting on rangeland ecosystems.

Radiant light from the sun is the ecosystem input source for energy. Radiant energy from the sun is necessary for photosynthesis (Manske 2011c). Intensity of sunlight can be greatly reduced by shading from taller plants. Nondefoliated live and standing dead leaves of grasses reduce light penetration to a similar degree as shrubs, even through shrub leaves are flat and wide and grass leaves are erect and linear (Kochy 1999). The light levels penetrating the leaf canopy can be about 20% of the light levels above the canopy (Peltzer and Kochy 2001).

Failure of a rangeland ecosystem to replenish essential elements at quantities equal to or greater than the annual amount of essential elements lost or removed from the ecosystem inhibits

ecosystem biogeochemical processes from functioning at potential levels causing incremental decreases in productivity and gradual degradation of the ecosystem.

Development of Ecosystem Mechanisms

Grass plants, rhizosphere microorganisms, and large grazing mammalian graminivores evolved together. Grazing mammals and grass plants appear in the fossil record at about the same time and coevolved during the period of 30 to 20 mya following the cooling of the global climate in the Eocene that reduced forest ecosystems and increased grassland ecosystems. The symbiotic relationships among grass plants, soil microorganisms, and large grazing graminivores developed during this period (Manske 2014).

The early grazing mammals had cecal fermentation digestive systems (small horses, rhinoceroses, tapirs, brontotheres, and chalicotheres) and primitive ruminant digestive systems (camels and oreodonts). Herbivore characteristics advanced with the development of deep, hard teeth that had enamel ridges on the crowns and with the improvement of digestive system effectiveness. The most successful group of herbivores to evolve are the bovine (deer, sheep, cattle, and antelope), which developed advanced true ruminant digestive systems, long legs with horny hooves, and hard, moon-shaped cusps on their teeth. Early large bison evolved in Asia and migrated to North America about a million years ago. Bison changed form with a gradual decrease in body and horn size (Manske 2008).

A sudden change in climate to drier and warmer summers but colder winters occurred about 10,000 years ago. This major change accelerated the melting of glacial ice and decreased the productivity of plant communities. The resulting increase in competition for grassland forage resource disadvantaged territorial animals. The mastodon, mammoth, camel, tapir, sloth, horse, large long-horned bison, middle-sized bison, and dire wolf became extinct between 10,000 and 8,000 years ago. Herding animals that were not confined to territories had an advantage. The caribou, musk oxen, and the small bison survived the climate change. The dramatic success of the bison following this period resulted in part from the extermination of previous prairie competitors (Manske 2008).

Free roaming bison were the dominant herbivore grazing North American grasslands between 5,000 and 130 years ago. Many authors

have estimated a peak population between 50 and 75 million bison in North America before the arrival of European immigrants. These high population estimates were based on an inaccurate assumption that the grasslands grazed by bison covered an area of 3.0 million square miles in North America. However, the region that contains all the tall grass, mixed grass, and short grass prairies, and parts of the eastern deciduous forest and aspen parkland extending from the foot of the Rocky Mountains to the Appalachian Mountains and from southern Texas to the Canadian Shield contain a total of 1,225,000 square miles. This smaller grassland grazing area could not realistically produce adequate forage to sustain a bison herd of 60 million head for one year. A more conservative estimate using 24 acres per bison per year would suggest that a peak population would not be greater than 30 million bison plus about 4 million animal unit equivalents for elk, deer, and pronghorn living on the Great Plains and Central Lowland Physiographic Regions of North America. Following the arrival of European settlers to North America, free roaming bison were eliminated in a very short period of about 150 years (Manske 1994).

The early grazing mammals are extinct and the large free roaming herds of bison have been eliminated. The grazing patterns of these large mammalian graminivores is not known. The 1862 Homestead Act of the United States and the 1872 Dominion Lands Act of Canada were implemented and divided North America into 160 acre parcels that have since been reapportioned. The possibility to manage large grazing graminivores as nomadic pastoral herds or free roaming herds has been removed and management of large graminivores has been restricted to pastures with defined boundaries. Fortunately, we have native grass plants, rhizosphere organisms, and domesticated graminivores, and recently, we have acquired an understanding of the defoliation resistance mechanisms, the ecosystem biogeochemical processes, and the grass resource competitiveness to a sufficient degree that we can activate these ecosystem mechanisms to function at potential level that then permit rangeland ecosystems to produce at potential level.

Activation of Ecosystem Mechanisms and Processes

The ecosystem mechanisms and processes are activated with partial defoliation by grazing of grass lead tillers at vegetative growth stages. Biologically effective management practices coordinate defoliation by grazing with grass phenological growth stages. Three to six rangeland

pastures are grazed from early June until mid October, with each of the pastures grazed during two periods per growing season. Each pasture in a rotation system is grazed for 7 to 17 days during the first period. The first grazing period is the 45 day interval from 1 June to 15 July when native grass lead tillers are between the 3.5 new leaf stage and the flower stage; these are the vegetative growth stages of grass tiller development at which partial defoliation by grazing activates the defoliation resistance mechanisms and the ecosystem biogeochemical processes. Activation of these mechanisms and processes does not occur at any other period during a growing season (Manske 1999a). The length of grazing on each pasture during the first period is the same percentage of 45 days as the percentage of the total season's grazable forage contributed by each pasture (Manske 2000a). The second grazing period is the 90 day interval from mid July to mid October and each pasture is grazed for double the number of days that it was grazed during the first grazing period. Livestock are removed from native rangeland pastures in mid October, towards the end of the perennial grass growing season, in order to allow the carryover tillers to store carbohydrates and nutrients that will maintain plant processes over the winter. Most of the upright vegetative tillers on rangeland ecosystems during fall are carryover tillers and will resume growth during the next growing season as lead tillers. Grazing carryover tillers after mid October causes termination of a large proportion of the population resulting in greatly reduced herbage biomass production during subsequent growing seasons (Manske 2011b).

Ecosystem Degradation

Traditional grazing management practices focus only on the aboveground components from the perspective of the "use" failing to consider rangelands as complex ecosystems and neglecting to address the biological needs of all above and belowground ecosystem components. The periods of defoliation by grazing are not coordinated with grass phenological growth stages resulting in decreases in the quantities of carbon exudates released through the grass roots into the rhizosphere, reducing the rhizosphere volume, decreasing the organism biomass and activity, and reducing the rates of mineralization of soil organic nitrogen into mineral nitrogen. Deficient quantities of available mineral nitrogen cause the defoliation resistance mechanisms to function at reduced levels resulting in incomplete recovery of grazed grass tillers replacing less leaf and stem material than the quantity removed by grazing decreasing tiller density and herbage production and

causing a steady decline in the biogeochemical processes and a reduction in grass resource competitiveness. This degradation of prairie communities results in creation of numerous large bare spaces between native grass plants. These open spaces, that lack competition from healthy native grasses, are suitable habitat for opportunistic “weedy” grasses, forbs, and shrubs to become established (Manske 2013).

Shrub Encroachment

The existence of a shrub component in a grassland plant community is not an ecological beneficial relationship. Shrubs and grasses are adversarial inhibitive competitors. Grasses and shrubs compete for sunlight, mineral nitrogen, and soil water.

The degree of difference in competitive abilities between prairie grasses and shrubs on the mixed grass prairie was investigated during 1994 to 1998 at the University of Regina, Saskatchewan, with direction from Dr. S.D. Wilson. The grass growth form has competitive advantages over the shrub growth form. The per gram of biomass effects on resource use efficiency are smaller for shrub growth forms than for grass growth forms (Kochy and Wilson 2000). Shrubs must use a portion of the photosynthates produced in the leaves to build and maintain their unproductive woody stems; the result is a great reduction in resource uptake efficiency. Shrubs require 6 times greater aboveground biomass than the grasses before grass production is decreased as a result of competition from the shrubs (Kochy 1999). Grass aboveground biomass is primarily productive photosynthetic leaves; the result is a high resource uptake efficiency. Grasses have a 1.4 times greater per gram of biomass resource efficiency effect than shrubs (Kochy 1999). Grasses on prairie habitat attenuated more light, took up more mineral nitrogen, and took up more soil water per gram of biomass than did shrubs on brush habitat (Kochy 1999, Kochy and Wilson 2000). Because grasses have high root : shoot ratios and no woody stems to maintain; grasses are good competitors for belowground resources and superior competitors for mineral nitrogen. Shrub’s taller growth form makes the plants superior competitors for aboveground resources (Kochy and Wilson 2000).

Competition between shrubs and grasses during early stages of shrub expansion into prairie habitat of healthy grasses is primarily for belowground resources of nutrients and soil water; under these initial conditions, grasses have the advantage and the shrubs are suppressed (Kochy and

Wilson 2000, Peltzer and Kochy 2001). Competition from healthy grasses also reduces the growth rates of shrub rhizomes and causes high mortality rates of young suckers, preventing expansion into healthy grass communities (Li and Wilson 1998). Seedlings of grasses and shrubs are also unable to compete effectively for resources in healthy established grass plant communities and are suppressed (Peltzer and Kochy 2001). Successful competition of grasses for belowground resources prevents shrubs from becoming established in healthy grass communities. Shrubs can compete for some of the belowground resources only after the grass plants have been degraded by antagonistic management practices.

Following the reduction in grass plant resource competitiveness, establishment of shrubs can occur in degraded grasslands, which frequently starts as clumps (Li and Wilson 1998). The belowground resources previously used by the healthy robust grasses, but no longer consumed by the smaller, less vigorous degraded grasses, are taken up by the shrub plants resulting in proportional increases of biomass production (Kochy and Wilson 2000). After grass competition for belowground resources is reduced, shrub rhizome suckers can regain the faster growth rates and higher survival rates (Li and Wilson 1998) resulting in greater shrub stem densities. As shrub stem density increases, the competition shifts to primarily the aboveground resources of light; under these different degraded conditions, shrubs have the advantage and the grasses are strongly suppressed (Kochy and Wilson 2000).

The reduction of the competitiveness of the grasses for belowground resources of mineral nitrogen and soil water in conjunction with diminution of the defoliation resistance mechanisms and degradation of the biogeochemical processes in the grass plant communities that resulted from antagonistic management practices fully explains the increase of woody shrubs and trees growing in degraded grassland ecosystems.

The increase of woody shrubs and trees in grass communities would have traditionally been explained as a result of fire suppression (Humphrey 1962, Stoddart, Smith, and Box 1975, Wright and Bailey 1982). The great increase of woody plants into grass communities has not been the result of fire suppression. The increased woody plant infestation has been caused by the greatly reduced competitiveness of the grasses and the degradation of the biogeochemical processes in the grass plant communities caused by management of grasslands for their “use”.

The presence of fire does not prove that grasslands need or are caused by fire (Heady 1975). In the Northern Plains prairie, fire cannot prevent the invasion of or cause the removal of shrubs and trees that reproduce by vegetative secondary suckers growing from crown (stem base) or rhizome buds (Wright and Bailey 1982, Manske et al. 2006a, Manske 2006b). Almost all deciduous woody plants growing in the Northern Plains grassland reproduce vegetatively, except big sagebrush.

The increase of undesirable introduced herbaceous grasses and forbs in grass communities has also often times been explained as a result of fire suppression (Wright and Bailey 1982). Kirsch and Kruse (1972) concluded that the cool season exotic grasses, Kentucky bluegrass and smooth brome grass, have invaded much of the northern mixed grass prairie in the absence of fire. Seedlings of trees, shrubs, weedy forbs, and introduced grasses cannot become established in healthy functioning grassland ecosystems with grasses that have retained full resource uptake competitiveness (Peltzer and Kochy 2001). Establishment of intrusive seedlings can occur only after the grass communities have been degraded by antagonistic management practices. Furthermore, fire cannot prevent establishment and expansion of undesirable seedlings into degraded grass communities unless the fire frequency restricts seed production of all invasive species in a region.

Repeated prescribed fire can change the percent composition of the aboveground vegetation biomass in degraded prairie invaded by shrubs. The composition of introduced cool season grasses, early succession and weedy forbs, and shrub aerial stems decrease temporarily from four repeated every-other-year prescribed fires (Manske 2007a, 2011a). However, the fundamental problems of low native grass competitiveness, diminished defoliation resistance mechanisms, and degraded biogeochemical processes remain in the grassland ecosystems following repeated fire events.

None of the physiological and asexual processes of the defoliation resistance mechanisms within grass plants and none of the biogeochemical processes performed by symbiotic rhizosphere organisms within grassland ecosystems are activated by fire. Fire does not stimulate vegetative reproduction by tillering. Fire does not increase native grass basal cover or density. Fire does not stimulate endomycorrhizal fungal colonization of perennial grass roots. Fire does not stimulate rhizosphere organism biomass and activity. Fire does not stimulate mineralization of soil organic nitrogen

into mineral nitrogen (Manske 2007a, 2011a). Fire does not improve prairie ecosystems biologically or ecologically. Fire does not replace partial defoliation by grazing for management of healthy and productive rangeland ecosystems.

Had the early grassland ecologists known about the conclusions from the grass-shrub competition research conducted at the University of Regina and understood the defoliation resistance mechanisms and the biogeochemical processes, it would appear extremely plausible that the conjectural observations of increasing shrubs and trees and undesirable forbs and grasses in grassland communities that were explained as results of fire suppression, would have been scientifically explained as shrubs and trees and introduced forbs and grasses effectively competing for a portion of the belowground resources of nutrients and soil water after the competitiveness of the grasses had been reduced as a result of degradation of the grass community caused by antagonistic management practices. The key to woody shrub and tree and herbaceous plant control in grass communities is to regain the competitive advantage of the grasses by restoration of the mechanisms and processes in the prairie ecosystem that results from biologically effective partial defoliation by large grazing graminivores.

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