Grassland Orchids of the Northern Plains

North Dakota State University
Dickinson Research Extension Center
2019

4034

Grassland Orchids of the Northern Plains

Llewellyn L. Manske PhD
Research Professor of Range Science

Project Assistant
Sheri A. Schneider

Western Prairie Fringed Orchid
Photo by L.L. Manske PhD
Sheyenne National Grasslands

North Dakota State University
Dickinson Research Extension Center
1041 State Avenue
Dickinson, North Dakota 58601

Tel. (701) 456-1118
Fax. (701) 456-1199

CONTENTS

Introduction

Botanical Description Summaries of Twelve Grassland Orchids

Grassland Orchids of the Northern Plains

Llewellyn L. Manske PhD
Research Professor of Range Science
North Dakota State University
Dickinson Research Extension Center
Report DREC 19-4034

Orchids are a highly advanced, intricate, and sophisticated group of plants dependent on complex relationships with insect pollinators and specific mycorrhizal fungi. The list of orchid species is huge. Orchids are one of the three largest families of angiosperms, consisting of about 10% of all known plant species. Much of the orchids unique characteristics had fully evolved by the early Eocene epoch, 45 to 55 million years ago (Poinar 2017), indicating that orchid ancestors originated much earlier. Few orchids have commercial value, a small quantity of genera and their hybrids are grown horticulturally for fancy house plants, a few varieties are desired as floral corsages, and one genus is the source of the popular spice, vanilla. Orchids are not forage for livestock or wildlife, other than curiosity nibbles. Orchids are not numerous enough to be considered as necessary components of ecosystems. Most orchids live in tropical and subtropical regions hanging from trees as epiphytes. Comparatively few orchids live in temperate North America with about 200 terrestrial species (0.6%), and only twelve species in five genera live in grassland habitats of the Northern Plains. These grassland orchids are rare and should be considered to be special and valued as heritage plants of the grasslands of the Northen Plains.

The grassland orchids have problems. They have never been abundant and have always lived in small isolated communities. However, the quantity of suitable habitat has been greatly reduced as a result of the high percentage of grassland acreage plowed and used for annual crop production. The remaining grasslands are critical for livestock agriculture and for orchid habitat. Unfortunately, the quantity of orchids surviving on these remaining grasslands is decreasing, primarily because the grassland ecosystems are degrading.

The intended purpose of this report is to present a management solution to these problems that can improve the quantity and quality of suitable habitat for grassland orchids, and that can provide the biological and physiological requirements to the forage grass plants, soil microorganisms, and grazing livestock, that can activate and maintain the grass plant growth mechanisms and the ecosystem biogeochemical processes, that can revitalize soil structure and functionality, that can increase forage growth and nutritional quality, and that can improve livestock growth and weight performance along with the capture of greater wealth per acre.

Twelve orchid species (table 1) have evolved grassland ecotypes in which a group of individual plants have developed genetic adaptations that permit survival on grassland habitat types in the Northern Plains. The Northern Plains is comprised of all or parts of the provinces of Alberta, Saskatchewan, and Manitoba, and the states of Minnesota, Iowa, North Dakota, South Dakota, Nebraska, Montana, and Wyoming. Four grassland orchids grow in Montana and Wyoming. Five grassland orchids grow in Alberta. Seven grassland orchids grow in Saskatchewan. Nine grassland orchids grow in South Dakota. Ten grassland orchids grow in Manitoba, North Dakota, and Nebraska. And eleven grassland orchids grow in Minnesota and Iowa (table 2).

Six major prairie vegetation types have developed in the Northern Plains based on stature of the major grass species, the annual soil temperature regimes, and the soil moisture regimes (Manske 2018a). Twelve grassland orchids grow in the Tall grass prairie. Eleven grassland orchids grow in the Moist mixed grass prairie. Eight grassland orchids grow in Sandhill prairies. Four grassland orchids grow in the Mixed grass prairie. Three grassland orchids grow in Foothill prairies. And one grassland orchid grows in the Northern shortgrass prairie (table 3).

Six grassland habitat types can potentially be occupied by grassland orchids in the Northern Plains. The mesic prairie habitat is suitable to be occupied by eleven grassland orchids. The wet meadow habitat is acceptable to be occupied by ten grassland orchids. Six grassland orchids are effective colonizers of disturbed areas. The dry prairie habitat can be occupied by four grassland orchids. Dune swales can be occupied by three grassland orchids. Natural springs seeps can be occupied by two grassland orchids (table 4).

Table 1. Twelve grassland orchids of the Northern Plains.

Platanthera praeclara	Sheviak & Bowles	Western prairie fringed orchid
Spiranthes cernua	(L.) Richard	Nodding lady's tresses
Spiranthes magnicamporium	Sheviak	Great Plains lady's tresses
Spiranthes romanzoffiana	Chamisso	Hooded lady's tresses
Spiranthes lacera	(Raf.) Rafinesque	Slender lady's tresses
Spiranthes vernalis	Engelmann & Gray	Twisted lady's tresses
Cypripedium candidum	Muhlenberg ex Willd.	White lady's slipper
Cypripedium parviflorum	Salisbury	Yellow lady's slipper
Cypripedium reginae	Walter	Showy lady's slipper
Platanthera aquilonis	Sheviak	Northern green orchid
Coeloglossum viride	(L.) Hartman	Longbracted frog orchid
Pogonia ophioglossoides	(L.) Ker-Gawler	Rose pogonia

Table 2. Distribution of twelve grassland orchids in Provinces and States of the Northern Plains.

Provinces and States	Pla pra	Spi cer	Spi mag	Spi rom	Spi lac	Spi ver	Cyp can	Cyp par	Cyp reg	Pla aqu	Coe vir	Pog oph	#/12
Alberta				X	X			X		X	X		5
Saskatchewn				X	X		X	X	X	X	X		7
Manitoba	X		X	X	X		X	X	X	X	X	X	10
Minnesota	X	X	X	X	X		X	X	X	X	X	X	11
Iowa	X	X	X	X	X	X	X	X	X	X	X		11
North Dakota	X	X	X	X			X	X	X	X	X	X	10
South Dakota	X	X	X	X		X	X	X		X	X		9
Nebraska	X	X	X	X	X	X	X	X		X	X		10
Montana				X				X		X	X		4
Wyoming				X				X		X	X		4
#/10	6	5	6	10	6	3	7	10	5	10	10	3	

Table 3. Distribution of twelve grassland orchids in the Prairie Vegetation Types of the Northern Plains.

Prairie Type	Pla pra	Spi cer	Spi mag	Spi rom	Spi lac	Spi ver	Cyp can	Cyp par	Cyp reg	Pla aqu	Coe vir	Pog oph	#/12
Tall grass	X	X	X	X	X	X	X	X	X	X	X	X	12
Moist mixed grass	X	X	X	X	X	X	X	X	X	X	X		11
Mixed grass		X	X	X							X		4
Short grass				X									1
Sandhill	X	X	X	X	X	X	X				X		8
Foothill				X				X			X		3
#/6	3	4	4	6	3	3	3	3	2	3	4	1	

Table 4. Occupied grassland habitat types by twelve grassland orchids of the Northern Plains.

Grassland Habitat	Pla pra	Spi cer	Spi mag	Spi rom	Spi lac	Spi ver	Cyp can	Cyp par	Cyp reg	Pla aqu	Coe vir	Pog oph	#/12
dry prairie		X	X		X	X							4
mesic prairie	X	X	X		X	X	X	X	X	X	X	X	11
wet meadow	X	X	X	X			X	X	X	X	X	X	10
spring seeps				X								X	2
dune swales				X	X	X							3
disturbed areas	X			X	X	X				X		X	6
#/6	3	3	3	4	4	4	2	2	2	3	2	4	

Orchid Flower

The orchid flower is much different than other flowers. Orchids have complex irregular zygomorphic (bilaterally symmetrical) flowers. The flower stalk (pedicel) of most orchids twists and rotates the flower 180° when the bud opens causing the flower to be resupinate (upside down). The perianth (collectively, the sepals and petals) consists of an outer calyx whorl of three sepals and an inner corolla whorl of three petals. The dorsal sepal is at the top in the twelve o'clock position. The two lateral sepals are similar to each other and sometimes fused. The two lateral petals are similar to each other and sometimes fused. The exceptional lip petal (labellum) is predominant in the six o'clock position and is larger and different from the other petals and sepals. A rearward extension of the lip petal of most orchids is a long curved spur that contains the nectar.

At the base of the lip petal, the male and female structures are placed for intentional contact by pollinator insects. The male stamen consists of anther and filament and the female pistil consists of stigma, style, and ovary. In orchid flowers, the male filament and female style have united into a single structure in the center of the flower called a column. The male anther (usually only one is fertile) at the top of the column have formed two pollen sacs in which the pollen is in firm masses called pollinium (pl. pollinia). The pollinia are attached by stalks called stipe or caudicles to sticky discs called viscidia, which are in turn attached to the rostellum. The rostellum is the stuctural portion of the column that separates the male anther at the top of the column from the female stigma towards the base of the column (Ballings and Wursten nd).

Most orchids require insect pollinators for cross pollination; a few orchids are able to self pollinate. The elaborate flower design, color, and fragrance are intended to lure specific selective groups of pollinator insects to the sexual parts located at the center of the flower. A pollinator insect is attracted to a flower, lands on the labellum (lip petal), moves toward the flower center searching for nectar, and comes in contact with the column. The sticky viscidia with attached pollinium become stuck unto the insects body, usually the head. The pollinium rotates downward and inward as one side of the caudicle dries causing the pollen mass to be positioned directly in front of the insect's head. After removal from the anther, pollen can remain viable for about 5 days. The pollinator and pollinium move to the next flower, the pollen in its new position, are brushed over and transferred to the female stigma,

and fertilizes that flower. Each fertilized flower produces a compound fruit capsule during the growing season that contains millions of minute seeds. When the capsule matures toward late summer, seeds are released (dehiscence) through slits in the capsule which continues through plant senescence at the end of the growing season. The minute seeds are designed to be dispersed over long distances by wind (Dearnaley and Cameron 2016). Potentially successful seeds will land on moist mineral soil, be moved below the soil surface by infiltrating water, and be located near that orchids specific mycorrhizal fungi.

Orchid Pollinators

The insect pollinators of grassland orchids of the Northern Plains are social bees, bumble bees, solitary bees, and sphinx moths (tables 5 and 6). The grassland orchids are vulnerably dependent on these insect pollinators. A summary of the pollinator life cycle indicates an extremely complex and precarious existence with numerous stages when small changes could cause tremendous failures.

Pollinator life cycles

Honey bees (Apis) are geologically the youngest of the apidae bees, are highly social (eusocial), introduced into North America from Europe, are attended by humans in apiaries, but are not considered to be domesticated insects. A hive is large with about 50,000 individuals, consisting of an egg producing queen that lives for 3 to 4 years, fertile male drones that are produced when needed to fertilize a new queen and then die, and female workers that start as cell cleaners, and feed larvae, advance to in hive house workers for 3 weeks, advance to field workers with short tongues that gather pollen, nectar, water, and propolis (tree wax) for 3 weeks, and then die.

Bumble bees (Bombus) developed during the late Cretaceous, 81 to 96 mya, are primitively social with between 50 and 400 individuals, in untidy underground nests. During autumn, a young queen leaves the old nest, mates, overwinters belowground in a state of diapause, in early spring, the fertilized queen selects a new underground nest site that is not in direct sunlight, makes egg containers, and produces female workers. The larvae are fed pollen for protein and nectar for carbohydrates. The female workers carry pollen in corbiculae "baskets" on their hind legs and nectar is stored in their crop and put into wax containers when they arrive back in the nest. Bumble bees do not store much pollen or nectar and do not

make honey; the male drones and female workers die during the fall.

Miner bees, or chimney bees (Authophora) develop gregarious clusters of ground nests, but are considered solitary bees because each female has her own nest. Miner bees appear to be small, fast bumble bees. The males emerge from the nest during early spring about 5 days before the females. Male and female mate on a flower. The female digs a tunnel usually on a slope in clay about 11 cm (4.3 in) long, and constructs a chimney like turret (or a protective overhang roof) over the entrance. The female then digs about 7 cells into the sidewall of the tunnel. Each cell is lined with secretions from a Dufour's gland at the base of the abdomen which waterproofs the cell. The female travels to numerous flowers, collects, and places pollen, nectar, and gland secretions into each cell, lays a single egg, and seals the cell with clay, leaving a single pore in the cap. The eggs hatch in 5 days, the larvae develop through 4 instar stages eating the pollen and nectar mixture. The larvae form a prepupae and overwinter. In the spring, the prepupal skin is shed and continue development for 2 and a half weeks, and emerge as adults.

Small carpenter bees (Ceratina) are dark with a metallic sheen and do not bore holes in wood, but develop tunnels in plants that have pithy or woody stems. The tunnels are long enough for 5 to 6 cell chambers. The wood or pith is not eaten. The adults are flower nectar feeders. The females collect pollen from several flowers, place it in the cell chambers, lay a single egg in each chamber, and seal the ends with wood pulp. The adult females can live longer than one year. They return to their bored chambers to overwinter, with sisters and daughters living near each other.

Solitary bees (Andrenidae, Halictidae, Megachilidae) are small. The adults emerge in early spring. The males are ahead of the females by a few days. There are no queen bees, each female is fertile. Males and females find each other and mate. The male dies soon after. The female builds her own nest. The location of the nest cavity and the material used to line each egg chamber is different for each species of solitary bee. Each egg is placed in a separate chamber in which the female has collected large masses of pollen from numerous flowers and mixed with nectar to provide food for each larvae. The eggs hatch in a few days after being laid. The larvae eats the pollen and nectar and develops through 4 instar stages, a pupal stage, and spins a cocoon for

overwinter or develops into an adult and hibernates during the winter.

Mining bees (Andrena, Calliopsis) developed during the Eocene-Oligocene boundary, 34 mya. They prefer small vertical holes belowground with mounds of soil around the entrance, usually in sand under a shrub to protect from heat and frost. The holes are 20-40 cm (8-16 in) deep, with 5 or so branches for separate egg chambers. Each cell is lined with Dufour's gland secretions to waterproof the cells. The female works alone at dusk collecting pollen and nectar to provide food for each larvae.

Sweat bees (Augochlorella, Agapostemon, Halictus, Lasioglossum) are small black, striped, or metallic green solitary ground nesting bees. The holes are dug by the females in bare soil in sunny locations. Each egg chamber is lined with Dufour's gland secretions and provided with pollen and nectar.

Mason bees (Osmia, Hoplitis) developed during mid Eocene, 45 mya. Mason bees are short, small waisted with robust metallic green or blue bodies and use clay mud masonry to build their nest. The female prefers a preexisting single tubular cavity aboveground with the egg chambers stacked on top of each other. Females can lay 1 or 2 eggs per day. A mud plug is placed at the bottom, nectar and pollen are added, then an egg is laid, and sealed with a thin mud partition. This process is repeated until that cavity is full and sealed with a mud cap. Then another cavity nest is built the same way. Female mason bees carry the pollen by a scopa on their bellies. The mated female stores semen, and uses it to fertilize the eggs she wants to be female, usually the lower egg cells. The unfertilized eggs become males, which are about 66% of the offsprings.

Resin bees (Anthidiellum) are very small solitary bees that build nests in preexisting holes aboveground in wood or trees. The female resin bee collects tiny balls of plant resin and sticks them together to form the egg chambers and the tubular nest. A mass of pollen and nectar is placed in each egg cell to feed the larvae.

Leafcutter bees (Megachile) cut 0.6-1.3 cm (0.25-0.5 in) circular pieces of thin smooth leaves to line preexisting cavities about 6 mm in diameter in wood, concrete, or soil. The circular leaf sections overlap forming strong individual egg cells, that include a ball of pollen and nectar to feed each larvae.

Sphinx moths (Sphingidae) are large size, fast and strong flyers that can hover. They overwinter

belowground in the papal stage. The adults emerge in the spring, are nocturnal or vespertine (dusk), feed on flower nectar with extremely long tongues. Following mating, the females deposit small eggs usually on the underside of host plant leaves, while hovering. Each species has specific host plants upon which the larvae feed. The larvae develop through 5 instar stages. Each species of larvae have a different color of tail or horn sticking out from their posterior, giving them the name hornworms.

Hermit sphinx (Lintneria eremitus) had a name change in 2007, prefer moist meadow habitat, adults are vespertine, and larvae feed on plants in the mint family.

Great ash sphinx (Sphinx chersis) prefer woodland and scrubland habitat, adults are vespertine, and larvae have a blue or pink horn and feed on ash, lilac, cherry, plum, and quaking aspen.

Laurel sphinx (Sphinx kalmiae) prefer woodland habitat, adults are nocturnal, and larvae have a blue horn and feed on ash, lilac, poplar, and honeysuckle. They do not feed on laurel (Kalmia), the moth was named after P. Kalm, a botanist who worked with C. Linnaeus.

Wild cherry sphinx (Sphinx drupiferarum), adults are nocturnal, and larvae feed on wild cherry, plum, apple, lilac, and hackberry.

Achemon sphinx (Eumorpha achemon) prefer wooded and scrubby habitats, adults are nocturnal, and larvae feed on wild and cultivated grapes, and virginia creeper.

Spurge hawkmoth (Hyles euphorbiae) was introduced from Europe and Asia for biological control of leafy spurge (Euphorbia) in 1965, prefers meadows near leafy spurge, adults are daylight flyers, and larvae have a very large dark horn and feed on leaves and bracts of leaf spurge. Larvae will not feed on poinsettia (Euphorbia).

Bedstraw hawkmoth (Hyles gallii) prefer open sandy meadow habitat, adults are vespertine but are often also nocturnal, and larvae have a red horn and feed on bedstraw (Galium), evening primrose, and fireweed.

Table 5. Grassland Orchid Insect Pollinators.

Phylum	Arthropoda	(arthropods)
Class	Insecta	(insects)
Order	Hymenoptera	(ants, bees, wasps)
Family	Apidae	(social bees, bumble bees)
Tribe	Apini	
Genus	Apis mellifera	European Honey bee
Tribe	Bombini	
Genus	Bombus bifarius	Twoform bumble bee
	Bombus borealis	Northern amber bumble bee
	Bombus flervidus	Yellow bumble bee
	Bombus flavifrons	Yellowhead bumble bee
	Bombus impatiens	Common eastern bumble bee
	Bombus insularis	Indiscriminate cuckoo bumble bee
	Bombus nevadensis	Nevada bumble bee
	Bombus pensylvanicus	American bumble bee
	Bombus perplexus	Confusing bumble bee
	Bombus sandersoni	Sanderson bumble bee
	Bombus ternarius	Tricolored bumble bee
	Bombus terricola	Yellowbanded bumble bee
	Bombus vagans	Halfblack bumble bee
Tribe	Authophorini	
Genus	Authophora abrupta	Miner bee
Subfamily	Xylocopinae	(carpenter bees)
Genus	Ceratina calcarata	Small carpenter bee
Family	Andrenidae	(mining bees)
Genus	Andrena barbilabris	Mining bee
	Andrena ziziae	Mining bee
Genus	Calliopsis andreniformis	Mining bee
Family	Halictidae	(sweat bees)
Tribe	Augochlorini	
Genus	Augochlorella aurata	Golden sweat bee

Table 5 cont. Grassland Orchid Insect Pollinators.

Tribe	Halictini	
Genus	Agapostemon spp	Striped sweat bee
Genus	Halictus confusus	Sweat bee
	Halictus ligatas	Sweat bee
Genus	Lasioglossum anomalum	Sweat bee
	Lasioglossum cinctipes	Sweat bee
	Lasioglossum cressonii	Sweat bee
	Lasioglossum hitchensi	Sweat bee
	Lasioglossum imitatum	Sweat bee
	Lasioglossum pilosum	Sweat bee
	Lasioglossum rohweri	Sweat bee
Family	Megachilidae	(mason, resin, leafcutter bees)
Tribe	Osmiini	(mason bees)
Genus	Osmia spp	Mason bee
Genus	Hoplitis truncata	Small mason bee
Tribe	Anthidiini	(resin bees)
Genus	Anthidiellum notatum	Rotund resin bee
Tribe	Megachilini	(leafcutter bee)
Genus	Megachile brevis	Leafcutter bee
	Megachile centuncularis	Leafcutter bee
	Megachile inermis	Leafcutter bee
	Megachile melanophaea	Leafcutter bee
Order	Lepidoptera	(butterflies, moths)
Family	Sphingidae	(sphinx moths)
Subfamily	Sphinginae	
Genus	Lintneria eremitus	Hermit sphinx
Genus	Sphinx chersis	Great ash sphinx
	Sphinx kalmiae	Laurel sphinx
	Sphinx drupiferarum	Wild cherry sphinx
Subfamily	Macroglossinae	
Genus	Eumorpha achemon	Achemon sphinx
Genus	Hyles euphorbiae	Spurge hawkmoth
	Hyles gallii	Bedstraw hawkmoth

Table 6. Insect pollinators of twelve grassland orchids of the Northern Plains.

Pollinators	Pla pra	Spi cer	Spi mag	Spi rom	Spi lac	Spi ver	Cyp can	Cyp par	Cyp reg	Pla aqu	Coe vir	Pog oph	#
Honey bees				1		1		2					2
Bumble bees		3	2	6	3	2						6	13
Miner bees									1				1
Carpenter bees							1	1					1
Mining bees					1		2	2					3
Sweat bees					1		9	2					11
Mason bees					1			1					2
Resin bees					1								1
Leafcutter bees					2				2				4
Sphinx moths	7												7
Stink bug							1						1
Scarab beetle									1				1
#	7	3	2	7	9	3	13	8	4	0	0	6	47

Data from North American Orchid Conservation Center.

Orchid Fungi Mycobionts

Orchids are dependent on mutualistic mycorrhizal fungi during life stages of germination, protocorm, and seedling stage, vegetative stage, flower stage, and prolonged underground dormancy stage. During the early development stages when the small plant is nonphotosynthetic and the fungi mycobiont supplies the carbon and essential elements, the type of nutrition is classified as full mycoheterotrophy. During the adolescent and adult stages when green leaves fix carbon during photosynthesis and the plant continues to augment their carbon, nitrogen, and other essential nutrient requirements with supplies from mycorrhizal fungi, the type of nutrition is classified as mixotrophy (Dearnaley et al. 2012) a category for orchids between autotrophy and heterotrophy (Dearnaley 2007). If the green plants do not receive supplemented nutrients from fungi, the type of nutrition is autotrophy. Orchid plants are able to survive underground for extended periods (for several months to several years), usually during environmental stress, and again relying totally on mycorrhizal fungi for carbon and essential nutrients, the type of nutrition is mycoheterotrophy (Dearnaley 2007).

The soil fungi that form symbiotic relationships with orchids are completely different from the endomycorrhizal and ectomycorrhizal fungi that form symbiotic relationships in the rhizosphere of grasses. The orchid mycorrhizal fungi are mostly free living soil saprophytes, and a few could be true one-sided parasites (usually associated with roots of woody plants) when the fungi are not colonized with an orchid in a mutualistic relationship (Nurfadilah et al. 2013, Rasmussen et al. 2015). The saprophytic fungi can breakdown the complex organic compounds in an ecosystem. These saprophytes can breakdown (catabolism) polysaccharides (cellulose, hemicellulose, lignin, pectin), polypeptides (proteins containing hundreds of amino acids), and inorganic and organic phosphorus compounds (Nurfadilah et al. 2013). These free living saprophytic fungi are important to the integrity of terrestrial ecosystems by decomposition of complex organic matter. The distribution of saprophytic fungi is independent of the presence of orchids and is related to the quantity and quality of the local organic matter (Rasmussen et al. 2015). The presence of orchids cannot occur without the preexistence of the fungi. The presence of these saprophytic fungi is good for grassland ecosystems and their biomass can be manipulated by the quantity of soil organic matter by using specific types of grazing management. Unlike the endo- and ectomycorrhizal fungi in the rhizosphere of grasses, most of the free living saprophyte fungi can be cultured in the laboratory (McCormick et al. 2004).

The majority of saprophytic fungi that form symbiotic mycorrhizal relationships with grassland orchids of the Northern Plains are from the fungal phylum Basidiomycota, class Agaricomycetes, and order Cantharellales. The major families are Ceratobasidiaceae and Tulasnellaceae (Dearnaley et al. 2012) (table 7). In the not to distant past, the orchid mycorrhizal fungi were lumped into a simple form category of asexual Rhizotonia, when the culture technology did not promote the development of taxonomically distinguishing characteristics like fruiting bodies (McCormick et al. 2004). With the improvements in culture techniques, DNA extraction, and sequencing of nuclear ribosomal DNA, the identification of orchid mycobionts has greatly advanced (McCormick et al. 2004, Dearnaley et al. 2012).

Table 7. Fungal mycobionts symbiotic with grassland orchids of the Northern Plains.

Fungi classification
    Phylum-Basidiomycota, Subphylum-Agaricomycotina,
        Class-Agaricomycetes, Order-Cantharellales

Orchid-Platanthera praeclara, western prairie fringed orchid

    Fungal Family-Ceratobasidiaceae

            Genus-Ceratobasidium

        asexual form-Ceratorhiza sp

                Ceratorhiza pernacatena Zelmer & Currah

    Fungal Family-Tulasnellaceae

            Genus-Tulasnella

        asexual form-Epulorhiza sp

Orchid-Spiranthes spp., lady's tresses

    Fungal Family-Tulasnellaceae

Orchid-Cypripedium candidum, white lady's slipper

    Fungal Family-Tulasnellaceae

Orchid-Cypripedium parviflorum, yellow lady's slipper

    Fungal Family-Tulasnellaceae

Orchid-Platanthera aquilonis, northern green orchid

    Fungal Family-Tulasnellaceae

            Genus-Tulasnella

        asexual form-Epulorhiza anaticular (Currah) Currah

Orchid-Coeloglossum viride, longbracted frog orchid

    Fungal Family-Ceratobasidiaceae

            Genus-Ceratobasidium cornigerum (Bourd.) Rogers

        asexual form-Ceratorhiza goodyerae-repentis (Costantin & Dufour) Moore

        asexual form-Moniliopsis anomala Burgeff ex Currah

Data from Currah et al. 1990, Zelmer and Currah 1995, Sharma et al. 2003, Dearnaley 2007, Tovar 2015.

Orchid Seedling

Orchid seeds are tiny at a weight of 0.3 to 14.0 micrograms (a millionth of a gram), they lack nutritive endosperm, but contain a few lipid (fat) stores and protein bodies. The embryo is undeveloped and lacks shoot and root meristematic tissue. All orchid seeds are dependent on symbiotic fungal colonization to provide organic materials, water, and mineral nutrients in order for development and growth from germination, to the preseedling stage of protocorm, to the seedling stage, through to the photosynthetic plant stage.

Following imbibition of water, the seed coat (testa) softens and forms a small slit, the protein bodies metabolize and ammonium is released into the environment with the intended purpose to entice fungal colonization (Dearnaley and Cameron 2016, Fochi et al. 2016, Chuan-Ming et al. 2019). The specific compatible mycorrhizal fungus must first degrade part of the seed coat which is composed of complex polysaccharides of cellulose, hemicellulose, and pectin. The fungi secretes extracellular (outside of the cell) enzymes of cellulase, carboxymethylcellulase, amylase, xylanase, and pectinase in order to breakdown each of the large polysaccharides into simple sugars which are then absorbed by the fungi (Nurfadilah et al. 2013). The fungi hyphae pass through the newly formed opening in the testa and enter the undifferentiated parenchyma cells (simple general tissue with thin walls) at the top (chalazal) of the embryo near the suspensor attachment point. The fungal hyphae pass through the cell walls but do not breach the cell plasma membrane. The space between the cell wall and the plasma membrane is expanded to make room for the hyphal coils called pelotons (Dearnaley et al. 2012). The fungal hyphae that enter the undifferentiated parenchyma cells of the undeveloped embryo contain an increased quantity of mitochondria resulting in increasing the metabolic capacity of the symbiotic pair and becomes the site for nutrient exchange from the fungi to the orchid embryo. The infected parenchyma cells develop enlarged nucleus as a result of increased DNA content which is correlated with differentiation of the simple parenchymal cells into meristematic tissue for shoot and root development.

A small protocorm develops, which is an intermediate structure before the seedling stage. All orchids growing in grassland habitats produce nonphotosynthetic, mycorrhiza dependent (mycoheterotrophic) subterranean (below the soil surface) protocorms (Dearnaley et al. 2012) to prevent desiccation and exposure to inhibitory light (Rasmussen et al. 2015). Development of the protocorm is very slow and may require several months to a few years.

The infected parenchyma cells increase in vigor and develop into active meristematic tissue. Early development of a stem arises from the apical region. At first the stem grows downward rather than upward to a depth of several centimeters (an inch or two) than turns to grow upward. The downward growth tends to move the protocorm deeper into the soil. Soon afterward, the first root forms in the apical region, growing upward. For a short time, the developing seedling appears to be upside down. The development and growth of the young seedling is slow. The stem develops leaf buds and then protoleaves. Chlorophyll does not develop until the enlarging stem and leaves are exposed to sunlight. The roots grow and increase in size. After the roots develop a cortex layer, just under the epidermis, the fungi can infect the cortex cells and develop pelotons between the cell wall and cell plasma membrane.

The fungi provides water, nitrogen, phosphorus, and carbon, with some nutrients in the organic form. While the orchid seedling is in the nonphotosynthetic stages, the orchid cells export ammonium to the mycobionts (Fochi et al. 2016, Chuan-Ming et al. 2019). After the orchid seedling develops chlorophyll, the orchid exports photosynthate carbon to the fungi (Cameron et al. 2006, Dearnaley and Cameron 2016). The association between orchid and mycorrhizal fungi is true mutualism (Dearnaley et al. 2012).

Botanical Description of Western Prairie Fringed Orchid

Western prairie fringed orchid, *Platanthera praeclara* Sheviak & Bowles, is a member of the orchid family, Orchidaceae, syn: Habenaria leucophaea (Nutt.) Gray var. praeclara Cronquist, and is a native, perennial, terrestrial (mineral soil), strongly mycotrophic (dependent on symbiotic fungi), monocot, herb, that requires full sunlight. Annual aerial growth is a single erect stem arising during mid April to late May from a perennating shoot bud developed on a crown (caudex) during the previous late summer. Adolescent plants remain vegetative with two or a few leaves during the growing season for an extended period of around 12 years. Adult plants produce a stem 38-85 cm (15-33 in) tall with 5 to 10 lanceolate to ovate-lanceolate glabrous (smooth) leaves 9-15 cm (3.5-5.9 in) long, 1.5-3.5 cm (0.6-1.4 in) wide, with lower leaves sheathing the stem. Leaf size decreasing upward, with upper leaves reduced to small bract like structures. A tuber and roots develop each growing season from buds formed during the previous late summer. The thick fleshy fusiform (thick in the middle and tapering at both ends) tuber is slightly larger than the roots. The numerous coarse fleshy roots are fused into fasciated bundles that extend from the caudex to around 12 cm (4.7 in) with some roots up to 16 cm (6.3 in) long but rarely do the roots descend below 10 cm (4 in) deep. Previous years tuber, roots, and shoot remnants wither with the salvaged contents used for growth of current year shoot, roots, and tuber. Inflorescence is an unbranched, terminal lax to dense raceme 5-15 cm (2-6 in) long, 5-9 cm (2-3.5 in) wide with 4 to 33, usually fewer than 20 showy, creamy white pedicellate flowers that mature from the bottom upwards. Each flower lasts for about 10 days. The flower period is from late June to late July with some years extending into August. Flowers are resupinate, upside down due to twisting of the pedicel (short stalk) 180 degrees when the bud opens. The floral bracts at the base of the perianth of each flower are green, 2.0-6.5 cm (0.8-2.5 in) long. Each irregular flower consists of three sepals and three petals with one of the petals forming the conspicuous labellum. The two lateral sepals are obliquely asymmetrical 9-14 mm long, 6-9 mm wide and are porrect (extending forward resembling a parrot beak). The dorsal sepal is ovate to suborbicular. The two lateral petals are flabelliform (fan shaped) 1.0-1.7 cm (0.4-0.7 in) long, 0-6-1.2 cm (0.2-0.5 in) wide with the apical margin shallowly and irregularly toothed. The lateral petals form a hood over the column (fused male filament and female style). The larger lip petal (labellum) predominant structure is 2.0-3.8 cm (0.8-1.5 in) wide,

divided into three major flabelliform (fan shaped) lobes. The two lateral descending lobes are deeply incised more than half way to the base producing extensive fringes. The primary middle lobe is incised less deeply but still producing a distinctive fringed margin. An extension of the lip is an extremely long curved spur 2.5-6.0 cm (1.0-2.4 in) long that contains the nectar. The insect pollinators are sphinx moths (table 8). The moths must be large enough to have a distance of 5.8 to 6.4 mm between the outer eye margins and a proboscis (elongated pipe like mouth part) ideally 34-43 mm long, however, 28 mm long is known to be effective. The viscidia are attached to the pollinia (firm mass of pollen) by a caudicle (stalk). When the moth inserts its proboscis into the spur for nectar, the sticky viscidia becomes attached unto the insects body (usually head or eyes), the caudicle dries rotating the pollinia to the front of the moths head, at the next flower, the pollinia are brushed over and transferred to the female stigma. Millions of minute seeds are produced in an ellipsoid to cylindric fruit capsule. The minute seeds are released through slits in the mature capsule during late summer, continuing through plant senescence. The small seeds contain an air pocket and can be dispersed great distances by wind, and also can be moved horizontally by spring melt water. Diploid chromosomes are 2n=42. Taxonomically, Western prairie fringed orchid, Platanthera praeclara, was separated in 1986 from Eastern prairie fringed orchid, P. leucophaea, based on morphological differences in pollination mechanisms and in geographic distribution (Sheviak and Bowles 1986). Platanthera praeclara was successfully hybridized with P. leucophaea through artificial fertilization (Sheviak and Bowles 1986). Two sphinx moths, Lintneria eremitus, Hermit sphinx, and Eumorpha achemon, Achemon sphinx, are known to sucessfully pollinate both orchids, and P. leucophaea has been known to populate areas west of the Mississippi River in Iowa, Nebraska, Missouri, and Oklahoma.

Geographic distribution of western prairie fringed orchid occurs in cental North America of Canada and the United States. In the Southern Plains, it has occurred in Kansas, Missouri, and Oklahoma. In the Northern Plains, it has occurred in se Manitoba, w & sw Minnesota, w & n Iowa, se North Dakota, e South Dakota, and e & c Nebraska. In North Dakota, it has been located in Cass, Ransom, and Richland counties (table 9). It was listed as threatened in the United States in 1989, and listed as endangered in Canada in 1993 due to habitat loss and degradation (Sather et al. 1996, Goedeke et al. 2008, US Fish and Wildlife Service 2009, COSEWIG 2016).

Preferred habitat of Platanthera praeclara is wet meadows and mesic prairie with calcareous or sandy soils in full sunlight, and it can colonize highly disturbed areas. In southeastern North Dakota, it grows primarily in the lowland grassland habitat type on the toe and lower foot slopes with fine sandy loam soil, high soil moisture, and dominant plants of Carex lanuginosa, wooly sedge, Calamagrotis inexpansa, northern reedgrass, and Juncus balticus, baltic rush, and it grows in the midland grassland habitat type on the back and upper foot slopes with loamy fine sand soil, low to moderate soil moisture, and dominant plants of Andropogon gerardii, big bluestem, Schizachyrium scoparium, little bluestem, and Panicum virgatum, switchgrass.

This botanical description summary of western prairie fringed orchid was based on works of Stevens 1963, Manske 1980, Great Plains Flora Association 1986, Sheviak and Bowles 1986, Smith 1993, Sather et al. 1996, Flora of North America Editorial Committee, eds. 2002, Sharma et al. 2003, Goedeke et al. 2008, US Fish and Wildlife Service 2009, and COSEWIC 2016.

Table 8. Pollinators of Platanthera praeclara, Western prairie fringed orchid.

Sphinx Moth	family	Sphingidae	
	subfamily	Sphinginae	
Lintneria eremitus		Hubner	Hermit sphinx
Sphinx chersis		Hubner	Great ash sphinx
Sphinx drupiferarum		Smith	Wild cherry sphinx
Sphinx kalmiae		Smith	Laurel sphinx
	subfamily	Macroglossinae	
Eumorpha achemon		Drury	Archemon sphinx
Hyles euphorbiae		Linnaeus	Spurge hawkmoth
Hyles gallii		Rottemburg	Bedstraw hawkmoth

Data from North American Orchid Conservation Center nd., Fauske 2016, Sheviak and Bowles 1986.

Table 9. North Dakota State University Herbarium specimens of Platanthera praeclara, Western prairie fringed orchid, collected before 1986.

Year	Date	County	Collector	Habitat
1890	-	Richland	Waldron	sandy soil
1908	Aug	Richland	Bell	sandy soil
1909	9 Jul	Ransom	Bell	low sandy meadow
1909	13 Jul	Ransom	Bell	low sandy
1929	1 Jul	Richland	Stevens	low prairie
1953	-	Ransom	Salerud	-
1960	21 Jul	Ransom	-	depression
1962	-	-	Schermeister	-
1970	21 Jul	Richland	Stevens	low place sandhills
1971	8 Jul	Richland	Seiler	lowland meadow
1971	15 Jul	Ransom	Seiler	lowland
1971	23 Jul	Richland	Seiler	moist road ditch
1972	12 Jul	Richland	Seiler	lowland meadow
1972	13 Jul	Ransom	Seiler	lowland meadow
1978	6 Jul	Ransom	Manske	wet meadow, mowed & grazed
1978	11 Jul	Richland	Manske	wet meadow prairie
1978	11 Jul	Richland	Manske	wet meadow, mowed
1982	15 Jul	Ransom	Warner	swale prairie

Botanical Description of Nodding lady's tresses

Nodding lady's tresses, *Spiranthes cernua* (L.) Richard, is a member of the orchid family, Orchidaceae, syn: Ophrys cernua L. and is a native, perennial, terrestrial (mineral soil), strongly mycotrophic (dependent on symbiotic fungi), monocot, herb. Annual aerial growth is a single erect unbranched stem arising during spring from a perennating shoot bud developed on a crown (caudex) during the previous late summer. Adolescent plants remain vegetative with two or a few leaves during the growing season for only two years. Adult plants produce a stem 10-40 cm (3.9-15.7 in) tall, green, glabrous below, pubescent with blunt hairs above. Two to six basal leaves sheathing the stem form a rosette, ascending to spreading, flaccid (not rigid), membranaceous blades with thickened mid ribs, lanceolate, linear to narrowly oblanceolate 6-28 cm long, 0.4-1.4 cm wide (2.4-11.0 in long, 0.2-0.6 in wide) and with 3 to 5 green stem (cauline) bracts that overlap upwards. Leaves are usually persisting through anthesis but are fugaceous (withering early). Roots are numerous, slender to tuberously thickened to 1 cm in diameter fused into fasciated bundles spreading horizontally and descending. New roots develop each growing season from root buds formed during the previous late summer. Previous years roots and shoot remnants wither with salvaged contents used for growth of current years shoot and roots. Inflorescence is a tight twisted spike 2.5-11.0 cm (1.0-4.3 in) long with 9 to 35 white, creamy, or ivory flowers densely packed in 2 or 3 ranks in spirally twisted stem with 3-4 flowers per cycle. The rachis (main axis of inflorescence) is pubescent with capitate trichomes (small hairs with spherical heads) and stalked glands producing a light fragrance. The flower period is the third week of July to the third week of September. The floral bracts at the base of the perianth are green ovate to acuminate, 7-17 mm long. The flowers are resupinate (upside down). The outer calyx whorl consists of three white, creamy, or ivory sepals, lanceolate 5.5-11.0 mm long, 1.2-2.2 mm wide. The inner corolla whorl consists of two lateral white, creamy, or ivory petals, linear-lanceolate 6-12 mm long with apex acute to obtuse and a lip petal (labellum) white, creamy, or ivory with a yellow-green center, ovate to oblong, bending downwards, slightly constricted near middle, 5.5-11.0

mm long, 3.0-6.0 mm wide, edge with ragged wavy margin and round apex. The three sepals and two lateral petals form a cylindrical tube that curves over the column. Two prominent calli (hard protuberances) are located at base of lip petal that are longer than wide at about 1.0 mm. There is no nectar spur. This orchid species is capable of agamospermy (formation of seed without fertilization). The insect pollinators are bumble bees (table 10). The viscidia are linear to linear-lanceolate attached to the pollinia. The sticky viscidia becomes attached unto the insects body, the pollinia rotate to the front of the insects head, are brushed over and transferred to the female stigma when the insect moves to the next flower. Millions of minute seeds are produced in a fruit capsule by the fertilized flower. Some of the seeds produced in the capsule are polyembryonic (multiple embryos). Diploid chromosomes are 2n=45,60. Until 1973, Spiranthes cernua was a polymorphic species that included S. magnicamporum. Spiranthes cernua can hybridize with S. lacera, S. romanzoffiana, and S. magnicamporum.

Geographic distribution of nodding lady's tresses occurs throughout eastern and central United States and eastern Canada. In the Northern Plains, it has occurred in w & c Minnesota, Iowa, e & c North Dakota, e South Dakota, and e Nebraska. In North Dakota, it has been located in Cass, Kidder, McHenry, Pembina, Ransom, Richland, and Stutsman counties. It is not listed as threatened or endangered in the United States or Canada.

Spiranthes cernua can occupy a wide range of habitat types of bogs, fens, marshes, open woodlands, lakeshores, and riverbanks, and it extends into the tall grass, eastern mixed grass, and sandhills prairie habitats of wet meadows, and moist to dry prairie with circumneutral soils and short or sparse herbaceous vegetation, and it is an effective colonizer of dunes, swales, ditches, roadsides, old fields, cemeteries, and lawns.

This botanical description summary of nodding lady's tresses was based on works of Stevens 1963, Great Plains Flora Association 1986, Smith 1993, Flora of North America Editorial Committee, eds. 2002.

Table 10. Pollinators of Spiranthes cernua, Nodding lady's tresses.

Bumble bees		
Bombus fervidus	Fabricius	Yellow bumble bee
Bombus impatiens	Cresson	Common eastern bumble bee
Bombus terricola	Kirby	Yellowbanded bumble bee

Data from North American Orchid Conservation Center.

Botanical Description of Great Plains lady's tresses

Great Plains lady's tresses, *Spiranthes magnicamporum* Sheviak, is a member of the orchid family, Orchidaceae, and is a native, perennial, terrestrial (mineral soil), strongly mycotrophic (dependent on symbiotic fungi), monocot, herb. Annual aerial growth is a single erect unbranched stem arising during spring from a perennating shoot bud developed on a crown (caudex) during the previous late summer. Adult plants produce a stem 15-42 cm (5.9-16.5 in) tall, green, pubescent above. Two to three basal leaves sheathing the stem, ascending, linear- lanceolate to oblanceolate, up to 14 cm (5.5 in) long, 1.2 cm (0.5 in) wide and with 4 to 6 green stem (cauline) bracts that overlap upwards. Basal leaves are fugaceous (withering early) about two weeks before flowers appear. Roots are few, stout and fleshy to tuberously thickened to 0.8 cm in diameter fused into fasciated bundles and descending. New roots develop each growing season from root buds formed during the previous late summer. Previous years roots and shoot remnants wither with salvaged contents used for growth of current years shoot and roots. Inflorescence is a tight twisted spike 2.5-10.0 cm (1.0-3.9 in) long with 13 to 48 white or ivory flowers densely packed in two or three ranks on a vertical spiraled stem with 3-4 flowers per cycle. The rachis (main axis of inflorescence) is moderately pubescent with capitate trichomes (small hairs with spherical heads) and obviously stalked glands producing a strong fragrance. The flower period is late August to late September. The floral bracts at the base of the perianth are green ovate to acuminate, 7-23 mm long. The flowers are resupinate (upside down). The outer calyx whorl consists of three white or ivory sepals, linear-lanceolate 7.0-11.0 mm long, 1.5-2.5 mm wide, curved and spreading forming an arch above the column. The inner corolla whorl consists of two lateral white or ivory petals, linear to lance-oblong 4.9-13 mm long, 1.0-2.0 mm wide, with margins crenulate (very small rounded teeth) and apex acute to obtuse and a lip petal (labellum) white or ivory with a yellow center, ovate to oblong, sharply curves downward, not constricted near middle, 7.0-11.0 mm long, 3.5-6.0 mm wide, curves evenly from base to tip, upper portion with ragged wavy margin. Two calli (hard protuberances) are located at base of lip petal and not prominent, less than 1 mm. There is no nectar spur. This orchid species is capable of agamospermy (formation of seed without fertilization). The insect pollinators are bumble bees (table 11). The viscidia are linear-lanceolate attached to the pollinia. The sticky viscidia becomes attached unto the insects body, the pollinia rotate to the front of the insects head, are brushed over and transferred to the female stigma when the insect moves to the next flower. Millions of minute seeds are produced in a fruit capsule by the fertilized flower. All of the seeds are monoembryonic (one embryo). Diploid chromosomes are 2n=30. Spiranthes magnicamporium was separated in 1973 from the polymorphic Spiranthes cernua. Spiranthes magnicamporium can hybridize with S. lacera and S. cernua.

Geographic distribution of Great Plains lady's tresses occurs in central Canada and in the northern and southern Great Plains, Great Lakes, mid western, and southern gulf regions of the United States. In the Northern Plains, it occurs in s Manitoba, w & s Minnesota, Iowa, e & c North Dakota, e & s South Dakota, and Nebraska. In North Dakota, it has been located in Benson, Cass, McHenry, Pembina, Ransom, Richland, and Stutsman counties. It is not listed as threatened or endangered in the United States or Canada.

Spiranthes magnicamporum can occupy habitat types of low moist open grassy spots and it extends into the tall grass, eastern mixed grass, and sandhills prairie habitats of wet meadows, and moist to dry prairie with circumneutral calcareous or gypsum soils and grassland vegetation.

This botanical description summary of Great Plains lady's tresses was based on works of Great Plains Flora Association 1986, Smith 1993, Flora of North America Editorial Committee, eds. 2002.

Table 11. Pollinators of Spiranthes magnicamporum, Great Plains lady's tresses.

Bumble bees		
Bombus fervidus	Fabricius	Yellow bumble bee
Bombus nevadensis	Cresson	Nevada bumble bee

Data from North American Orchid Conservation Center.

Botanical Description of Hooded lady's tresses

Hooded lady's tresses, *Spiranthes romanzoffiana* Chamisso is a member of the orchid family, Orchidaceae, syn: S. stricta (Rydb.) A. Nelson, and is a native, perennial, terrestrial (mineral soil), strongly mycotrophic (dependent on symbiotic fungi), monocot, herb. Annual aerial growth is a single erect stem arising during spring from a perennating shoot bud developed on a crown (caudex) during the previous late summer. Adult plants produce a stem 13-46 cm (5.1-18.1 in) tall, green, glabrous below, pubescent above. Two to five basal leaves sheathing the stem, ascending to spreading, linear to narrowly lanceolate or oblanceolate 5-24 cm (2.0-9.4 in) long, 2.5-9.0 mm wide with middle and upper stem (cauline) leaves much reduced to bracts. Basal and lower stem leaves persist through flowering. Roots are few to several long, thick and fleshy to tuberous mostly to l cm in diameter, spreading and descending. New roots develop each growing season from root buds formed during the previous late summer. Previous years roots and shoot remnants wither with salvaged contents used for growth of current years shoot and roots. Inflorescence is a twisted spike 2.5-13.0 cm (1.0-5.1 in) long with 11 to 45 white to ivory or cream flowers in two or three ranks on vertical columns spirally twisted on the stem. The rachis (main axis of inflorescence) is glabrous (smooth) and fragrant. The flower period is from mid July to late August. The floral bracts at the base of the perianth are green ovate to acuminate 8-20 mm long. The flowers are resupinate (upside down). The outer calyx whorl consists of three white to ivory or cream sepals. The two lateral sepals are lanceolate. The inner corolla whorl consists of two lateral white to ivory or cream petals linear to obtuse 7-11 mm long and the lip petal (labellum). The dorsal sepal and two lateral petals are connivent (converging together but not actually fused) forming a hood over the column. The labellum is 6.0-11.5 mm long, 3.0-4.5 mm wide, strongly constricted above middle producing a fiddle shape (pandurate), with a ragged wavy margin above constriction. Two calli (hard protuberances) located at base of lip petal are small. There is no nectar spur. This orchid species is completely dependent on insects for pollination. The insect pollinators are bumble bees and a honey bee (table 12). The viscidia are linear -lanceolate attached to the pollinia. The sticky viscidia become attached unto the insects body, the pollinia rotate to the front of the insects head, are brushed over and transferred to the female stigma when the insect moves to the next flower. Millions of minute seeds are produced in a fruit capsule 6-7 mm long, 3-4 mm wide by the fertilized flower. All of the seeds are monoembryonic (one embryo). Diploid chromosomes are 2n=44, 66, 88. Spiranthes romanzoffiana can hybridize with S. lacera and S. cernua. This species was named for Count Romanzoff.

Geographic distribution of Hooded lady's tresses is wide across most of Canada, most of central and southern Alaska, across the northern portions, and the mountains and foothills of western United States. In the Northern Plains, it occurs in Alberta, Saskatchewan, Manitoba, n & w Minnesota, nc & nw North Dakota, w South Dakota, Montana, and Wyoming. In North Dakota, it has been located in Benson, Burke, and McHenry counties, which seems to be greatly undersampled. It is not listed as threatened or endangered in the United States or Canada.

Spiranthes romanzoffiana can occupy a wide range of habitat types in tundra, fens, marshes, open wet herbaceous areas in coniferous forests, and sandy, gravelly, and rocky lakeshores, and it extends south into the tall grass, sandhills, mixed grass, and shortgrass prairie habitats of sedge meadows, wet meadows, natural spring seeps, moist prairies, and dunes.

This botanical description summary of Hooded lady's tresses was based on works of Looman and Best 1979, Great Plains Flora Association 1986, Smith 1993, Flora of North America Editorial Committee, eds. 2002.

Table 12. Pollinators of Spiranthes romanzoffiana, Hooded lady's tresses.

Bumble bees and a honey bee		
Apis mellifera	Linnaeus	European honey bee
Bombus bifarius	Cresson	Twoform bumble bee
Bombus flavifrons	Cresson	Yellowhead bumble bee
Bombus insularis	Smith	Indiscriminate cuckoo bumble bee
Bombus perplexus	Cresson	Confusing bumble bee
Bombus terricola	Kirby	Yellowbanded bumble bee
Bombus vagans	Smith	Halfblack bumble bee

Data from North American Orchid Conservation Center.

Botanical Description of Northern slender lady's tresses

Northern slender lady's tresses, *Spiranthes lacera* (Raf.) Rafinesque, is separated into two varieties: var. lacera and var. gracilis, is a member of the orchid family, Orchidaceae, syn: Neottia lacera Raf. and N. gracilis Bigelow, and is a native, perennial, terrestrial (mineral soil), strongly mycotrophic (dependent on symbiotic fungi), monocot, herb. Annual aerial growth is a single erect stem arising during spring from a perennating shoot bud developed on a crown (caudex) during the previous late summer. Adult plants produce a stem 15-65 cm (5.9-25.6 in) tall, sparsely pubescent to glabrous (smooth, no hairs). Two to five short basal leaves, sheathing the stem, form a rosette, spreading, ovate to elliptic, 1.5-6.5 cm (0.6-2.6 in) long, 1-2.5 cm (0.4-1.0 in) wide, with the upper stem (cauline) bracts sheathing stem. Basal leaves of var. lacera are usually persisting through anthesis, and basal leaves of var. gracilis are usually absent at anthesis. Roots are few to several slender to stout, fleshy, mostly to 0.75 cm in diameter fused into fasciated bundles spreading and descending. New roots develop each growing season from root buds formed during the previous late summer. Previous years roots and shoot remnants wither with salvaged contents used for growth of current years shoot and roots. Inflorescence is a spike with up to 40 white flowers, secund (all on one side) to loosely (lax) to very tightly spiraled, with or without space between proximal (lower) flowers. The rachis (main axis of inflorescence) is glabrous to sparsely pubescent with trichomes capitate (small hairs with spherical heads) or clavate (small hairs club-shaped) and glands obviously stalked. The flower period usually is long for four months, and is variable with location from June to October. The floral bracts at the base of the perianth are green ovate to ovate-lanceolate 5-10 mm long, 1-3 mm wide. The flowers are resupinate (upside down). Dorsal sepal is white, elliptic-oblong to oblong-lanceolate, 4-5.5 mm long, 1 mm wide. Lateral sepals are white, lanceolate, 4-5.5 mm long, 1 mm wide. Lateral petals are white, lanceolate, 4-5.5 mm long, 1 mm wide. Lip petal (labellum) is white with distinctive green or yellowish green spot, ovate to oblong, 4-6 mm long, 2-2.5 mm wide, apex dilated (flattened), margin crenate (with small rounded teeth) and crisped (curled inward). Two calli (hard protuberances) are located at base of lip petal, are erect with short point and about 1.0 mm. There is no nectar spur. The insect pollinators are solitary bees and bumble bees (table 13). The viscidia are linear - lanceolate attached to the pollinia. The sticky viscidia become attached unto the insects body, the pollinia rotate to the front of the insects head, are brushed over and transferred to the female stigma when the insect moves to the next flower. Millions of minute seeds are produced in a fruit capsule 3-7 mm long, 2-4 mm wide by the fertilized flower. All of the seeds are monoembryonic (one embryo). Diploid chromosomes are 2n=30. Spiranthes lacera can hybridize with S. romanzoffiana and S. vernalis.

Geographic distribution of Northern slender lady's tresses is spread across eastern and central Canada and throughout eastern United States. In the Northern Plains, it occurs in se Alberta, c Saskatchewan, s Manitoba, w Minnesota, w Iowa, and e Nebraska. It is not listed as threatened or endangered in the United States or Canada.

Spiranthes lacera can occupy a wide range of habitat types of open woodlands and barrens and it extends into the tall grass and sandhills prairie habitats of moist meadows, and moist to dry prairies, and it is an effective colonizer of dunes, old fields, roadsides, cemeteries, and lawns.

This botanical description summary of Northern slender lady's tresses was based on works of Great Plains Flora Association 1986, Smith 1993, Flora of North America Editorial Committee, eds. 2002.

Table 13. Pollinators of Spiranthes lacera, Northern slender lady's tresses.

Bees and Bumble bees		
Anthidiellum notatum	Latreille	Rotund resin bee
Calliopsis andreniformis	Smith	Mining bee
Hoplitis truncata	Wu	Small mason bee
Lasioglossum imitatum	Smith, Walker	Sweat bee
Megachile brevis	Say	Leafcutter bee
Megachile inermis	Provancher	Leafcutter bee
Bombus perplexus	Cresson	Confusing bumble bee
Bombus terricola	Kirby	Yellowbanded bumble bee
Bombus vagans	Smith	Halfblack bumble bee

Data from North American Orchid Conservation Center.

Botanical Description of Twisted lady's tresses

Twisted lady's tresses, *Spiranthes vernalis* Engelmann & Gray, is a member of the orchid family, Orchidaceae, syn: Ibidium vernale (Eng. & Gray) House, and is a native, perennial, terrestrial (mineral soil), strongly mycotrophic (dependent on symbiotic fungi), monocot, herb. Annual aerial growth is a single erect stem arising during spring from a perennating shoot bud developed on a crown (caudex) during the previous late summer. Adult plants produce a stem 20-65 cm (7.9-25.6 in) tall, green, densely pubescent above. Four to five basal leaves sheathing the stem, spreading, linear-lanceolate, keeled, 5-25 cm (2.0-9.8 in) long, 1 cm (0.4 in) wide, with upper stem (cauline) reduced to bracts, linear to narrowly lanceolate. Leaves are usually persisting through anthesis. Roots are numerous, coarse, fusiform (stout in middle) mostly to 1 cm in diameter fused into fasciated bundles spreading. New roots develop each growing season from root buds formed during the previous late summer. Previous years roots and shoot remnants wither with salvaged contents used for growth of current years shoot and roots. Inflorescence is a spike loosely to tightly spiraled with up to 50 white to cream flowers in one rank with 3-7 flowers per cycle. The rachis (main axis of inflorescence) is densely pubescent with reddish or whitish articulate (jointed) hairs with pointed tip and absent of glands. The flower period is long, variable with location from June to October. The floral bracts at the base of the perianth are green ovate to oblong-lanceolate, 7-23 mm long, 4-7.5 mm wide. The flowers are resupinate (upside down). Lateral sepals and lateral petals are equal, lanceolate, 5-10 mm long, 2 mm wide, margin linear, apex obtuse. Lip petal (labellum) is fleshy, ovate 5-8 mm long, 4 mm wide, creamy yellow with two orange or brown spots near center, veins are straight with parallel branches. Two calli (hard protuberances) located at base of lip petal are conic (cone shaped) about 1 mm. There is no nectar spur. The insect pollinators are bumble bees and a honey bee (table 14). The viscidia are linear -lanceolate attached to the pollinia. The sticky viscidia become attached unto the insects body, the pollinia rotate to the front of the insects head, are brushed over and transferred to the female stigma when the insect moves to the next flower. Millions of minute seeds are produced in a fruit capsule obliquely ovoid to elliptic 6-9 mm long, 3.5-6 mm wide by the fertilized flower. All of the seeds are monoembryonic (one embryo). Diploid chromosomes are 2n=30. Spiranthes vernalis can hybridize with S. lacera.

Geographic distribution of twisted lady's tresses is spread across eastern and southcentral United States and expands northward into the southern portion of the Northern Plains. In the Northern Plains, it occurs in w Iowa, e Nebraska, and se South Dakota. It is not listed as threatened or endangered in the United States or Canada.

Spiranthes vernalis can occupy habitat types of moist to dry open herbaceous vegetation and it extends into the southern portions of the northern tall grass prairie habitats of moist meadows and moist to dry prairies and it is an effective colonizer of dune hollows, old fields, roadsides, cemeteries, and lawns.

This botanical description summary of Twisted lady's tresses was based on works of Great Plains Flora Association 1986, and Flora of North America Editorial Committee, eds. 2002.

Table 14. Pollinators of Spiranthes lacera, Twisted lady's tresses.

Honey bee and Bumble bees		
Apis mellifera	Linnaceus	European honey bee
Bombus impatiens	Cresson	Common eastern bumble bee
Bombus pensylvanicus	DeGeer	American bumble bee

Data from North American Orchid Conservation Center.

Botanical Description of White lady's slipper

White lady's slipper, *Cypripedium candidum* Muhlenberg ex Willdenow, is a member of the orchid family, Orchidaceae, and is a native, perennial, terrestrial (mineral soil), strongly mycotrophic (dependent on symbiotic fungi), monocot, herb that is intolerant of shade. Annual aerial growth is a single erect stem arising during spring from a perennating shoot bud developed on a crown (caudex) during the previous late summer. Adolescent plants remain vegetative with two or a few leaves during the growing season for about twelve to maybe sixteen years. Adult plants are long lived, produce a stem 10-35 cm (3.9-13.8 in) tall, green, glabrous (smooth). Two to four crowded leaves develop in the middle portion of stem, alternate, erect, ascending, with blade lanceolate or elliptic to oblanceolate, glabrous (smooth), 5.0-15.0 cm (2.0-5.9 in) long, 2.0-6.0 cm (0.8-2.4 in) wide, and with 2 to 4 bladeless sheaths at lower portion of stem. Rhizomes are short, horizontal forming dense clumps with up to 50 stems or more. Roots are numerous, long, and cordlike. New roots develop each growing season from root buds formed during the previous late summer. Previous years roots and shoot remnants wither with salvaged contents used for growth of current years shoot and roots. Inflorescence is solitary (rarely two) nearly sessile flower that begins development while shoot is still emerging. The flower period is from 19 May-22 June. The floral bracts at the base of the perianth appear early with stem leaves, are green, foliaceous (leaflike), narrowly elliptical 3.3-11.0 cm (1.3-4.3 in) long, 0.9-3.2 cm (0.4-1.3 in) wide. The flowers are resupinate (upside down). The outer calyx whorl consists of three sepals that are green to pale brownish yellow, usually spotted and striped with reddish brown or madder (red). Dorsal sepal is ovate to ovate-lance acuminate (gradually tapering to a sharp point) 1.5-3.5 cm (0.6-1.4 in) long, 0.7-1.3 cm (0.3-0.5 in) wide. Lateral sepals are connate (fused) to form a single sepal (synsepalous) with tip split, located ventrally (directly below the lip petal), 1.3-3.5 cm (0.5-1.4 in) long, 0.7-1.5 cm (0.3-0.6 in) wide. Lateral petals are lanceolate to linear-lanceolate, same color as sepals, spirally or helically twisted, 2.1-4.1 cm (0.8-1.6 in) long, 2.4-4.0 mm wide. Small lip petal (labellum) is calceolate (an inflated pouch, shoe-shaped) ovoid 1.7-2.5 cm (0.7-1.0 in) long, white with faint purple veins or spots and may have purple streaks on the inside. There is no nectar spur. The insect pollinators are small solitary bees and a stink bug (table 15). Insects visit the small labellum to collect nectar and pollen, and transfer the pollen to the female stigma of the next flower. Millions of minute seeds are produced in a fruit capsule that is ellipsoid, 2-3 cm long by the fertilized flower. Diploid chromosomes are 2n=20. Cypripedium candidum can hybridize with C. parviflorum.

Geographic distribution of White lady's slipper is in south central Canada and in the Great Lakes, mid west and Great Plains regions of the United States. In the Northern Plains, it occurs in se Saskatchewan, s Manitoba, w & s Minnesota, Iowa, nc & e North Dakota, e & se South Dakota and c & e Nebraska. In North Dakota, it has been located in Benson, Cass, Dickey, Eddy, Griggs, Richland, Sargent, and Walsh counties. It is not listed as threatened or endangered in the United States or Canada.

Cypripedium candidum can occupy a wide range of habitat types of calcareous fens, edges of marshes, and shrubby to open herbaceous areas in deciduous woodlands and it extends into the tall grass, moist mixed grass, and sandhills prairie habitats of wet meadows, and moist to mesic prairies with calcareous soils in full sunlight.

This botanical description summary of White lady's slipper was based on works of Stevens 1963, Looman and Best 1979, Great Plains Flora Association 1986, Smith 1993, and Flora of North America Editorial Committee, eds. 2002.

Table 15. Pollinators of Cypripedium candidum, White lady's slipper.

Solitary Bees and a stink bug		
Andrena barbilabris	Kirby	Mining bee
Andrena ziziae	Robertson	Mining bee
Augochlorella aurata	Smith	Golden sweat bee
Ceratina calcarata	Robertson	Small carpenter bee
Halictus confusus	Smith	Sweat bee
Halictus ligatus	Say	Sweat bee
Lasioglossum anomalum	Robertson, Rayment	Sweat bee
Lasioglossum cinctipes	Provancher	Sweat bee
Lasioglossum cressonii	Robertson	Sweat bee
Lasioglossum hitchensi	Gibbs	Sweat bee
Lasioglossum pilosum	Smith	Sweat bee
Lasioglossum rohweri	Ellis	Sweat bee
Cosmopepla lintneriana	Kirkaldy	Twice stabbed stink bug

Data from North American Orchid Conservation Center.

Botanical Description of Yellow lady's slipper

Yellow lady's slipper, *Cypripedium parviflorum* Salisbury, has been separated into several varieties that form an overlapping continuum of a single polymorphic taxon, is a member of the orchid family, Orchidaceae, and is a native, perennial, terrestrial (peat and mineral soil), strongly mycotrophic (dependent on symbiotic fungi), monocot, herb, that is tolerant of both shade and direct sunlight. Annual aerial growth is a single erect stem arising during spring from a perennating shoot bud developed on a crown (caudex) during the previous late summer. Adolescent plants remain vegetative with two or a few leaves during the growing season for nine to twelve years. Adult plants are long lived, produce a stem 12-60 cm (4.7-23.6 in) tall, pubescent (hairy) with glands that can produce a rash upon contact with susceptible people. Two to five stem (cauline) leaves develop evenly spaced along the stem, are alternate, erect or spreading, with blade ovate to elliptical, elliptic-lanceolate, 6.0-20.0 cm (2.4-7.9 in) long, 2.5-10.0 cm (1.0-3.9 in) wide, and with 2 to 4 bladeless sheaths at lower portion of stem 5-15 cm long. Rhizomes are stout creeping horizontally, forming large colonies with up to 10 stems per rhizome. Roots are numerous, fibrous, long, and cordlike. New roots develop each growing season from root buds formed during the previous late summer. Previous years roots and shoot remnants wither with salvaged contents used for growth of current years shoot and roots. Inflorescence is solitary (rarely two) nearly sessile. The flower period is from 10 May-12 July. The floral bracts at the base of the perianth are green, foliaceous (leaflike), ovate to ovate-elliptical, 2.5-10.0 cm (1.0-3.9 in) long, 0.6-4.0 cm (0.2-1.6 in) wide. The flowers are resupinate (upside down). The outer calyx whorl consists of three sepals that are greenish, or yellowish with spots or strips tinted dark reddish, brown, or red. Dorsal sepal is ovate to ovate-lanceolate, acuminate (gradually tapering to a sharp point) 2.0-7.0 cm (0.8-2.8 in) long, 0.5-3.0 cm (0.2-1.2 in) wide, located arched above lip petal. Lateral sepals are connate (fused) to form a single sepal (synsepalous) with tip split, located ventrally (directly below the lip petal), 1.1-8.0 cm (0.4-3.0 in) long, 0.5-3.4 cm (0.2-1.3 in) wide. Lateral petals are lance-linear, spirally twisted, 2.5-9.5 cm (1.0-3.7 in) long, 3.0-6.0 cm (1.2-2.4 in) wide, same color as sepals. Lip petal (labellum) is calceolate (an inflated pouch or sac, shoe-shaped) obovate, 1.6-6.0 cm (0.6-2.4 in) long, pale to deep yellow, orifice is basal, 10-17 mm. There is no nectar spur. The insect pollinators are small bees (table 16). Insects visit the labellum to collect nectar and pollen, and transfer the pollen to the female stigma of the next flower. Millions of minute seeds are produced in a fruit capsule that is ellipsoid, 2-3.5 cm long, 1 cm wide, by the fertilized flower. Diploid chromosomes are 2n=20. Cypripedium parviflorum can hybridize with C. candidum and C. montanum.

Geographic distribution of Yellow lady's slipper is spread throughout eastern, central, and western provincial Canada, and across the Great Lakes, mid west and northern rocky mountain regions of the United States. In the Northern Plains, it occurs in Alberta, Saskatchewan, Manitoba, n & w Minnesota, Iowa, e & nc North Dakota, w South Dakota, nw Nebraska, w Montana, and w Wyoming. In North Dakota, it has been located in Benson, Bottineau, Grand Forks, McHenry, Pembina, Ransom, Rolette, Sargent, and Walsh counties. It is not listed as threatened or endangered in the United States or Canada.

Cypripedium parviflorum can occupy a wide range of habitat types of fens, peat swamps, openings on slopes with herbaceous or thicket vegetation in the eastern, northern, and Rocky Mountain coniferous, deciduous, and aspen woodlands, and it extends into the tall grass prairie and moist mountain meadow habitats of wet meadows and moist prairies in shade or direct sunlight.

This botanical description summary of Yellow lady's slipper was based on works of Stevens 1963, Looman and Best 1979, Great Plains Flora Association 1986, Smith 1993, Flora of North America Editorial Committee, eds. 2002, and Larson and Johnson 2007.

Table 16. Pollinators of Cypripedium parviflorum, Yellow lady's slipper.

Bees		
Agapostemon spp		Striped sweat bee
Andrena barbilabris	Kirby	Mining bee
Andrena ziziae	Robertson	Mining bee
Apis mellifera	Linnaeus	European honey bee
Ceratina calcarata	Robertson	Small carpenter bee
Eristalis spp		Honeybee drone
Osmia spp		Mason bee
Lasioglossum rohweri	Ellis	Sweat bee

Data from North American Orchid Conservation Center.

Botanical Description of Showy lady's slipper

Showy lady's slipper, *Cypripedium reginae* Walter, is a member of the orchid family, Orchidaceae, syn: C. spectabile Salisbury, and is a native, perennial, terrestrial (peat and mineral soil), strongly mycotrophic (dependent on symbiotic fungi), monocot, herb, that is tolerant of both shade and direct sunlight. Annual aerial growth is a single erect stem arising during spring from a perennating shoot bud developed on a crown (caudex) during the previous late summer. Adolescent plants remain vegetative with two or a few leaves during the growing season for fourteen or sixteen years. Adult plants are long lived at about fifty years, produce a stem 30-60 cm (11.8-23.6 in) tall, densely pubescent with soft glandular hairs that are capable of producing an irritation resulting in a poison ivy like rash in most people. Three to nine stem (cauline) leaves develop evenly spaced along the stem, are alternate, ascending to spreading, with blade ovate or elliptic-lanceolate to broadly elliptical 12.0-25.0 cm (4.7-9.8 in) long, 4-14.0 cm (1.6-5.5 in) wide, and with one to three bladeless sheaths at lower portion of stem. Leaves are pubescent, covered with soft hairs. Rhizomes are coarse and knotty, creeping horizontally, forming colonies with up to 20 stems arising per rhizome. Rhizomes are long lived, for 100 years or more. Roots are numerous, long, and cordlike. New roots develop each growing season from root buds formed during the previous late summer. Previous years roots and shoot remnants wither with salvaged contents used for growth of current years shoot and roots. Inflorescence of one or often two flowers with short pedicels. The flower period is from early June to mid July. The floral bracts at the base of the perianth are green, foliaceous (leaflike), elliptical to elliptic-lanceolate 6.0-14.0 cm (2.4-5.5 in) long, 2.6-7.0 cm (1.0-2.8 in) wide. The flowers are resupinate (upside down). The outer calyx whorl consists of three sepals that are white. Dorsal sepal is ovate-orbicular to broadly elliptical 3.0-5.0 cm (1.2-2.0 in) long, 2.6-7.0 cm (1.0-2.8 in) wide, located arched above lip petal. Lateral sepals are connate (fused) to form a single sepal (synsepalous) ovate to broadly elliptical 3.0-4.5 cm (1.2-1.8 in) long, 1.8-3.5 cm (0.7-1.4 in) wide, oblique and flat, not twisted, located ventrally (directly below the lip petal). Lateral petals are oblong to elliptic, flat, white, 3.0-4.5 cm (1.2-1.8 in) long, 1.8-3.5 cm (0.7-1.4 in) wide. Lip petal (labellum) is calceolate (an inflated pouch or sac, shoe-shaped) subglobose (not spherical) 3.0-5.5 cm (1.2-2.2 in) long, white streaked with pale pink, pink, to crimson, or magenta (vivid purplish red), oriface is basal. There is no nectar spur. The insect pollinators are small bees and a beetle (table 17). Insects visit the labellum to collect nectar and pollen, and transfer the pollen to the female stigma of the next flower. Millions of minute seeds are produced in a fruit capsule that is ellipsoid to oblong-ellipsoid, 2.5-4.5 cm long, by the fertilized flower. Diploid chromosomes are 2n=20.

Geographic distribution of Showy lady's slipper is a westwardly expanded Great Lakes region of Canada and the United States. In the Northern Plains, it occurs in se Saskatchewan, s Manitoba, n & nw Minnesota, e Iowa, and e & nc North Dakota. In North Dakota, it has been located in Benson, Cavalier, Eddy, Pembina, Ransom, and Richland counties. It is not listed as threatened or endangered in the United States or Canada.

Cypripedium reginae can occupy habitat types of peat swamps, fens, natural seeps, shrub swamps, and wet herbaceous dominated openings in coniferous and deciduous forests, and it extends into the tall grass and moist mixed grass prairie habitats of sedge meadows, wet meadows, and mesic prairies with limy neutral soils in shade or direct sunlight.

This botanical description summary of Showy lady's slipper was based on works of Stevens 1963, Looman and Best 1979, Great Plains Flora Association 1986, Smith 1993, and Flora of North America Editorial Committee, eds. 2002.

Table 17. Pollinators of Cypripedium reginae, Showy lady's slipper.

Bees and a beetle		
Anthophora abrupta	Say	Miner bee
Megachile centuncularis	Linnaeus	Leafcutter bee
Megachile melanophaea	Smith	Leafcutter bee
Trichiotinus assimilis	Kirby	Hairy flower scarab

Data from North American Orchid Conservation Center.

Botanical Description of Northern green orchid

Northern green orchid, *Platanthera aquilonis* Sheviak, is a member of the orchid family, Orchidaceae, syn: Limnorchis viridiflora (Cham.) Rydb., has repeatedly been confused with tetraploid P. hyperborea (L.) Lindl. of Greenland and Iceland, and is a native, perennial, terrestrial (peat and mineral soil), strongly mycotrophic (dependent on symbiotic fungi), monocot, herb, that is tolerant of both shade and direct sunlight. Annual aerial growth is a single erect stem arising during spring from a perennating shoot bud developed on a crown (caudex) during the previous late summer. Adult plants produce a stem 15-60 cm (5.9-23.6 in) tall, green, stout, glabrous (smooth). Two to six leaves develop sheathing the stem, with size gradually reduced to bracts, oblong to linear-lanceolate, 2.7-25 cm (1.1-9.8 in) long, 0.4-4.0 cm (0.2-1.6 in) wide. Roots are fleshy, elongate, and slender. New roots and a tuber develop each growing season from root and tuber buds formed during the previous late summer. Previous years roots, tuber, and shoot remnants wither with salvaged contents used for growth of current years shoot, tuber, and roots. Inflorescence is a terminal raceme 4-25 cm (1.6-9.8 in) tall, loosely or densely flowered with 13 to 65 small, green, yellowish green, or greenish white, scentless, flowers. The flower period is from 16 June to 11 August. The floral bracts at the base of the perianth are green, lanceolate, 0.6-2.8 cm (0.2-1.1 in) long. The flowers are resupinate (upside down). Dorsal sepal located above the lip petal is ovate to ovate-elliptical, 2.8-6.0 mm long, 1.8-3.0 mm wide. Lateral sepals are spreading to reflexed (bent backward), long and narrow ovate to elliptic-lanceolate. Lateral petals are fleshy, as long as lateral sepals, rhombic-ovate-lanceolate, asymmetrical and falcate (sickle shaped), dilated (flattened) at base, connivent (converging, but not fused) with dorsal sepal to form a vague hood over the column. Lip petal (labellum) is descending, dilated (flattened) at base, lanceolate 3.0-6.0 mm long, 0.8-2.2 mm wide. Nectar spur is 2.5-6.5 mm long with clavate (club shaped) or cylindric (cylinder shaped) tube. The flowers are commonly self-pollinating. As each flower matures, the pollinia rotate forward and downward out of the pollen sacs and the pollen spills onto the female stigma. Millions of minute seeds are produced in a fruit capsule that is obliquely ellipsoid, 1-1.5 cm long, 4-7 mm wide, by the self-fertilized flower. Diploid chromosomes are 2n=42, 84. Platanthera aquilonis can hybridize with P. dilatata.

Geographic distribution of Northern green orchid is extensive across most of Canada, most of Alaska, and extends across the northern, and rocky mountain regions of the United States. In the Northern Plains, it occurs in Alberta, Saskatchewan, Manitoba, n & w Minnesota, ne Iowa, se & nc North Dakota, w South Dakota, nw Nebraska, Montana, and Wyoming. In North Dakota, it has been located in Barnes, Bottineau, LaMoure, and Ransom counties. It is not listed as threatened or endangered in the United States or Canada.

Platanthera aquilonis can occupy a wide range of habitat types of tundra, fens, marshes, bogs, swamps, streambanks, lakeshores, and wet herbaceous dominated areas in mesic deciduous forests in peat or mineral soils with a wide range of pH, in shade or full sunlight, and it extends into the tall grass, and mesic mixed grass prairie habitats of sedge meadows, wet meadows, grass swales, and is an effective colonizer of ditches, roadsides, and borrow pits in mineral soils with a wide range of pH.

This botanical description summary of Northern green orchid was based on works of Stevens 1963, Looman and Best 1979, Great Plains Flora Association 1986, Currah et al. 1990, Smith 1993, Flora of North America Editorial Committee, eds. 2002, and Larson and Johnson 2007.

Botanical Description of Longbracted frog orchid

Longbracted frog orchid, *Coeloglossum viride* (L.) Hartman, is a member of the orchid family, Orchidaceae, syn: Habenaria viridis (L.) Brown, it is morphologically different but has little molecular divergence from a separate but closely related genera of Dactylorhiza viridis (L.) Bateman, Pridgeon & Chase, and is a native, perennial, terrestrial (well drained mineral soil), strongly mycotrophic (dependent on symbiotic fungi), monocot, herb, that prefers full shade. Annual aerial growth is a single erect stem arising during spring from a perennating shoot bud developed on a crown (caudex) during the previous late summer. Adult plants produce a stem 14-53 cm (5.5-20.9 in) tall, green, glabrous (smooth). Two to six stem (cauline) leaves develop, the middle ones are elliptical to oblong or obovate 5.0-13.0 cm (2.0-5.1 in) long, 0.8-6.5 cm (0.3-2.6 in) wide and rather blunt, the upper leaves are lanceolate and reduced to long floral bracts, and the lower ones are bladeless sheaths. Roots are few, fleshy, and palmately spreading from caudex. New roots and a tuber develop each growing season from root and tuber buds formed during the previous late summer. Previous years roots, tuber, and shoot remnants wither with salvaged contents used for growth of current years shoot, tuber, and roots. Inflorescence is a terminal spicate raceme 4.5-24.0 cm (1.8-9.5 in) long with 11 to 76 greenish flowers tinted with dull red or brown. The flower period is from 20 May to 9 August, with the flowers persisting for weeks after pollination. The long floral bracts at the base of the perianth of each flower are green, widely spreading foliaceous (leaflike) lanceolate 1.0-5.5 cm (0.4-2.2 in) long, 0.3-1.2 cm (0.1-0.5 in) wide, which is 2 to 3 times longer than the flowers and is the bases for the common name. The outer calyx whorl consists of three sepals and the inner corolla whorl consists of three petals. Dorsal sepal is broadly ovate to nearly elliptical, 3.0-5.5 mm long, 1.7-3.0 mm wide and forms a hood over the column. The two lateral sepals are ovate oblique (with uneven sides) 4.2-7.0 mm long, 2.0-4.0 mm wide. The two lateral petals are linear to lance-linear, 3.5-4.5 mm long, 0.6 mm wide. Lip petal (labellum) is descending, oblong or strap shaped 4.0-11.0 mm long, 0.8-3.5 mm wide, with truncate (squared off) apex that has two long blunt parallel teeth. The nectar spur is an inconspicuous spherical pouch shaped bag, 2.0-2.7 mm across. If this orchid has insect pollinators, they are unknown. The flowers are capable of autogamy (self-pollination). Millions of minute seeds are produced in an ascending ellipsoid fruit capsule 7-14 mm long, 4-5 mm wide. Diploid chromosomes are 2n=40. This orchid has widely variable characteristics and hybrids are not known.

Geographic distribution of Longbracted frog orchid covers a wide global circumboreal expanse across Eurasia, most of Canada, and the Appalachia, Great Lakes, and Rocky Mountain regions of the United States. In the Northern Plains, it occurs in Alberta, Saskatchewan, Manitoba, nw & c Minnesota, w Iowa, e & w Nebraska, w South Dakota, and sw & c North Dakota. In North Dakota, it has been located in McLean, Morton, and Stark counties. It is not listed as threatened or endangered in the United States or Canada.

Coeloglossum viride can occupy a wide range of habitat types of tundra, coastal heaths, thickets, bogs, and moist to wet deciduous and coniferous forests in well drained acidic mineral soils with full shade, and it extends into the tall grass, and mixed grass prairie habitats of open herbaceous dominated areas in woodlands, wet meadows, and mesic prairies.

This botanical description summary of Longbracted frog orchid was based on works of Stevens 1963, Great Plains Flora Association 1986, Currah et al. 1990, Smith 1993, Flora of North America Editorial Committee, eds. 2002, and Larson and Johnson 2007.

Botanical Description of Rose pogonia

Rose pogonia, *Pogonia ophioglossoides* (L.) Ker-Gawler, is a member of the orchid family, Orchidaceae, syn: Arethusa ophioglossoides L., and is a native, perennial, terrestrial (peat and mineral soil), strongly mycotrophic (dependent on symbiotic fungi), monocot, herb. Annual aerial growth is a single erect unbranched stem arising during spring from a perennating shoot bud developed on a crown (caudex) during the previous late summer. Adult plants produce a stem 20-30 cm (7.9-11.8 in) tall, green, slender and glabrous (no hairs). One solitary leaf develops about mid stem is sessile (no stalk), the blade is veiny, elliptical, lanceolate, lance-ovate, or oblong 4-5 cm (1.6-2.0 in) long, 1-2 cm (0.4-0.8 in) wide. Lateral stolons (aboveground off shoots) gives rise to aerial shoots at intervals of 10 cm (3.9 in) or more. Roots are few, fibrous. New roots develop each growing season from root buds formed during the previous late summer. Previous years roots, and shoot remnants wither with salvaged contents used for growth of current years shoot, and roots. Inflorescence is a terminal solitary flower (rarely two) on a pedicel. The flower period is from 14 June to 30 July. Flowers are resupinate, upside down due to twisting of pedicel when bud opens. The floral bracts at the base of the perianth are prominent, green, foliaceous (leaflike), oblong, ovate, to elliptical 1.2-5.0 cm (0.5-2.0 in) long, 2-10 mm wide. The outer calyx whorl consists of three sepals and the inner corolla whorl consists of three petals, pink to purple, rarely white or blueish. Three sepals are widely spreading, oblong, elliptical, or lanceolate, 1.3-2.4 cm (0.5-0.9 in) long, 2.0-6.0 mm wide. Lateral petals are broadly elliptical to lance-obovate 1.3-2.3 cm (0.5-0.9 in) long, 0.7-1.2 cm (0.3-0.5 in) wide. Lip petal (labellum) is narrowly oblong to spatulate (spatula shape) widest near apex and tapering to base 1.4-2.1 cm (0.6-0.8 in) long, 5-10 mm wide, pinkish to dark pink with conspicuous beard of red short fleshy bristles rising vertically from a crest on the upper portion of the lip and a row of red fleshy bristles at the apical margin. The enlarged receptacle disk around the base of the ovary is bearded with three veins of yellow bristles. The curved column is pink, 8-11 mm long. The insect pollinators are bumble bees (table 18). A bumble bee lands on the fragrant labellum, puts its head deep into the flower, brushes against the anther and a pollinia attaches to the bee's head, and transfers pollen to the female stigma of the next flower. Millions of minute seeds are produced in a fruit capsule that is erect ellipsoid 1.4-3.0 cm (0.6-1.2 in) long, 0.4-0.8 cm (0.2-0.3 in) wide. Diploid chromosomes are 2n=18.

Geographic distribution of Rose pogonia occurs in southern east and central Canada and spread throughout eastern United States and expands westward into the north central region. In the Northern Plains, it occurs in se Manitoba, n Minnesota, and ne North Dakota. In North Dakota, it has been located in Grand Forks county. It is not listed as threatened or endangered in the United States or Canada.

Pogonia ophioglossoides can occupy habitat types of swamps, bogs, and fens with strongly to weakly acidic peat soils, and open herbaceous areas in coniferous and deciduous forests, open woodlands, savannas, and streambanks with wet to moist mineral soils, and it extends into the tall grass prairie habitats of marshy meadows, sedge meadows, wet meadows, moist prairies, and natural spring seeps with partial shade, and it is an effective colonizer of ditches and roadcuts.

This botanical description summary of Rose pogonia was based on works of Great Plains Flora Association 1986, Smith 1993, and Flora of North America Editorial Committee, eds. 2002.

Table 18. Pollinators of Pogonia ophioglossoides, Rose pogonia.

Bumble bees		
Bombus borealis	Kirby	Northern amber bumble bee
Bombus fervidus	Fabricius	Yellow bumble bee
Bombus sandersoni	Franklin	Sanderson bumble bee
Bombus ternarius	Say	Tricolored bumble bee
Bombus terricola	Kirby	Yellowbanded bumble bee
Bombus vagans	Smith	Halfblack bumble bee

Data from North American Orchid Conservation Center.

Management of Grassland Orchid Habitat

Grasslands are complex ecosystems; exceedingly more complex than the most complicated machines ever built by humans. Grassland ecosystems are comprised of biotic and abiotic components. The indispensable biotic components are grass vegetation, rhizosphere organisms, and domesticated graminivores which have biological and physiological requirements. The abiotic components include radiant energy from sunlight, the major essential elements of carbon, hydrogen, nitrogen, and oxygen, and the minor essential elements of macro - and micro - nutrients required by living organisms and environmental conditions. Grass plants, rhizosphere organisms, and grazing graminivores have developed complex symbiotic relationships. Grazing graminivores depend on grass plants for nutritious forage. Grass plants depend on rhizosphere organisms for mineralization of essential elements from the soil organic matter. Rhizosphere organisms, which are achlorophyllous, depend on grass plants for short chain carbon energy that is exudated through the roots of lead tillers at vegetative growth stages following partial defoliation by grazing graminivores. Grass plants produce double the leaf biomass than is needed for photosynthesis in order to attract the vital partial defoliation by grazing graminivores on which they depend.

The indispensable rhizosphere microorganisms are responsible for the performance of the ecosystem biogeochemical processes that determine grassland ecosystem productivity and functionality. Biogeochemical processes transform stored essential elements from organic forms or ionic forms into plant usable mineral 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 soil organic matter for later use. Biogeochemical processes decompose complex unusable organic material into compounds and then into reusable major and minor essential elements (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).

Perpetuation of life on earth requires that the abiotic major and minor essential elements be reused over and over. Recycling of the essential elements is performed by rhizosphere microorganisms. The essential elements are required for life to exist by ensuring growth and development of organisms and the maintenance of all life functions (table 19). Animals require twenty one elements and plants require seventeen elements. Sixteen of the same essential elements are required by both animals and plants. The four major essential elements: carbon (C), hydrogen (H), nitrogen (N), and oxygen (O) are required in very large amounts by animals and plants. A portion of the major essential elements is lost annually from grassland ecosystems by natural processes and a portion is removed from grassland ecosystems as weight biomass produced by insects and wildlife and as animal growth from essential elements transferred from grass plants to grazing livestock. When greater quantities of major essential elements are lost and removed than the quantities accumulated, the ecosystem degrades (declines). When greater quantities of major essential elements are accumulated than the quantities removed, the ecosystem aggrades (improves). Biologically effective management strategies can replenish the quantity of lost or removed major essential elements by capturing input essential elements from the surrounding environment through ecosystem biogeochemical processes performed by the indispensable rhizosphere microorganisms.

Animals and plants require large amounts of the same five macronutrients: potassium (K), calcium (Ca), phosphorus (P), magnesium (Mg), and sulfur (S). Animals require one additional macronutrient: sodium (Na) and require chlorine (Cl) as a macronutrient. Warm season plants and cacti use some sodium (Na). Animals and plants require very small amounts of the same seven micronutrients or trace elements: iron (Fe), manganese (Mn), zinc (Zn), copper (Cu), molybdenum (Mo), and nickel (Ni). Animals require four additional micronutrients: iodine (I), cobalt (Co), selenium (Se), and chromium (Cr). Plants require one additional micronutrient: boron (B), and require chlorine (Cl) as a micronutrient. A few plants and rhizobia use some cobalt (Co).

The ecosystem source for all of the minor essential elements required by animals and plants is weathered parent material. The elemental content of the parent material greatly influences the quantity of macro - and micronutrients in the soil. The minor essential elements are stored in the soil organic matter as unavailable organic forms or as ions adsorbed by colloidal complexes and are biologically and chemically immobilized, respectively. While in these stable forms, the minor essential elements are not subjected to potential losses through volatilization or leaching movement (Legg 1975, Gibson 2009). The

immobilized minor essential elements are made available through the ecosystem biogeochemical cycles performed by rhizosphere microorganisms (McGill and Cole 1981, Cheng and Johnson 1998, Manske 2012b, 2014c). The quantity of available minor essential elements is detemined by the recycling rates of soil organic matter decomposition and mineralization that are directly regulated by the biomass of active rhizosphere microorganisms.

Table 19. Essential Elements Required by Animals and Plants.

Major Essential Elements required by animals and plants

Carbon (C), Hydrogen (H), Nitrogen (N), Oxygen (O)

Minor Essential Elements

Macronutrients required by animals and plants

Potassium (K), Calcium (Ca), Phosphorus (P), Magnesium (Mg), Sulfur (S)

Macronutrients required by animals

Sodium (Na), Chlorine (Cl)

Micronutrients required by animals and plants

Iron (Fe), Manganese (Mn), Zinc (Zn), Copper (Cu)

Molybdenum (Mo), Nickel (Ni)

Micronutrients required by animals

Iodine (I), Cobalt (Co), Selenium (Se), Chromium (Cr)

Micronutrients required by plants

Boron (B), Chlorine (Cl)

Blue elements required by both animals and plants, Red elements required by animals, Green elements required by plants.

The quantity of ecosystem biogeochemical processes conducted is also dependent on the quantity of rhizosphere microorganism biomass (Coleman et al. 1983). The greater the microbial biomass, the greater the grassland ecosystem productivity. The greater the productivity, the greater the annual increase in soil organic matter. Increases in the organic matter content of a soil improves the stability of soil aggregates, improves the physical and chemical properties, improves soil air and water infiltration and water holding capacity, improves soil fertility, and increases cation exchange capacity (Schimel, Coleman, and Horton 1985, Six et al. 1998, 2004).

The indispensable grass vegetation provides nutritious forage to large grazing graminivores. Grass plants use the major and minor essential elements in the inorganic form to synthesize vital organic components of carbohydrates, proteins, and nucleic acids for growth. Grass plants have four primary internal plant growth mechanisms that help grass tillers withstand and recover from partial defoliation by grazing graminivores. The primary mechanisms are: compensatory physiological mechanisms (McNaughton 1979, 1983; Briske 1991); vegetative reproduction by tillering (Mueller and Richards 1986, Richards et al. 1988, Murphy and Briske 1992, Briske and Richards 1994, 1995); nutrient resource uptake (Crider 1955, Li and Wilson 1998, Kochy and Wilson 2000, Peltzer and Kochy 2001); and water use efficiency (Wight and Black 1972, 1979).

Compensatory physiological mechanisms give grass plants the capability to replace lost leaf and shoot biomass following partial grazing defoliation by increasing meristematic tissue activity, increasing photosynthetic capacity, and increasing allocation of carbon and nitrogen. Fully activated mechanisms can produce replacement foliage at 140% of the herbage weight that was removed during grazing (Manske 2000a, b, 2010a, b, 2014a, b). The growth rates of replacement leaves and shoots increase after partial defoliation by grazing. The enhanced activity of meristematic tissue produces larger leaves with greater mass (Langer 1972, Briske and Richards 1995). Developing leaf primordia not fully expanded at time of defoliation have increased growth rates and tend to grow larger than leaves on undefoliated tillers (Langer 1972). Partial defoliated tillers increase photosynthetic rates of remaining mature leaves and rejuvenated portions of older leaves not completely senescent (Atkinson 1986, Briske and Richards 1995). Changes in cytokinin levels and other signals produced as a result of the increase in the root-shoot

ratio rejuvenate the photosynthetic apparatus, inhibit or reduce the rate of senescence, and increase the life span and leaf mass of remaining mature leaves (Briske and Richards 1995). Activation of the compensatory physiological mechanisms after partial defoliation of grass tillers by grazing require alternative sources of abundant carbon and nitrogen (Coyne et al. 1995). Carbon fixed during current photosynthesis in remaining mature leaf and shoot tissue and rejuvenated portions of older leaves is preferentially allocated to areas of active meristematic tissue (Ryle and Powell 1975, Richards and Caldwell 1985, Briske and Richards 1995, Coyne et al. 1995). The quantity of leaf area required to fix adequate quantities of carbon is 67% to 75% of the predefoliated leaf area (Manske 1999, 2011b, 2014c). Very little, if any, of the carbon and nitrogen stored in the root system is remobilized to support compensatory growth (Briske and Richards 1995). The mobilizable nitrogen pools in the shoot tissue are reduced following partial defoliation. This loss in nitrogen from the shoot increases preferential use of the quantities of mineral nitrogen available in the media around the roots (Millard et al. 1990, Ourry et al. 1990). This available soil mineral nitrogen has been converted from soil organic nitrogen by active rhizosphere organisms, absorbed though the roots, and moved to areas of active meristematic tissue.

Vegetative secondary tillers are shoots that develop on lead tillers from growth of axillary buds by the process of tillering (Dahl 1995). 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 (Briske and Richards 1995). Tiller growth from axillary buds is inhibited indirectly by auxin interference with the metabolic function of cytokinin, a growth hormone (Briske and Richrds 1995). Partial defoliation of young leaf material at vegetative growth stages temporarily reduces the production of the blockage hormone, auxin (Briske and Richards 1994). The abrupt reduction of plant auxin in the lead tiller allows for cytokinin synthesis or utilization in multiple axillary buds, stimulating the development of vegetative secondary tillers (Murphy and Briske 1992, Briske and Richards 1994). 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 gradationally 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. This developing secondary tiller produces auxin that hormonally

suppresses development of additional axillary buds (Briske and Richards 1995). Vegetative tiller growth is the dominant form of reproduction in semiarid and mesic grasslands (Belsky 1992, Chapman and Peat 1972, Briske and Richards 1995, Chapman 1996, Manske 1999) not sexual reproduction and the development of seedlings. 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.

Grass plant dominance within a grassland community is related to the plants competitiveness at nutrient and water resource uptake. Crider (1955) found that grass tillers with 50% or more of the aboveground leaf material removed reduce root growth, root respiration, and root nutrient absorption resulting in reduced functionality of these grass plants. Reduction of active root biomass caused diminishment of grass plant health and vigor (Whitman 1974) that resulted in a loss of resource uptake efficiency and a suppression of the competitiveness of grass plants to take up mineral nitrogen, essential elements, and soil water (Li and Wilson 1998, Kochy 1999, Kochy and Wilson 2000, Peltzer and Kochy 2001). The loss of active root length contributed to the reduction of rhizosphere biomass and the decline of ecosystem biogeochemical processes (Coleman et al. 1983, Klein et al. 1988). The nutrient resource uptake competitiveness of healthy grasses is able to suppress the expansion of shrubs and prevent successful establishment of grass, forb, and shrub seedlings into grasslands (Peltzer and Kochy 2001). The grass growth form has competitive advantages of nutrient uptake over the shrub growth form (Kochy and Wilson 2000). Grass aboveground biomass is primarily productive photosynthetic leaves resulting in a high resource uptake efficiency. Grasses are good competitors for belowground nutrient resources and superior competitors for mineral nitrogen because of a high root: shoot ratio and no woody stems to maintain. Shrubs have a great reduction in resource uptake efficiency because a large portion of the photosynthates produced in the leaves must be used to build and maintain their unproductive woody stems. However, the taller woody stems make shrubs superior competitors for aboveground sunlight resources (Kochy and Wilson 2000). Competition for belowground nutrient resources from healthy grasses reduce the growth

rates of shrub rhizomes and cause high mortality rates of young sucker (Li and Wilson 1998). Shrubs can compete for some of the belowground resources only after the grass plants have been degraded by ineffective management. Following the reduction in grass plant resource uptake competitiveness, the belowground resources 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). With greater nutrient resources, shrub rhizome suckers are able to establish a faster growth rate and a higher survival rate (Li and Wilson 1998). The resulting greater shrub stem density increases the competition for the aboveground resources of light causing strong suppression of the grasses (Kochy and Wilson 2000). Traditionally, the observation of increasing woody shrubs and trees into grasslands would have been explained as a result of fire suppression (Humphrey 1962, Stroddart, Smith, and Box 1975, Wright and Bailey 1982). The invasion of the cool season exotic grasses, Kentucky bluegrass, and smooth bromegrass, into much of the northern mixed grass prairie was presumed to be caused by the absence of fire (Kirsch and Kruse 1972). 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).

Grasslands of the Northern Plains managed with traditional practices are notorious for their inhibitory deficiency in available soil mineral nitrogen (Goetz et al. 1978) which has been determined to cause the observed low herbage production. Deficiencies in mineral nitrogen limit herbage production more often than water deficiencies in temperate grasslands (Tilman 1990). Total herbage biomass production on grassland ecosystems has been shown to increase with increases in the quantity of available soil mineral nitrogen (Rogler and Lorenz 1957; Whitman 1957, 1963, 1976; Smika et al. 1965; Goetz 1969, 1975; Power and Alessi 1971; Lorenz and Rogler 1972; Taylor 1976; Wight and Black 1979). Greater quantities of available soil mineral nitrogen has been shown to also cause the soil water use efficiency to improve in grassland plants (Smika et al. 1965, Wight and Black 1972, Whitman 1976, 1978). Using a proxy method, Wight and Black (1972) found that precipitation (water) use efficiency of grass plants improved when soil mineral nitrogen was available at threshold quantities of 100 lbs/ac (112 kg/ha) and greater. The inhibitory deficiencies of mineral nitrogen on grasslands that had less than 100 lbs/ac of available

soil mineral nitrogen caused the weight of herbage production per inch of precipitation received to be reduced an average of 49.6% below the weight of herbage produced per inch of precipitation on the grassland ecosystem that had greater than 100 lbs/ac of mineral nitrogen and did not have mineral nitrogen deficiencies (Wight and Black 1979). The efficiency of water use in grass plants function at low levels when mineral nitrogen is deficient, and function at high levels when mineral nitrogen is available at threshold quantities of 100 lbs/ac or greater. The level of water use efficiency determines the level of herbage biomass productivity on grasslands. Manske (2010a, b) found that the threshold quantity of 100 lbs/ac of available mineral nitrogen was also critical for functionality for two internal grass plant growth mechanisms of the vegetative reproduction by tillering and the compensatory physiological mechanisms. Both of these mechanisms function at high potential levels on grasslands that have 100 lbs/ac or greater available soil mineral nitrogen and do not function or function at extremely low levels on grasslands that have mineral nitrogen deficiencies (Manske 2009c, 2010a, b, c, 2011c).

Production of herbage biomass on grassland ecosystems at potential biological levels requires mineral nitrogen to be available at the threshold amount of 100 lbs/ac or greater. The biogeochemical processes of the nitrogen cycle in grassland ecosystems that convert organic nitrogen into mineral nitrogen are a function of the complex symbiotic interactions among rhizosphere organisms, grass plants, and large grazing graminivores. Soil organic matter in grassland ecosystems generally contains about three to eight tons of organic nitrogen per acre. Organic nitrogen is a form of nitrogen not directly usable by grass plants. Organic nitrogen must be transformed into inorganic (mineral) nitrogen in order to be usable by plants. In grassland ecosystems, the transformation of plant usable mineral nitrogen from soil organic nitrogen requires active rhizosphere organisms comprised of several trophic levels of microbes existing in the narrow zone of soil around active roots of perennial grass plants (Harley and Smith 1983, Campbell and Greaves 1990, Caesar-TonThat et al. 2001b).

The nitrogen cycle within grassland soils functions with two major biogeochemical processes. Immobilization is the process of assimilation of mineral nitrogen into organic forms of living organisms. Mineralization is the process of converting organic nitrogen into mineral (inorganic) nitrogen. Mineralization is a complex biogeochemical process conducted by saprotrophic

and heterotrophic soil microorganisms that convert immobilized organic nitrogen from soil organic matter detritus into mineral (inorganic) nitrogen (Power 1972). Ammonium salts are the first inorganic nitrogen compounds produced by microbial digestion. Complex proteins and other organic nitrogen compounds are simplified by enzymatic digestion that hydrolyze the peptide bonds and liberate and degrade the amino acids by deamination to produce ammonia (NH_3) and carbon dioxide, or other low molecular weight carbon compounds (Power 1972, Brady 1974). Most of the ammonia released is readily hydrolyzed into stable ammonium (NH_4). The ammonium ions are fairly immoble and some can be oxidized during nitrification producing nitrite (NO_2) and then nitrate (NO_3) (Brady 1974, Legg 1975, Coyne et al. 1975). The quantity of available nitrate in soil increases when the soil moisture content is abundant (Brady 1974). Mineral nitrogen (NH_4 and NO_3) have several optional biological and chemical pathways and are not available for very long. The quantity of available mineral nitrogen varies with changes in soil microorganism biomass and plant phenological growth and development during the growing season (Whitman 1975) and is the net difference between the total quantity of organic nitrogen mineralized by soil microorganisms and the quantity of mineral nitrogen immobilized into organic forms by plants and soil microbes (Brady 1974, Legg 1975). Maintaining available mineral nitrogen at the threshold quantity of 100 lbs/ac or greater requires a very large biomass of soil microorganisms.

Rhizosphere organism biomass and activity are limited by access to simple carbon chain energy (Curl and Truelove 1986) because the microflora trophic levels lack chlorophyll and have low carbon (energy) content. Partial defoliation by large indispensable grazing graminivores that removes 25% to 33% of the aboveground leaf and shoot weight from grass lead tillers in vegetative phenological growth between the three and a half new leaf stage and the flower stage (Manske 1999) causes large quantities of exudates containing simple carbon compounds to be released through the plant roots into the rhizosphere (Hamilton and Frank 2001). With the increase in availability of energy from simple carbon compounds in the rhizosphere, microorganism activity (Elliot 1978, Anderson et al. 1981, Whipps 1990) and biomass (Gorder, Manske, and Stroh 2004) greatly increase. The elevated biomass and activity of the microfauna trophic levels results in heavy grazing on the low carbon, high nitrogen content microflora trophic levels resulting in ingestion of greater quantities of nitrogen than the microfauna

organisms need for a balanced diet based on energy (carbon); the excess nitrogen is excreted as ammonium (NH_4). As a result of the increase in availability of energy from the exuded simple carbon chains, the biomass and activity of rhizosphere organisms greatly increased, transforming greater quantities of organic nitrogen into mineral nitrogen (Coleman et al. 1983, Klein et al. 1988, Burrows and Pfleger 2002, Rillig et al. 2002, Bird et al. 2002, Driver et al. 2005).

The increased available mineral nitrogen is absorbed into grass plant roots and through complex processes, the plant combines the mineral nitrogen with carbon, hydrogen, and oxygen to synthesize different kinds of amino acids which are combined into large organic compounds to produce various types of proteins, nucleotides, and chlorophyll, resulting in greatly increased herbage biomass production at or near potential biological levels (Manske 1999, 2003). As a result of the great increase in ecosystem net primary productivity, much greater quantities of organic nitrogen are returned annually back to the grassland ecosystem pool of soil organic matter which will raise the ecosystem functionality. Without the stimulation from the partial defoliation of grass lead tillers by the indispensable grazing graminivores none of the ecosystem biogeochemical processes and the internal grass plant mechanisms are activated and do not function.

Management of grassland orchid habitat without large grazing graminivores is not sustainable. Forty-five years of research have been devoted to the development of a biologically effective grazing management strategy that can improve and maintain grassland ecosystems at their potential biological levels and improve the quality of habitat for grassland orchids and their mycobionts and pollinators.

Biologically Effective Management of Grassland Ecosystems

The biologically effective twice-over rotation strategy was designed to coordinate partial defoliation events with grass phenological growth stages, to meet the nutrient requirements of the grazing graminivores, the biological requirements of the grass plants and the rhizosphere microorganisms, to enhance the ecosystem biogeochemical processes, and to activate the internal grass plant growth mechanisms in order for grassland ecosystems to function at the greatest achievable levels.

The twice-over rotation grazing management strategy uses three to six native grassland pastures. Each pasture is grazed for two periods per growing season. The number of grazing periods is determined by the number of sets of tillers: one set of lead tillers and one set of vegetative secondary tillers per growing season. The first grazing period is 45 days long, ideally, from 1 June to 15 July, with each pasture grazed for 7 to 17 days (never less or more). The number of days of the first grazing period on each pasture is the same percentage of 45 days as the percentage of the total season's grazeable forage contributed by each pasture to the complete system. The forage is measured as animal unit months (AUM's). The average grazing season month is 30.5 days long (Manske 2012a). The number of days grazed are not counted by calendar dates but by the number of 24-hr periods grazed from the date and time the livestock are turned out to pasture. The second grazing period is 90 days long, ideally from 15 July to 14 October, each pasture is grazed for twice the number of days as in the first period. The length of the total grazing period is best at 135 days; 45 days during the first period plus 90 days during the second period. There is some flexibility in the grazing period dates. The starting date has a variance of plus or minus 3 days with a range of start dates from 29 May to 4 June. This gives an extreme early option to start on 29 May with the first period to 12 July and with the second period to 11 October. The extreme late alternative option can start on 4 June with the first period to 18 July and with the second period to 17 October. There is also the option to add a total of 2 days to the total length of the grazing period. These 2 days can be used when a scheduled rotation date occurs on an inconvenient date by adding one day to each of two rotation dates. The limit of additional days is two per year resulting in a total length of 137 days. If inconvenient rotation dates occur during 3 or more times, an equal number of days greater than two must be subtracted from the grazing season, so total number of days grazed per year does not exceed 137 days. If the start date is later than 4 June, the scheduled rotation dates must remain as if the start date were on 4 June, in order to maintain the coordinated match of the partial defoliation events with the grass phenological growth stages. The total number of days grazed will be 135 days minus the number of days from 4 June to the actual start date. However, it is best to start on 1 June each year.

During the first period, partial defoliation that removes 25% to 33% of the leaf biomass from grass lead tillers between the 3.5 new leaf stage and the flower stage increases the rhizosphere microbe

biomass and activity, enhances the ecosystem biogeochemical processes, and activates the internal grass plant growth mechanisms. Manipulation of these processes and mechanisms does not occur at any other time during a growing season. During the second grazing period, the lead tillers are maturing and declining in nutritional quality and defoliation by grazing is only moderately beneficial to grass development. Adequate forage nutritional quality during the second period depends on the activation of sufficient quantities of vegetative secondary tillers from axillary buds during the first period. Livestock are removed from intact grassland pastures in mid October, towards the end of the perennial grass growing season, in order to allow the carryover tillers to store the carbohydrates and nutrients which will maintain plant mechanisms over the winter. Most of the upright vegetative tillers on grassland ecosystems during the autumn will be carryover tillers which will resume growth as lead tillers during the next growing season. Almost all grass tillers live for two growing seasons, the first season as vegetative secondary tillers and the second season as lead tillers. Grazing carryover tillers after mid October causes the termination of a large proportion of the population, resulting in greatly reduced herbage biomass production in subsequent growing seasons. The pasture grazed first in the rotation sequence is the last pasture grazed during the previous year. The last pasture grazed has the greatest live herbage weight on 1 June of the following season (Manske 2018a).

Stocking rates are based on peak herbage biomass on seasonlong grazing practices. The starting stocking rate on the "new" twice-over grazing practice is usually 80% to 100% of the seasonlong stocking rate. It usually requires three grazing seasons with the twice-over strategy stocked at 100% to increase the rhizosphere microbe biomass to be great enough to mineralize 100 lbs/ac of mineral nitrogen (nitrate NO_3 and ammonium NH_4). After the increased rhizosphere microbe biomass can mineralize 100 lbs/ac of mineral nitrogen, the stocking rate can be increased at 10% per year until the system is stocked at 140% of the seasonlong stocking rate. This has been the maximum biological potential reached on North American grasslands from the twice-over rotation strategy.

Once a rotation date scheduled has been determined, do not change that schedule greater than one day for any worldly reason. If you do not like your neighbors bull, build a fence that the bull cannot jump. If you have water sources that sometimes go dry, put in a water tank system on a pipeline. Fix the

problems that develop with solutions that do not change the rotation schedule.

Grasslands of the Northern Plains managed by traditional practices are low in available mineral nitrogen. This low nitrogen availability has long been known to be responsible for the reduced herbage productivity and below genetic potential calf weight gains per acre perceived by grassland livestock producers. However, intact grasslands have adequate nitrogen, usually at 5 to 6 tons of organic nitrogen per acre, which is not available to plants. Organic nitrogen must be mineralized by soil microorganisms in order for it to be available for plant use in the inorganic form. Unfortunately, traditionally grazing management practices do not elevate the soil microorganism biomass high enough to support mineralization of organic nitrogen at a level that can yield a supply at the threshold quantity of 100 lbs/ac or greater (Wight and Black 1972, 1979), which will permit the four major grass plant growth mechanisms and all of the ecosystem biogeochemical processes to function at potential biological levels.

Changing traditional grazing management practices' rotation dates is not the first thing livestock producers think of when they realize they need to increase soil mineral nitrogen. Implementation of some quick fix agronomic practice is usually attempted first. The application of nitrogen fertilizer to grassland ecosystems does not solve the complex problems related to the cause of low soil mineral nitrogen (Manske 2014d). It was found that nitrogen fertilization of native grasslands caused a synchronization of grass tiller growth stage development, resulting in a small increase in herbage biomass which later produced a high rate of leaf senescence and an early season decrease in forage nutritional quality compared to nonfertilized grasslands (Manske 2014d). It also caused a short term shift in plant species composition, with an increase in mid cool season grass (e.g. western wheatgrass) and a decrease in short warm season grasses (e.g. blue grama) (Manske 2009a, 2014d). Initially, these changes were considered by most observers to be beneficial (Manske 2009d). However, close examination of the data showed that the costs of the additional herbage weight were excessive (Manske 2009b), and that the long term disruptions of ecosystem biogeochemical processes were detrimental to desirable plant composition (Manske 2010c). The reduction of short warm season grasses caused a decrease in total live plant basal cover, thus exposing greater amounts of soil to higher levels of solar radiation and erosion (Goetz et al. 1978). These large areas of open space became ideal

invasion sites for undesirable plants, resulting in a long term plant species compositional shift towards a replacement community of domesticated and introduced mid cool season grasses, and in the removal of nearly all the native plant species (Manske 2009c, 2010c, 2018a).

Implementation of the strategy to interseed alfalfa into intact semiarid native grassland does not solve the complex problems related to the cause of low soil mineral nitrogen (Manske 2005). The introduction of alfalfa increased demand on the existing low levels of soil mineral nitrogen because almost all of the alfalfa plants' nitrogen requirements had to be taken from the soil. The interseeded alfalfa plants had extremely low levels of nodulation of rhizobium bacteria on the roots and, consequently, almost no nitrogen fixation. The inoculated rhizobium had been consumed by the resident soil microbes before the alfalfa seedlings had grown sufficient root material to permit infection (Manske 2004). The low amounts of mineral nitrogen available in the soil resulted in slower rates of growth and higher rates of mortality for the interseeded alfalfa plants than those for alfalfa plants solid seeded into cropland (Manske 2005). In addition, the high water use of the interseeded alfalfa plants depleted soil water levels within a 5 foot radius from each crown to an average of 35% below ambient soil water levels, causing drought stress conditions in the adjacent grass plants and, subsequently, further reducing grass herbage production (Manske 2004, 2005). Agronomic strategies implemented on grassland ecosystems slowly stifled grass internal growth mechanisms and ecosystem biogeochemical processes to ineffectiveness (Manske 2018a).

Grassland ecosystems should be managed with sound ecological principles. The ecological method to increase the quantity of available mineral nitrogen to 100 lbs/ac or greater in grassland ecosystems is to increase the biomass of the rhizosphere microorganisms. The rhizosphere is the narrow zone of soil bonded by extra cellular adhesive polysaccharides around active roots of perennial grassland plants. The primary biologically active rhizosphere microbes are the endomycorrhizal fungi, ectomycorrhizal fungi, low carbon: high nitrogen bacteria, and normal carbon: nitrogen protozoa. The rhizosphere microbes do not possess chlorophyll nor do they have direct access to sunlight, as a consequence, these microbes are deficient of energy and require an outside source of simple carbon energy. Contrary to common assumptions, there isn't enough short chain carbon energy in recently dead grass material and there isn't enough energy from

natural plant leakage to support a large active biomass of soil microbes. The only readily accessible source of large quantities of short chain carbon energy is the surplus fixed carbon energy photosynthesized by grass lead tillers at vegetative phenological growth stages. Grass plants fix a great deal more carbon energy than they use, furthermore, grass plants do not store the surplus fixed energy until during the winter hardening period, which starts in mid August and lasts to hard frost. Surplus carbon energy not programed for use, is broken down during night respiration. However, grass lead tillers at vegetative growth stages, between the three and a half new leaf stage and the flower (anthesis) stage, can be manipulated to exudate most of the surplus carbon energy into the rhizosphere through the roots following partial removal of 25% to 33% of the aboveground leaf biomass by grazing graminivores. This technique supplies sufficient quantities of short chain carbon energy into the rhizosphere initiating the production of large increases in microbe biomass and activity when 60% to 80% of the grass lead tiller population are partially defoliated by grazing graminivores over a period of 7 to 17 days on each pasture during the 45 day stimulation period from 1 June to 15 July.

Initiation of a twice-over strategy on native grassland that had previously been managed by nongrazing or traditional seasonlong practices will have a rhizosphere microbe biomass that is low to very low and it will require about three growing seasons to increase the microbe biomass large enough to mineralize 100 lbs/ac of mineral nitrogen. The response from the rhizosphere microbes is not instantaneous and rhizosphere weight changes respond differently to different management treatments. Annual changes in microbe weight on a nongrazed control treatment were small and appeared to be related to small changes in growing season precipitation during the first five years, with a relatively large change in microbe weight during the sixth year that corresponded with a substantial increase in growing season precipitation (table 20, figure 1). The rhizosphere weights on the twice-over managed pastures were not significantly different from those on the nongrazed control during the first two years. The microbe weights increased by 33% during the third year on the grazed pastures and continued to increase at a mean rate of 30.5 kg/m^3 per year from year 3 to 6, reaching a weight of 214.3 kg/m^3, which was 64.2% greater than the microbe weight on the nongrazed control (table 20, figure 1). After six years of management with the twice-over rotation strategy, 214 kg/m^3 of rhizosphere microbes

were mineralizing 99.4 lbs/ac (111.3 kg/ha) of mineral nitrogen (Manske 2018c).

During treatment year 20, the effects from three management practices were evaluated monthly for changes in rhizosphere volume (Gorder, Manske, Stroh 2004). The management practices were nongrazed, seasonlong, and twice-over rotation. The rhizosphere volume changed little during the growing season months on the nongrazed and seasonlong treatments (table 21, figure 2). The test pasture of the twice-over system was the third pasture grazed. During the 14 day grazing period from 1 to 15 July, surplus carbon energy was exudated from partially defoliated lead tillers through the roots into the rhizosphere. The microbe biomass and rhizosphere volume increased and the biogeochemical processes that mineralize organic nitrogen into mineral nitrogen greatly increased. By the mid August sample period, the rhizosphere volume had increased 85.7% from the July volume (table 21, figure 2).

The relationship between microbe biomass, rhizosphere volume, and the quantity of available mineral nitrogen is not linear. As the grassland ecosystem aggrades and the quantity of herbage biomass increases, the biomass of rhizosphere microbes must also increase in order to mineralize the threshold quantity of mineral nitrogen at 100 lb/ac (112 kg/ha).

During treatment year 24, the largest rhizosphere biomass for the twice-over strategy was measured at 406.44 kg/m^3, which is now considered to be the Standard Reference Rhizosphere Weight. The apparent quantity of mineralized nitrogen was 176 kg/ha (157 lbs/ac). The twice-over rotation system is the only management strategy known to be able to maintain a large biomass of rhizosphere microbes that can mineralize nitrogen at or above the threshold quantity of 100 lbs/ac (112 kg/ha) (Manske 2018c).

Available mineral nitrogen at or above the threshold quantity of 100 lbs/ac permits grassland vegetation to be produced near the biological potential level. For thirty years, 1983 to 2012, the monthly herbage biomass data for standard biotype categories was collected by standard clipping methods on the silty ecological sites from the biologically effective concepts of twice-over management compared to the herbage biomass on the silty sites from the traditional concept of seasonlong management (Manske 2018b). In general, the mean monthly herbage biomass values for the cool and warm season grasses on the biologically effective

concept were substantially greater than those on the traditional concept (tables 22 and 23, figures 3 and 4). The mean monthly herbage biomass values for the upland sedges and forbs on the biologically effective concept were lower than those on the traditional concept, except the mean herbage weight of upland sedge in October (tables 22 and 23, figures 3 and 4).

The cool season grasses on the biologically effective concept (table 22, figure 3) produced an impressively great lead tiller peak of 760.51 lbs/ac in July and then produced a greater secondary vegetative tiller peak of 826.89 lbs/ac in September. The secondary vegetative tillers were at growth stages greater than the three and a half new leaf stage and contained similar nutrient quality as the lead tillers had during the same growth stages. The cool season grasses on the traditional concept (table 23, figure 4) produced a 20.3% lower lead tiller peak of 606.10 lbs/ac in July and then produced a 33.6% lower secondary vegetative tiller peak of 548.70 lbs/ac in September.

The warm season grasses on the biologically effective concept (table 22, figure 3) produced a lead tiller peak at 333.21 lbs/ac in August which was 16.1% greater than the lead tiller peak of 287.08 lbs/ac produced in August on the traditional concept (table 23, figure 4) and then produced a secondary vegetative tiller herbage peak above 300 lbs/ac during September and October that was 29.9% greater than that on the traditional concept (tables 22 and 23, figure 3 and 4).

The herbage biomass production of upland sedge on the biologically effective concept was at a 12.4% lower mean weight than that produced on the traditional concept. The peak upland sedge biomass in July on the biologically effective concept was 204.99 lbs/ac (table 22, figure 3) which was 13.8% lower than the peak upland sedge biomass in July at 237.83 lbs/ac on the traditional concept (table 23, figure 4). During the initial stages after implementation of the biologically effective management concept, the upland sedge component greatly increased filling bare spaces in the plant community. The ecosystem continued to improve and develop. Around year 15, the cool and warm season grasses increased sufficiently to expand into the areas of upland sedge causing the upland sedges to decrease.

The herbage biomass production of forbs on the biologically effective concept was at a 28.6% lower mean weight than that produced on the

traditional concept. The peak forb biomass in July on the biologically effective concept was 193.27 lbs/ac (table 22, figure 3) which was 34.2% lower than the peak forb biomass in July at 293.73 lbs/ac on the traditional concept (table 23, figure 4).

There is a huge biological advantage for grass plants to grow in an ecosystem in which the biogeochemical processes are performed by a large biomass of rhizosphere microbes functioning at potential levels and in which the four main grass plant growth mechanisms are functioning at biological levels with available quantities of mineral nitrogen at or above 100 lbs/ac and with adequate quantities of major and minor essential elements which are all made possible by the beneficial effects from the biologically effective twice-over rotation strategy. Greater quantities of live cool and warm season grasses with greater quantities of nutrients are available during the entire grazing period from 1 June to 15 October.

Grazing period dates must be coordinated with the grass plant herbage biomass production curves and the nutritional quality curves in order for cow and calf weight performance to be at genetic potential. The optimum coordinated dates for native grassland pastures in the Northern Plains is to graze from early June to mid October, ideally 1 June to 14 October. Cow and calf weight performance on the biologically effective concept of the twice-over rotation strategy were compared to those on the traditional concept of the seasonlong treatment. Pasture costs were determined using pasture rent value of $8.76 per acre and market value per pound of calf pasture accumulated live weight gain was determined from the low market value of $0.70 per pound, with both values occurring during 1993 and 1994 at the start of this sample period. The three native grassland pastures managed with the twice-over rotation strategy were stocked at 8 cows per 80 acres with 10.34 ac/AU and 2.30 ac/AUM. The one native grassland pasture managed with the seasonlong treatment was stocked at 7 cows per 80 acres with 11.69 ac/AU and 2.60 ac/AUM. Both treatments were replicated two times. The increased herbage biomass production permitted the greater stocking rate on the twice-over strategy (Manske 2018d).

The greater herbage biomass production and the improved herbage nutritional quality from mid July to mid October permitted greater cow and calf accumulated live weight performance of the biologically effective concept. On the twice-over system, calf weight gain was 380.47 lbs per head, 2.89 lbs per day, and 37.66 lbs per acre and cow

weight gain was 86.92 lbs per head, 0.66 lbs per day, and 8.68 lbs per acre (table 24). On the seasonlong system, calf weight gain was 354.37 lbs per head, 2.65 lbs per day, and 30.61 lbs per acre and cow weight gain was 67.11 lbs per head, 0.50 lbs per day, and 5.91 lbs per acre (table 24). The cow and calf accumulated weight gain on the twice-over system was greater than those on the seasonlong system. Calf weight was 26.10 lbs per head greater, 0.24 lbs per day greater, and 7.05 lbs per acre greater and cow weight was 19.81 lbs per head greater, 0.16 lbs per day greater, and 2.77 lbs per acre greater (table 24). The dollar value captured was greater on the twice-over system than those on the seasonlong system. The pasture cost was $11.82 lower, calf pasture weight gain value was $15.16 greater, net return per cow-calf pair was $30.09 greater, and net return per acre was $4.37 greater (table 25).

On the seasonlong system managed with the traditional concept, cow daily weight gain decreased at an average of 47% per month from 1 June to 15 September (figure 5). Lead tillers of native cool season and warm season grasses decrease in crude protein content at an average rate of 24% and 23% per month, respectively, from 1 June to 15 September. The cow daily weight gain decreased 377% from 15 September to 15 October. The seasonlong cows lost weight the last month of the grazing period during 82% of the growing seasons. Calf daily weight gain averaged 2.79 lbs/day from 1 June to 15 September, then daily weight gain decreased to 2.11 lbs/day during the last month (figure 5). Cow weight accumulation occurred at about 28 lbs/month from 1 June to 15 September, then cows lost 26 lbs during the last month, which was more then 26% of their accumulated weight. Calf weight accumulation occurred at about 81 lbs/month during the entire grazing period (figure 6).

On the twice-over system managed with the biologically effective concept, cow daily weight gain decreased at an average of 34% during the first month (June), then the rate of daily weight gain increased each time the cows returned to pastures 1 and 2 for the second grazing period. A small increase in daily weight gain is assumed to occur for longer than 2 weeks when the cows returned to pasture 3 for the second grazing period, however, weight performance data was not collected during late season interim dates. The cows lost an average of 0.51 lbs/day during the first 2 weeks of October. This loss of cow weight occurred 36% of the time which experienced one month per growing season with severe water deficiency at 22% of LTM during August, September, or October resulting in an average cow weight loss of

1.93 lbs/day. During the other 64% of the growing seasons, the cow weight gain averaged 0.34 lbs/day during the first 2 weeks of October (figure 5). Calf daily weight gain averaged 3.08 lbs/day from 1 June to 15 September, then daily weight gains decreased to 2.28 lbs/day during the last month (figure 5). Cow weight accumulation occurred at about 32 lbs/month from 1 June to 15 September, then the cows lost an average of 17 lbs during the last month, which was about 15% of their accumulated weight. Calf weight accumulation occurred at about 88 lbs/month during the entire grazing period (figure 6).

Grazing native grassland for 4.5 months from 1 June to 15 October (137 days) is the ideal period for the best potential cow and calf weight performance to occur. Grazing earlier than 1 June, before the grass lead tillers produce 3.5 new leaves is extremely detrimental for grass herbage biomass production with reductions ranging between 20% and 45% losses that result in secondary problems from lost animal weight gains. Grazing later than 15 October when all native grasses are deficient of crude protein, cows lose weight and calf weight gains greatly decrease, and removing leaf biomass by grazing living carryover grass tillers causes great reductions in grass density and herbage biomass production during the following growing season.

The 45 day period from 1 June to 15 July is the only time that the internal grass plant growth mechanisms of compensatory physiological mechanisms, vegetative reproduction by tillering, nutrient resource uptake, and water use efficiency can be activated and the ecosystem biogeochemical processes performed by rhizosphere microorganisms can be enhanced by short chain carbon energy exudated from photosynthetic surpluses in grass lead tillers, through the roots into the rhizosphere and available to the microbes, resulting in increased activity that result in greater quantities of soil organic nitrogen to be mineralized providing mineral nitrogen at quantities at or greater than the threshold level of 100 lbs/ac. All of these mechanisms and processes require partial defoliation by grazing graminivores that removes 25% to 33% of the aboveground leaf material from grass lead tillers that are at phenological growth stages between the three and a half new leaf stage and the flower stage.

Prescribed fire and mowing grass hay cannot activate the grass plant growth mechanisms or the ecosystem biogeochemical processes because these practices remove too much of the leaf area preventing adequate quantities of carbon energy to be fixed through leaf photosynthesis. Stored carbohydrates

are not mobilzed for compensatory replacement growth following defoliation events (Briske and Richards 1995).

Many grassland ecologists have retained the belief that grassland ecosystems can be managed with fire because they have accepted the observational concept that fire prevents the intrusion of shrubs and trees into grasslands (Weaver 1954, Humphrey 1962, Daubenmire 1974, Stoddart, Smith, and Box 1975, Wright and Bailey 1982). However, the presence of fire does not prove that grasslands need or are caused by fire (Heady 1975). The existence of a shrub component in a grassland is not a ecologically beneficial relationship as shrubs and grasses are adversarial inhibitive competitors. They compete for sunlight, mineral nitrogen, other essential elements, and soil water. Fire in grasslands cannot prevent the invasion of, or cause the removal of, shrubs and trees that are able to reproduce by vegetative secondary suckers (Wright and Bailey 1982; Manske 2006a, b). Almost all deciduous woody plants reproduce vegetatively, except big sagebrush (Artemisia tridentata) (Manske 2019). Seedlings of trees, shrubs, weedy forbs, and introduced grasses cannot become established in grasslands containing grasses with full nutrient resource uptake competitiveness (Peltzer and Kochy 2001). Intrusive seedlings can only be established after a grassland has been degraded by poor management practices. Repeated prescribed fire can modify the composition of the aboveground vegetation in degraded grasslands which have been invaded by shrubs. The composition of introduced cool season grasses may change, and early succession and weedy forbs, and shrub aerial stems decrease temporarily after four repeated prescribed fires (Manske 2007a, 2011a). However, the fundamental problems of weak nutrient resource uptake, reduced water use efficiency, nonfunctional compensatory physiological mechanisms, impaired vegetative reproduction by tillering and diminished biogeochemical processes will remain in the degraded grassland ecosystem following repeated fire events. None of the biological, physiological, or asexual mechanisms within grass plants and none of the rhizosphere microbes or biogeochemical processes they perform are activated by fire (Manske 2007a, 2011a). Almost all of the essential elements in the aboveground herbage are volatilized when a grassland is burned, and if the soil is dry, some of the belowground essential elements are also lost (Russelle 1992). When the losses of essential elements are greater than the quantity of captured essential elements, the result is degradation of the grassland (McGill and Cole 1981). Fire does not improve grassland ecosystems biologically or

ecologically and fire cannot replace the partial defoliation achieved by grazing graminivores in managing healthy and productive grassland ecosystems (Manske 2018a).

Often times, livestock grazing is removed to protect a grassland ecosystem based on naive presumptions that livestock grazing causes damage to grassland ecosystem. Livestock grazing is not what causes damage to grasslands; poor management of grazing livestock can cause serious damage to grasslands. The greatest antagonistic effects to grassland ecosystem occur from no livestock-idle land management concepts that rest grasslands from grazing defoliation. The term "rest" is a misnomer; resting a grassland does not cause revitalizations of crucial biological and ecological processes. Resting a grassland by withholding partial defoliation by grazing results in regression of ecosystem processes and biological growth mechanisms. Several negative changes occur relatively soon after grazing graminivores are removed from grasslands; the live root biomass of grasses decrease (Whitman 1974), standing dead leaves and litter accumulate (Brand and Goetz 1986), and ecosystem biogeochemical processes diminish (Manske 2011b).

The reduction of live root surface area causes a decrease in active root length for interaction with symbiotic rhizosphere organisms and causes a decrease in absorption of water and nutrients from the soil. Reduction of active root biomass and diminishment of grass plant health vigor result in a loss of resource uptake efficiency and a suppression of competitiveness of grass plants to take up mineral nitrogen, essential elements, and soil water (Kochy 1999, Kochy and Wilson 2000).

Grass plants produce double the quantity of leaf biomass than needed for normal plant growth and maintentance (Crider 1955, Coyne et al. 1995). Without grazing graminivores to remove the surplus herbage production, the standing leaf material accumulates rapidly and changes from an asset to a detriment. The accumulation of nondefoliated live and standing dead leaves of grasses reduce light penetration below native grass light saturation points (Peltzer and Kochy 2001). Native grasses have high light saturation points and require near full sunlight. Warm season grasses have higher light saturation points than cool season grasses (Kochy 1999, Kochy and Wilson 2000). Shading reduces native warm season grasses more than native cool season grasses. Introduced cool season domesticated grasses have lower light saturation points than native grasses, permitting domesticated grass to live in low light

conditions. The accumulating standing dead leaves shade the lower leaves, increasing the rate of leaf senescence and reducing the rate of photosynthesis, causing a decrease in the supply of carbohydrates (Coyne et al. 1995) that results in a reduction in growth of leaves and roots (Langer 1972, Briske and Richards 1995). Grass leaves grown under shaded conditions become longer but narrower, thinner, and lower in weight (Langer 1972) than leaves in sunlight. Shaded grass plants shift to erect growth forms with a small number of tillers (Briske and Richards 1995). Lack of grazing reduces grass tiller densities by decreasing tiller development and increasing tiller mortality through shading (Manske 2013). After a few years, shading reduces the composition of native grass species in the ecosystem and increases the composition of shade-tolerant or shade-adapted replacement species, like smooth bromegrass and Kentucky bluegrass.

Standing dead material not in contact with soil does not decompose through microbial activity. Dead plant material on nongrazed treatments breaks down slowly over several years by leaching and weathering and builds up into a thick mulch layer. Thick mulch effectively blocks sunlight from reaching understory young grass leaves. Thick mulch modifies soil temperatures. Thick mulch ties up and holds organic nutrients above the soil surface preventing accession to the soil organic matter which limits nutrient cycling through biogeochemical processes increasing the deficiencies of essential elements causing great reductions in grass growth of leaves and roots. Thick mulch absorbs and holds precipitation for later evaporation preventing the water from infiltrating into the soil diminishing soil water to deficiency quantities (Wright and Bailey 1982, Manske 2000a, 2011a).

The loss of active root length is a contributing factor in the reduction of rhizosphere biomass. The primary cause for the reduction in rhizosphere biomass is, however, the great reduction in the quantity of carbohydrate energy exudated from the grass roots into the rhizosphere zone. Without partial defoliation by grazing, only a small quantity of short carbon chain energy leaks from the grass roots into the rhizosphere; this low amount of simple carbon compounds is barely enough to sustain a very small rhizosphere microbe biomass. A small biomass of rhizosphere organisms function at greatly reduced rates of organic material decomposition, and can mineralize only small quantities of nitrogen and other essential elements (Anderson et al. 1981, Coleman et al. 1983, Curl and Truelove 1986, Klein et al. 1988, Whipps 1990).

Grazing graminivores perform several indispensable functions for grassland ecosystems. Partial defoliation by grazing graminivores activate the four major internal grass plant growth mechanisms, enhance rhizosphere microorganisms activity and increase their biomass large enough to perform the ecosystem biogeochemical processes and to mineralize greater than 100 lbs/ac of mineral nitrogen plus the other essential elements, and they remove the surplus grass leaf biomass produced by grass plants before it can become a detriment to the ecosystem each growing season.

Grazing graminivores have difficulty in properly defoliating the grassland communities that grow on subirrigated soils. The grasses and sedges that grow below the switchgrass ring deposit silicate crystals in the leaf tissue. Because of the presence of these crystals in mature plants, graminivores consume only about 10% of the mature forage growing in these highly productive wet meadow communities. The ungrazed standing plant biomass restricts growth of young grass plants and this old material needs to be removed by mowing or burning periodically. The unpredictability of wet and dry conditions of subirrigated soils requires a flexible treatment schedule. A simple strategy would be to organize the wet meadow areas into three groups, with each group containing wet meadow areas from each of the grazed pastures, and all of the wet meadow areas in the same group would receive treatment during the same year. All of the wet meadows in each group would receive a mowing or burning treatment one time in a cycle of three to five years as conditions permit.

Grazing graminivores is biologically beneficial for grass plants and for grassland ecosystems when grazing periods are coordinated with grass phenological growth stages. The four primary physiological growth mechanisms within grass plants that perform the herbage replacement processes are activated with partial defoliation by grazing graminivores when 25% to 33% of leaf weight is removed from 60% to 80% of lead tillers during vegetative phenological growth stages between the three and a half new leaf and the flower stage when a threshold quantity of 100 lbs/ac of mineral nitrogen is available. Unavailable soil organic nitrogen must be mineralized by soil microbes in order for nitrogen to be usable by grass plants. A large biomass of rhizosphere microorganisms is required to mineralize a large quantity of nitrogen yielding 100 lbs/ac. Grassland microbes are achlorphyllous and cannot fix their own carbon energy. Large quantities of surplus short chain carbon energy are produced by healthy vegetative lead tillers that can be exudated into the microbial rhizosphere when 25% to 33% of the leaf weight is removed with partial defoliation by grazing graminivores while lead tillers are between the three and a half new leaf stage and the flower stage. The four primary physiological growth mechanisms are not functional when less than 100 lbs/ac of mineral nitrogen is available and are not activated when zero % or greater than 33% of the leaf weight of lead tillers is removed during vegetative growth stages.

Grazing graminivores receive nutritious forage from healthy grass plants. However, providing forage for graminivores is not the only purpose for grazing grasslands. Grass plants have biological requirements and have four primary physiological growth mechanisms that must be activated by partial defoliation by grazing. Rhizosphere microorganisms are needed in large quantities to perform all of the ecosystem biogeochemical processes, but are unable to fix carbon energy and require exudated short chain carbon energy that can be provided by partial defoliation by grazing. The three indispensable biotic components of grasslands; grass vegetation, rhizosphere organisms, and large graminivores; must have their biological requirements provided with partial defoliation by grazing graminivores in order for grassland ecosystems to function at achievable levels.

Summary

Orchids have been successful and prolific for a long time. Terrestrial orchids with C_3 photosynthesis emerged during the late Cretaceous (76-84 mya). These ancestral orchids underwent a polyploidization event (whole-genome duplication WGD) which doubled their genetic material and allowed them to successfully survive the Cretaceous-Paleogene (K/Pg) boundary mass biological extinction of 66 mya that eliminated all nonavian dinosaurs and caused a loss of 76% of all species, resulting in widespread destruction of every ecological system. Because of their polyploid advantage, orchids were able to recover rapidly and experience accelerated evolution. Redundant genes provides more than one gene to do a specific job. Which means that one gene can mutate, while the duplicate gene can still maintain proper functions, or if the mutation is useful, the plant can evolve into a new species faster than other organisms could. Four major genetic mutations have given orchids their high speciation rate and their remarkable adaptability to successfully colonize a wide diversity of habitats.

The genetic fusion of the male filament with the female style formed the central column and reduced the number of male stamen to 3, 2, or 1, with 99% of all orchid species having a single stamen. This mutation also permitted the development of pollen masses into pollinium which improved the precision of pollen transfer by selected pollinators to the female stigma and reduced the amount of pollen grains lost between flowers greatly improving the rate of successful fertilization.

The polyploidy event also provided a different set of genes to govern the development of the specialized petal, the labellum, and another set of genes that controlled the other petals. This combination of additional sets of genes produced the bilaterally symmetrical flower structure resulting in great improvements in the selection efficiency of specific pollinators and ensuring improved reproductive success.

The set of genes that regulated the development of seed endosperm were lost causing orchids to produce seeds without endosperm which has enabled orchids to transfer energy into the production of tens of thousands of seeds in a single fruit permitting wide dispersal of the tiny seeds into new and distant habitats and has led to the extensive development of obligate symbiotic relationships with specific mycorrhizal fungi which has greatly improved seedling and photosyntheic adult plant survival rates.

The sets of genes involved in cell differentiation of roots growing underground were lost in some tropical orchids during the Eocene epoch (35 mya) causing a different type of lateral root to appear which facilitated orchids clinging to trees and rocks. This mutation led to the rapid evolution of the aerial lifestyle of the epiphytic orchid growth form and opened up numerous new areas for colonization and greatly increased diversification to the point that 70% of all orchid species grow as tropical epiphytes. The exposure of the lateral roots to the environment caused a problem with water conservation. In order to save water, the epiphytic orchids developed a different type of photosysthesis, which was crassulacean acid metabolism (CAM) that helped them to survive on just fog and rain.

Near the end of the Eocene epoch, around 34 mya, global cooling expanded. As the climate cooled, the dominant closed forest ecosystems were reduced, increasing the openness of savannah ecosystems that later developed into open grasslands. The symbiotic relationships among grass species, rhizosphere microorganisms, and large grazing mammalian graminivores developed complex grassland ecosystems. The northern portion of North America experienced periodic glaciation during a two million year period. Following the retreat of the last glacial ice and the stabilization of a continental climate in the interior of North America, grassland components were able to migrate northward by different mechanisms, at different times and rates, and form grassland communities in the Northern Plains. All of the plants and animals considered to be native to the Northern Plains region originated in other areas. The grassland orchids migrated into the Northern Plains as grassland orchids or as woodland orchids, then to have genetic changes and move into the grassland habitats later.

Polyploidy, beneficial gene mutations, and never ceasing evolutionary development has permitted orchid plants to produce 30,000 species and to successfully colonize a multitude of habitat types.

In spite of that, this report has concentrated on only the grassland biome of the Northern Plains which consists of six prairie vegetation types divided into three grassland habitat types and three subtypes of which can potentially be occupied by twelve species in five genera of grassland orchids. The successful sustainability of occupancy of grassland orchids on these grassland habitats depends upon the implementation of biologically effective management strategies that can provide the biological and physiological requirements of the forage grass plants, soil microorganisms, and grazing graminivores, that can activate and maintain the grass plant growth mechanisms and the ecosystem biogeochemical processes, that can revitalize soil structure and functionality, that can increase forage growth and nutritional quality, that can improve livestock growth and weight performance along with the capture of greater wealth per acre, and that can improve the quantity and quality of suitable habitat for grassland orchids.

Table 20. Rhizosphere weight (kg/m^3) for the nongrazed control pasture and grazed pastures during six years of twice-over rotation management.

	Control Pasture kg/m^3	Grazed Pastures kg/m^3	% Difference
Pregrazing	52.23	77.99	49.32
Year 1	64.24x	83.28x	29.64
Year 2	77.82x	92.22x	18.50
Year 3	70.67y	122.61x	73.50
Year 4	82.88y	140.32x	69.31
Year 5	86.85y	183.00x	110.71
Year 6	130.56y	214.34x	64.17

Means in the same row and followed by the same letter (x, y) are not significantly different (P<0.05).
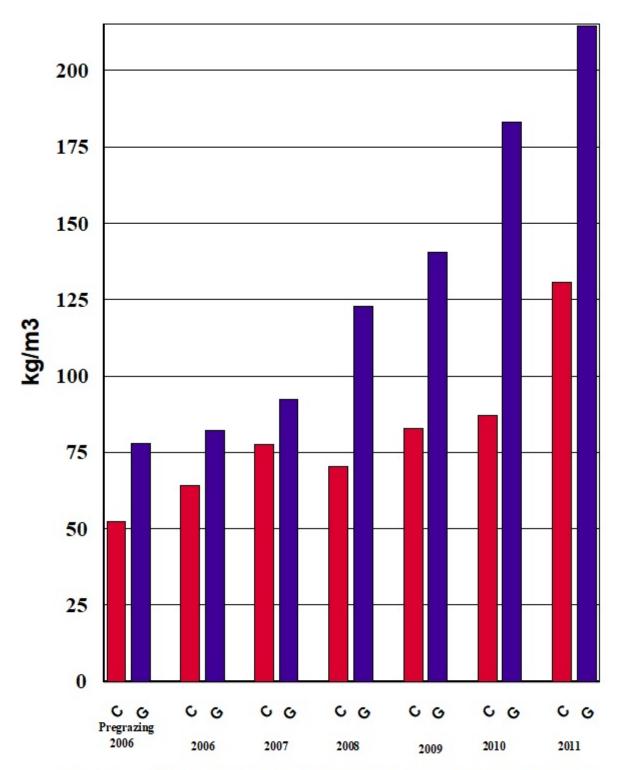
Figure 1.   Rhizosphere weight (kg/m3) for the control pasture (red) and grazed pastures (blue) during six years of twice-over rotation management, 2006-2011.

Table 21. Rhizosphere volume in cubic centimeters per cubic meter of soil (cm^3/m^3), 2002, year 20.

Grazing Management	May	Jun	Jul	Aug	Sep	Oct
Nongrazed		1725.24a	2804.61a	2391.97b	2438.47b	
Seasonlong		1800.93a	642.21b	1963.02b	1802.97b	
Twice-over		3214.75a	3867.54a	7183.27a	6586.06a	

Means in the same column and followed by the same letter are not significantly different (P<0.05).
Data from Gorder, Manske, and Stroh, 2004.

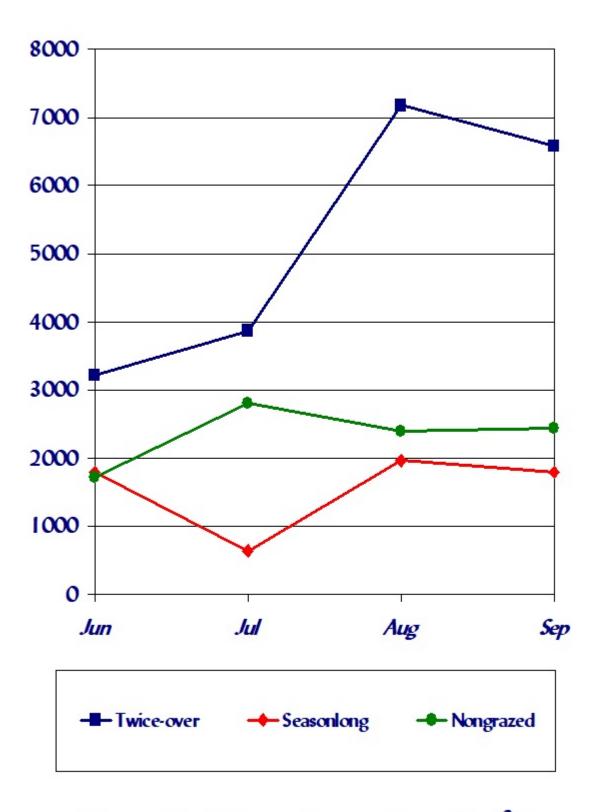Figure 2. Rhizosphere volume (cm^3)
per cubic meter of soil

Table 22. Mean monthly herbage biomass (lbs/ac) by biotype categories on the silty ecological sites of the Biologically Effective concept, 1983-2012.

Silty Site	May	Jun	Jul	Aug	Sep	Oct
Cool Season	397.73	637.66	760.51	670.20	826.89	698.80
Warm Season	179.90	217.06	304.43	333.21	300.86	302.53
Upland Sedge	165.99	199.29	204.99	175.74	127.28	137.21
Forbs	145.26	146.55	193.27	187.79	164.72	159.88
Grasses	577.63	854.72	1064.94	1003.41	1127.75	1001.33
Graminoids	743.62	1054.01	1269.93	1179.15	1255.03	1138.54
Total	888.88	1200.56	1463.20	1366.94	1419.75	1298.42

Table 23. Mean monthly herbage biomass (lbs/ac) by biotype categories on the silty ecological sites of the Traditional concept, 1983-2012.

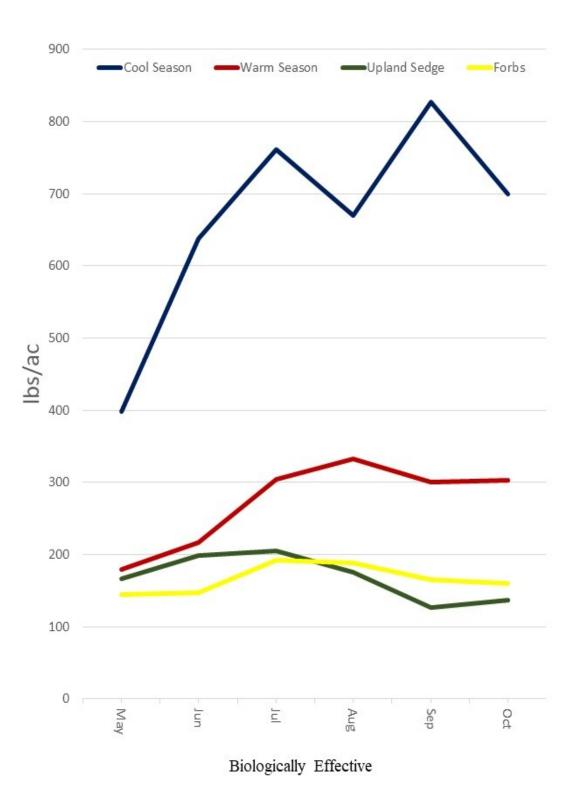| Silty Site	May	Jun	Jul	Aug	Sep	Oct
Cool Season	308.46	483.96	606.10	515.39	548.70	542.12
Warm Season	123.98	157.64	244.45	287.08	222.68	241.69
Upland Sedge	168.26	226.16	237.83	222.50	151.45	126.55
Forbs	166.47	218.24	293.73	253.01	212.18	216.13
Grasses	432.44	641.60	850.55	802.47	771.38	783.81
Graminoids	600.70	867.76	1088.38	1024.97	922.83	910.36
Total	767.17	1086.00	1382.11	1277.98	1135.01	1126.49

Figure 3. Mean monthly herbage biomass (lbs/ac) by biotypes on the silty site of the Biologically Effective concept, 1983-2012.
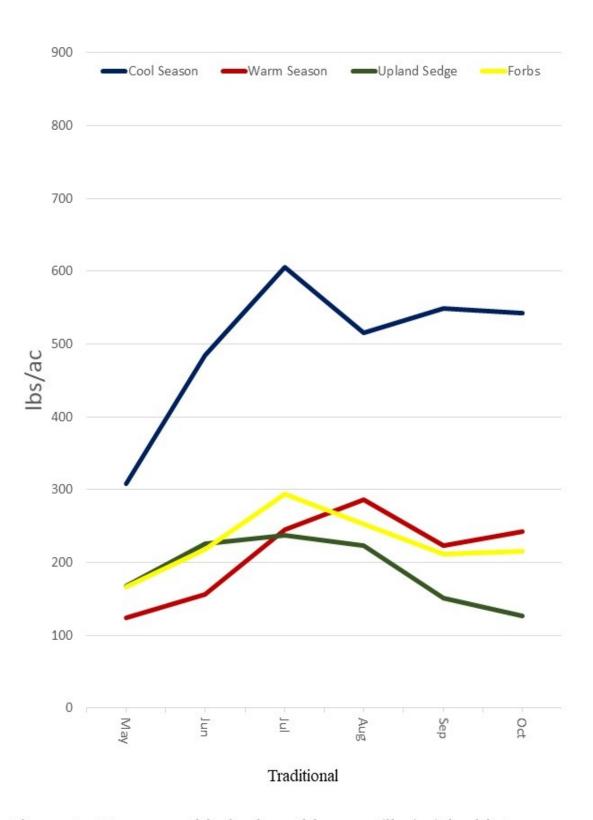
Figure 4. Mean monthly herbage biomass (lbs/ac) by biotypes on the silty site of the Traditional concept, 1983-2012.

Table 24. Cow and calf weight performance grazing summer native rangeland pastures managed by the biologically effective concept compared to pastures managed by the traditional concept.

Native Rangeland	Traditional Concept			Biologically Effective Concept			Biological Gain		
	Wt Gain lbs	Gain per Day lbs	Gain per Acre lbs	Wt Gain lbs	Gain per Day lbs	Gain per Acre lbs	Wt Gain lbs	Gain per Day lbs	Gain per Acre lbs
1995-2005	One Pasture, 11.69 ac/AU Seasonlong			Three Pastures, 10.34 ac/AU Twice-over rotation					
Calf	354.37	2.65	30.61	380.47	2.89	37.66	26.10	0.24	7.05
Cow	67.11	0.50	5.91	86.92	0.66	8.68	19.81	0.16	2.77

Table 25. Value captured gain in dollars from summer native rangeland pastures managed by the biologically effective concept compared to pastures managed by the traditional concept.

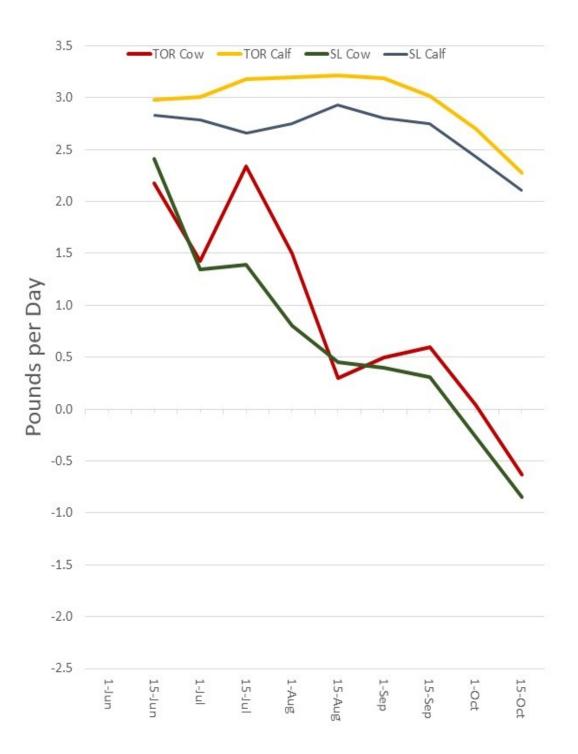| Native Rangeland	Traditional Concept				Biologically Effective Concept				Value Captured Gain			
	Pasture Cost $	Pasture Weight Gain Value $	Net Return per C-C pr $	Net Return per Acre $	Pasture Cost $	Pasture Weight Gain Value $	Net Return per C-C pr $	Net Return per Acre $	Pasture Cost $	Pasture Weight Gain Value $	Net Return per C-C pr $	Net Return per Acre $
1995-2005	One Pasture, 11.69 ac/AU Seasonlong				Three Pastures, 10.34 ac/AU Twice-over rotation							
Cow-Calf pair	102.42	248.06	145.64	12.67	90.60	263.22	175.73	17.04	-11.82	15.16	30.09	4.37

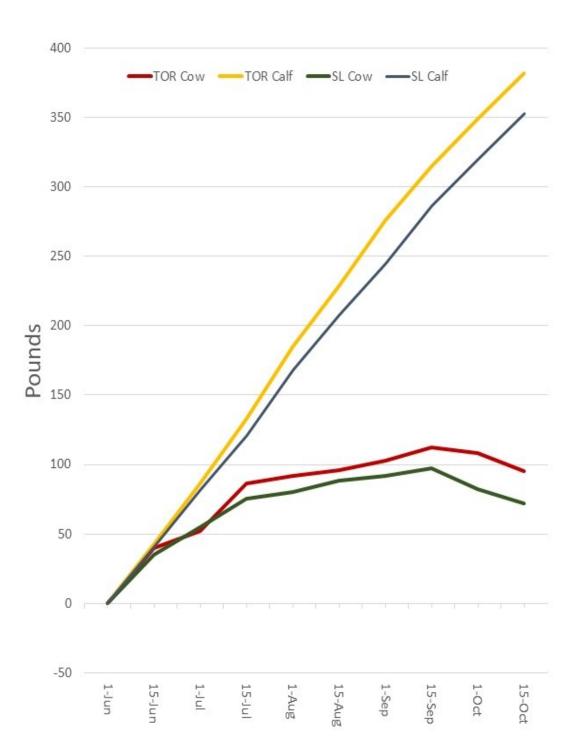Figure 5. Cow and calf daily gain on the seasonlong and twice-over grazing systems, 1995-2005.

Figure 6. Cow and calf accumulated weight gain on the seasonlong and twice-over grazing systems, 1995-2005.

Literature Cited

Anderson, R.V., D.C. Coleman, C.V. Cole, and E.T. Elliott. 1981. Effect of nematodes *Acrobeloides sp.* and *Mesodiplogaster lheritieri* on substrate utilization and nitrogen and phosphorus mineralization. Ecology 62:549-555.

Atkinson, C.J. 1986. The effect of clipping on net photosynthesis and dark respiration rates of plants from an upland grassland, with reference to carbon partitioning in *Festuca ovina.* Annals of Botany 58:61-72.

Ballings, P. and B. Wursten. nd. Orchids of Zimbabwe. Vumba-Nature.com

Belsky, A.J. 1992. Effects of grazing competition, disturbance and fire on species composition and diversity in grassland communities. Journal of Vegetation Science 3:187-200.

Bird, S.B., J.E. Herrick, M.M. Wander, and S.F. Wright. 2002. Spatial heterogeneity of aggregate stability and soil carbon in semi-arid rangeland. Environmental Pollution 116:445-455.

Brady, N.C. 1974. The nature and properties of soils. MacMillan Publishing Co., Inc., New York, NY. 639p.

Brand, M.D., and H. Goetz. 1986. Vegetation of exclosures in southwestern North Dakota. Journal of Range Management 39:434-437.

Briske, D.D. 1991. Developmental morphology and physiology of grasses. p. 85-108. *in* R.K. Heitschmidt and J.W. Stuth (eds.). Grazing management: an ecological perspective. Timber Press, Portland, OR.

Briske, D.D., and J.H. Richards. 1994. Physiological responses of individual plants to grazing: current status and ecological significance. p. 147-176. *in* M. Vavra, W.A. Laycock, and R.D. Pieper (eds.). Ecological implications of livestock herbivory in the west. Society for Range Management, Denver, CO.

Briske, D.D., and J.H. Richards. 1995. Plant response to defoliation: a physiological, morphological, and demographic evaluation. p. 635-710. *in* D.J. Bedunah and R.E. Sosebee (eds.). Wildland plants: physiological ecology and developmental morphology. Society for Range Management, Denver, CO.

Burrows, R.L., and F.L. Pfleger. 2002. Arbuscular mycorrhizal fungi respond to increasing plant diversity. Canadian Journal of Botany 80:120-130.

Caesar-TonThat, T.C., D.H. Branson, J.D. Reeder, and L.L. Manske. 2001b. Soil-aggregating basidiomycetes in the rhizosphere of grasses under two grazing management systems. Poster. American Society of Agronomy. Charlotte, NC.

Cameron, D.D., J.R. Leake, and D.J. Read. 2006. Mutualistic mycorrhiza in orchids: evidence from plant-fungus carbon and nitrogen transfers in the green-leaved terrestrial orchid Goodyera repens. New Phytologist 171:405-416.

Campbell, R., and M.P. Greaves. 1990. Anatomy and community structure of the rhizosphere. p. 11-34. *in* J.M. Lynch (ed.). The rhizosphere. John Wiley and Sons, New York, NY.

Chapman, G.P., and W.E. Peat. 1992. An introduction to the grasses. C.A.B. International, Wallingford, UK. 111p.

Chapman, G.P. 1996. The biology of grasses. C.A.B. International, Wallingford, UK. 273p.

Cheng, W. and D.W. Johnson. 1998. Elevated CO_2, rhizosphere processes, and soil organic matter decomposition. Plant and Soil 202:167-174.

Chuan-Ming, Y., KwiMi, C., Chieh-Kai, L., and Wen-Chieh, T. 2019. New insights into the symbiotic relationship between orchids and fungi. Journal of Applied Sciences 9(3):585-603.

Coleman, D.C., C.P.P. Reid, and C.V. Cole. 1983. Biological strategies of nutrient cycling in soil ecosystems. Advances in Ecological Research 13:1-55.

Committee on the Status of Endangered Wildlife in Canada (COSEWIC). 2016. Western prairie fringed orchid. Platanthera praeclara, Assessment and Status Report in Canada. Environment and Climate Change Canada. Canadian Wildlife Service, Ottawa, ON. 47p.

Coyne, P.I., M.J. Trlica, and C.E. Owensby. 1995. Carbon and nitrogen dynamics in range plants. p. 59-167. in D.J. Bedunah and R.E. Sosebee (eds.). Wildland plants: physiological ecology and developmental morphology. Society for Range Management, Denver, CO.

Crider, F.J. 1955. Root-growth stoppage resulting from defoliation of grass. USDA Technical Bulletin 1102. 23p.

Curl, E.A., and B. Truelove. 1986. The rhizosphere. Springer-Verlag, New York, NY.

Currah, R.S., E.A. Smreciu, and S. Hambleton. 1990. Mycorrhizae and mycorrhizal fungi of boreal species of Platanthera and Coeloglossum (Orchidaceae). Canadian Journal of Botany 68(6):1171-1181.

Dahl, B.E. 1995. Developmental morphology of plants. p. 22-58. in D.J. Bedunah and R.E. Sosebee (eds.). Wildland plants: physiological ecology and developmental morphology. Society for Range Management, Denver, CO.

Daubenmire, R.F. 1974. Plants and Environment: A textbook of plant autecology. 3rd ed. John Wiley & Sons. New York, NY. 422p.

Dearnaley, J.D.W. 2007. Further advances in orchid mycorrhizal research. Mycorrhiza 17(6):475-486.

Dearnaley, J.D.W., F. Martos, and M.A. Selosse. 2012. Orchid mycorrhizas: Molecular ecology, physiology, evolution, and conservation aspects. Mycota 9:207-230.

Dearnaley, J.D.W. and D.D. Cameron. 2016. Nitrogen transport in the orchid mycorrhizal symbiosis-further evidence for a mutualistic association. New Phytologist 213:10-12.

Driver, J.D., W.E. Holben, and M.C. Rillig. 2005. Characterization of glomalin as a hyphal wall component of arbuscular mycorrhizal fungi. Soil Biology and Biochemistry 37:101-106.

Elliot, E.T. 1978. Carbon, nitrogen and phosphorus transformations in gnotobiotic soil microcosms. M.S. Thesis. Colorado State University, Ft. Collins, CO.

Fauske, G.M. 2016. Hawk moths of the northern Great Plains. Poster. NDSU, Fargo, ND.

Flora of North America Editorial Committee, eds. 2002. Flora of North America North of Mexico. Vol. 26. Oxford University Press, New York and Oxford.

Fochi, V., W. Chitarra, A. Kohler, S. Voyron, V.S. Singan, E.A. Lindquist, K.W. Barry, M. Girlanda, I.V. Grigoriev, F. Martin, R. Balestrini, and S. Perotto. 2016. Fungal and plant gene expression in the Tulasnella calospora-Serapias vomeracea symbiosis provides clues about nitrogen pathways in orchid mycorrhizas. New Phytologist 213:365-379.

Gibson, D.J. 2009. Grasses and grassland ecology. Oxford University Press Inc., New York, NY. 305p.

Goedeke, T., J. Sharma, P. Delphey, and K. Marshall Mattson. 2008. Platanthera praeclara. The International Union for Conservation of Nature and Natural Resources (IUCN) Red List of Threatened Species. 14p.

Goetz, H. 1969. Composition and yields of native grassland sites fertilized at different rates of nitrogen. Journal of Range Management 22:384-390.

Goetz, H. 1975. Availability of nitrogen and other nutrients on four fertilized range sites during the active growing season. Journal of Range Management 28:305-310.

Goetz, H., P.E. Nyren, and D.E. Williams. 1978. Implications of fertilizers in plant community dynamics of Northern Great Plains rangelands. Proceedings of the First International Rangeland Congress. p. 671-674.

Gorder, M.M., L.L. Manske, and T.L. Stroh. 2004. Grazing treatment effects on vegetative tillering and soil rhizospheres of western wheatgrass. NDSU Dickinson Research Extension Center. Range Research Report DREC 04-1056. Dickinson, ND. 13p.

Great Plains Floral Association. 1986. Flora of the Great Plains. University of Kansas, Lawrence, KS.

Hamilton, E.W., and D.A. Frank. 2001. Can plants stimulate soil microbes and their own nutrient supply? Evidence from a grazing tolerant grass. Ecology 82:2397-2402.

Harley, J.L., and S.E. Smith. 1983. Mycorrhizal symbiosis. Academic Press, New York, NY. 483p.

Heady, H.F. 1975. Rangeland management. McGraw-Hill Book Company, New York, NY. 460p.

Humphrey, R.R. 1962. Range Ecology. The Ronald Press Co. New York, NY. 234p.

Ingham, R.E., J.A. Trofymow, E.R. Ingham, and D.C. Coleman. 1985. Interactions of bacteria, fungi, and the nemotode grazers: effects of nutrient cycling and plant growth. Ecological Monographs 55:119-140.

Kirsch, L.M., and A.D. Kruse. 1972. Prairie fires and wildlife. Proceedings of Tall Timbers Fire Ecology Conference. 12:289-303.

Klein, D.A., B.A. Frederick, M. Biondini, and M.J. Trlica. 1988. Rhizosphere microorganism effects on soluble amino acids, sugars, and organic acids in the root zone of *Agropyron cristatum, A. smithii,* and *Bouteloua gracilis*. Plant and Soil 110:19-25.

Kochy, M. 1999. Grass-tree interactions in western Canada. Ph.D. Dissertation. University of Regina. Regina, SK, Canada.

Kochy, M., and S.D. Wilson. 2000. Competitive effects of shrubs and grasses in prairie. Oikos 91:385-395.

Langer, R.H.M. 1972. How grasses grow. Edward Arnold, London, Great Britain.

Larson, G.E., and J.R. Johnson. 2007. Plants of the Black Hills and Bear Lodge Mountains. 2nd Edition. South Dakota State University, Brookings, SD.

Legg, J.O. 1975. Influence of plants on nitrogen transformation in soils. pg. 221-227. *in* M.K. Wali (ed.). Prairie: A multiple view. University of North Dakota Press. Grand Forks, ND.

Li, X., and S.D. Wilson. 1998. Facilitation among woody plants establishing in an old field. Ecology 79:2694-2705.

Looman, J., and K.F. Best. 1979. Budd's Flora of the Canadian Prairie Provinces. Publication 1662. Agriculture Canada.

Lorenz, R.J., and G.A. Rogler. 1972. Forage production and botanical composition of mixed prairie as influenced by nitrogen and phosphorus fertilization. Agronomy Journal 64:244-249.

Manske, L.L. 1980. Habitat, phenology, and growth of selected Sandhills range plants. PhD Thesis, North Dakota State University, Fargo, ND. 154p.

Manske, L.L. 1999. Can native prairie be sustained under livestock grazing? Provincial Museum of Alberta. Natural History Occasional Paper No. 24. Edmonton, AB. p. 99-108.

Manske, L.L. 2000a. Management of Northern Great Plains prairie based on biological requirements of the plants. NDSU Dickinson Research Extension Center. Range Science Report DREC 00-1028. Dickinson, ND. 12p.

Manske, L.L. 2000b. Grazing before grass is ready. NDSU Dickinson Research Extension Center. Range Management Report DREC 00-1032. Dickinson, ND. 6p.

Manske, L.L. **2003.** Effects of grazing management treatments on rangeland vegetation. NDSU Dickinson Research Extension Center. Summary Range Research Report DREC 03-3027. Dickinson, ND. 6p.

Manske L.L. **2004.** Evaluation of interseeding seeding-date, seeding-rate, and rhizobium-inoculation techniques. NDSU Dickinson Research Extension Center. Summary Range Research Report DREC 04-3036. Dickinson, ND. 13p

Manske, L.L. **2005.** Evaluation of alfalfa interseeding techniques. NDSU Dickinson Research Extension Center. Rangeland Research Outreach Program DREC 05-4008. Dickinson, ND. 140p.

Manske, L.L. **2006a.** Chemical management of silver sagebrush. NDSU Dickinson Research Extension Center. Range Research Report DREC 06-1065. Dickinson, ND. 38p.

Manske, L.L. **2006b.** Management of western snowberry aka wolfberry and buckbrush. NDSU Dickinson Research Extension Center. Rangeland Research Outreach Program DREC 06-4009. Dickinson, ND. 107p.

Manske, L.L. **2007a.** Effects from prescribed burning treatments on mixed grass prairie. NDSU Dickinson Research Extension Center. Summary Range Research Report DREC 07-3044. Dickinson, ND. 19p.

Manske, L.L. **2009a.** Evaluation of plant species shift on fertilized native rangeland. NDSU Dickinson Research Extension Center. Range Research Report DREC 09-1071. Dickinson, ND. 23p.

Manske, L.L. **2009b.** Cost of herbage weight for nitrogen fertilization treatments on native rangeland. NDSU Dickinson Research Extension Center. Range Research Report DREC 09-1072. Dickinson, ND. 10p.

Manske, L.L. **2009c.** Grass plant responses to defoliation. NDSU Dickinson Research Extension Center. Range Research Report DREC 09-1074. Dickinson, ND. 47p.

Manske, L.L. **2009d.** Influence of soil mineral nitrogen on native rangeland plant water use efficiency and herbage production. NDSU Dickinson Research Extension Center. Summary Range Management Report DREC 09-3053. Dickinson, ND. 3p.

Manske, L.L. **2010a.** Leaf stage development of western wheatgrass tillers. NDSU Dickinson Research Extension Center. Range Research Report DREC 10-1075. Dickinson, ND. 48p.

Manske, L.L. **2010b.** Evaluation of the defoliation resistance mechanisms influence on vegetative tiller initiation and tiller density. NDSU Dickinson Research Extension Center. Range Research Report DREC 10-1076. Dickinson, ND. 13p.

Manske, L.L. **2010c.** Long-term plant species shift caused by nitrogen fertilization of native rangeland. NDSU Dickinson Research Extension Center. Summary Range Research Report DREC 10-3055. Dickinson, ND. 16p.

Manske, L.L. **2011a.** Grazing and burning treatment effects on soil mineral nitrogen and rhizosphere volume. NDSU Dickinson Research Extension Center. Range Research Report DREC 11-1066c. Dickinson, ND. 15p.

Manske, L.L. **2011b.** Biology of defoliation by grazing. NDSU Dickinson Research Extension Center. Range Management Report DREC 11-1067b. Dickinson, ND. 25p.

Manske, L.L. **2011c.** Soil mineral nitrogen increased above the threshold quantity of 100 pounds per acre in rangeland ecosystems. NDSU Dickinson Research Extension Center. Summary Range Management Report DREC 11-3056. Dickinson, ND. 8p.

Manske, L.L. **2012a** Length of the average grazing season month. NDSU Dickinson Research Extension Center. Range Management Report DREC 12-1021c. Dickinson, ND. 2p.

Manske, L.L. 2012b. Degradation and biological restoration of mixed grass prairie ecosystems. NDSU Dickinson Research Extension Center. Summary Range Research Report DREC 12-3058. Dickinson, ND. 16p.

Manske, L.L. 2013. Effects from long-term nongrazing after 75 years. NDSU Dickinson Research ExtensioCenter. Rangeland Research Outreach Program DREC 13-4016a. Dickinson, ND. 85p.

Manske, L.L. 2014a. Grass vegetative tillering responses to partial defoliation. NDSU Dickinson Research Extension Center. Range Research Report DREC 14-1086. Dickinson, ND. 35p.

Manske, L.L. 2014b. Vegetative forage tiller development in response to partial defoliation. NDSU Dickinson Research Extension Center. Range Research Report DREC 14-1087. Dickinson, ND. 26p.

Manske, L.L. 2014c. Grazingland management based on native rangeland ecosystem mechanisms and processes. NDSU Dickinson Research Extension Center. Summary Range Management Report DREC 14-3062. Dickinson, ND. 18p.

Manske, L.L. 2014d. Evaluation of nitrogen fertilization on native rangeland. 2nd Ed. NDSU Dickinson Research Extension Center. Rangeland Research Outreach Program DREC 14-4013b. Dickinson, ND. 193p.

Manske, L.L. 2018a. Restoring degraded grasslands. pp. 325-351. in A. Marshall and R. Collins (ed.). Improving grassland and pasture management in temperate agriculture. Burleigh Dodds Science Publishing, Cambridge, UK.

Manske, L.L. 2018b Grass Vegetation: An indispensable biotic component of the Northern Mixed Grass Prairie. NDSU Dickinson Research Extension Center. Rangeland Research Outreach Program DREC 18-4029. Dickinson, ND. 53p.

Manske, L.L. 2018c Rhizosphere Organisms: An indispensable biotic component of the Northern Mixed Grass Prairie. NDSU Dickinson Research Extension Center. Rangeland Research Outreach Program DREC 18-4030. Dickinson, ND. 91p.

Manske, L.L. 2018d Domesticated Graminivores: An indispensable biotic component of the Northern Mixed Grass Prairie. NDSU Dickinson Research Extension Center. Rangeland Research Outreach Program DREC 18-4031. Dickinson, ND. 26p.

Manske, L.L. 2019. Evaluation of processes that inhibit of encroachment of woody species into native rangelands of the Northern Plains. NDSU Dickinson Research Extension Center. Rangeland Research Outreach Program DREC 19-4022b. Dickinson, ND. 49p.

McCormick, M.K., D.F. Whigham, and J. O'Neill. 2004. Mycorrhizal diversity in photosynthetic terrestrial orchids. New Phytologist 163:425-438.

McGill, W.B., and C.V. Cole. 1981. Comparative aspects of cycling of organic C, N, S, and P through soil organic matter. Geoderma 26:267-286.

McNaughton, S.J. 1979. Grazing as an optimization process: grass-ungulate relationships in the Serengeti. American Naturalist 113:691-703.

McNaughton, S.J. 1983. Compensatory plant growth as a response to herbivory. Oikos 40:329-336.

Millard, P., R.J. Thomas, and S.T. Buckland. 1990. Nitrogen supply affects the remobilization of nitrogen for the growth of defoliation *Lolium perenne* L.J. Experimental Botany 41:941-947.

Mueller, R.J., and J.H. Richards. 1986. Morphological analysis of tillering in *Agropyron spicatum* and *Agropyron desertorum.* Annals of Botany 58:911-921.

Murphy, J.S., and D.D. Briske. 1992. Regulation of tillering by apical dominance: chronology, interpretive value, and current perspectives. Journal of Range Management 45:419-429.

Nurfadilah, S., N.D. Swarts, K.W. Dixon, H. Lambers, and D.J. Merritt. 2013. Variation in nutrient acquisition patterns by mycorrhizal fungi of rare and common orchids explains diversification in a global biodiversity hotspot. Annals of Botany 111:1233-1241.

Orchid Committee. nd. Fact sheets on twelve orchid species. North American Orchid Conservation Center. org. 3 to 4 pg each.

Ourry, A., J. Boucaud, and J. Salette. 1990. Partitioning and remobilization of nitrogen during regrowth in nitrogen-deficient ryegrass. Crop Science 30:1251-1254.

Peltzer, D.A., and M. Kochy. 2001. Competitive effects of grasses and woody plants in mixed grass prairie. Journal of Ecology 89:519-527.

Poinar, G. 2017. Researchers identify evidence of oldest orchid fossil on record. Oregon State University News Release.

Power, J.F., and J. Alessi. 1971. Nitrogen fertilization of semiarid grasslands: plant growth and soil mineral N levels. Agronomy Journal 63:277-280.

Power, J.F. 1972. Fate of fertilizer nitrogen applied to a Northern Great Plains rangeland ecosystem. Journal of Range Management 25:367-371.

Rasmussen, H.N., K.W. Dixon, J. Jersakova, and T. Tesitelova. 2015. Germination and seedling establishment in orchids: a complex of requirements. Annals of Botany 116(3):391-402.

Richards, J.H., and M.M. Caldwell. 1985. Soluble carbohydrates, concurrent photosynthesis and efficiency in regrowth following defoliation: a field study with *Agropyron* species. Journal of Applied Ecology 22:907-920.

Richards, J.H., R.J. Mueller, and J.J. Mott. 1988. Tillering in tussock grasses in relation to defoliation and apical bud removal. Annals of Botany 62:173-179.

Rillig, M.C., S.F. Wright, and V.T. Eviner. 2002. The role of arbuscular mycorrhizal fungi and glomalin in soil aggregation: comparing effects of five plant species. Plant and Soil 238:325-333.

Rogler, G.A., and R.J. Lorenz. 1957. Nitrogen fertilization of Northern Great Plains rangelands. Journal of Range Management 10:156-160.

Russelle, M.P. 1992. Nitrogen cycling in pastures and range. Journal of Production Agriculture. 5:13-23.

Ryle, G.J., and C.E. Powell. 1975. Defoliation and regrowth in the graminaceous plant: the role of current assimilate. Annals of Botany 39:297-310.

Sather, N., C. Freeman, L. Manske, J. Milton Jr., L. Potts, and C. Hull Sieg. 1996. Platanthera praeclara (western prairie fringed orchid) recovery plan. US Fish and Wildlife Service, Ft Snelling, MN. vi + 101p.

Schimel, D.S., D.C. Coleman, and K.A. Horton. 1985. Soil organic matter dynamics in paired rangeland and cropland toposequences in North Dakota. Geoderma 36:201-214.

Sharma, J., L.W. Zettler, J.W. Van Sambeek, M.R. Ellersieck, and C.J. Starbuck. 2003. Symbiotic seed germination and mycorrhizae of federally threatened Platanthera praeclara (Orchidaceae). The American Midland Naturalist 149(1):104-120.

Sheviak, C.J., and M.L. Bowles. 1986. The prairie fringed orchids: A pollinator-isolated species pair. Rhodora 88(854):267-289.

Six, J., E.T. Elliot, K. Paustian, and J.W. Doran. 1998. Aggregation and soil organic matter accumulation in cultivated and native grassland soils. Soil Science Society of America 62:1367-1377.

Six, J., H. Bossuyt, S. Degryze, and K. Denef. 2004. A history of research on the link between (micro) aggregates, soil biota, and soil organic matter dynamics. Soil & Tillage Research 79:7-31.

Smika, D.E., H.J. Haas, and J.F. Power. 1965. Effects of moisture and nitrogen fertilizer on growth and water use by native grass. Agronomy Journal 57:483-486.

Smith, W.R. 1993. Orchids of Minnesota. University of Minnesota Press. Minneapolis, MN.

Stevens, O.A. 1963. Handbook of North Dakota plants. North Dakota Institute for Regional Studies. Fargo, ND.

Stoddart, L.A., A.D. Smith, and T.W. Box. 1975. Range Management. 3rd ed. McGraw-Hill Book Co. New York, NY. 532p.

Taylor, J.E. 1976. Long-term responses of mixed prairie rangeland to nitrogen fertilization and range pitting. Ph.D. Thesis, North Dakota State University, Fargo, ND. 97p.

Tilman, D. 1990. Constraints and tradeoffs: toward a predictive theory of competition and succession. Oikos 58:3-15.

Tovar, P.A. 2015. Spatial and temporal variation in mycorrhizal associations in a rare North American orchid. MS Thesis, Texas Tech University, Lubbock, TX. 164p.

Weaver, J.E. 1954. North American Prairie. Johnsen Publishing Co. Lincoln, NE. 348p.

Whipps, J.M. 1990. Carbon economy. p. 59-97. in J.M. Lynch (ed.). The rhizosphere. John Wiley and Sons, New York, NY.

Whitman, W.C. 1957. Influence of nitrogen fertilizer on native grass production. Annual Report. Dickinson Experiment Station. Dickinson, ND. p. 16-18.

Whitman, W.C. 1963. Fertilizer on native grass. Annual Report. Dickinson Experiment Station. Dickinson, ND. p. 28-34.

Whitman, W.C. 1974. Influence of grazing on the microclimate of mixed grass prairie. p. 207-218. in Plant Morphogenesis as the basis for scientific management of range resources. USDA Miscellaneous Publication 1271.

Whitman, W.C. 1975. Native range fertilization and interseeding study. Annual Report. Dickinson Experiment Station, Dickinson, ND. p. 11-16.

Whitman, W.C. 1976. Native range fertilization and interseeding studies. Annual Report. Dickinson Experiment Station. Dickinson, ND. p. 11-17.

Whitman, W.C. 1978. Fertilization of native mixed prairie in western North Dakota. Annual Report. Dickinson Experiment Station. Dickinson, ND. p. 20-22.

Wight, J.R., and A.L. Black. 1972. Energy fixation and precipitation use efficiency in a fertilized rangeland ecosystem of the Northern Great Plains. Journal of Range Management 25:376-380.

Wight, J.R., and A.L. Black. 1979. Range fertilization: plant response and water use. Journal of Range Management 32:345-349.

Wilson, A.M., and D.D. Briske. 1979. Seminal and adventitious root growth of blue grama seedlings on the central plains. Journal of Range Management 32:209-213.

Wright, H.A., and A.W. Bailey. 1982. Fire Ecology: United States and southern Canada. John Wiley & Sons. New York, NY. 501p.

US Fish and Wildlife Service. 2009. Western prairie fringed orchid (Platanthera praeclara) 5-year review: Summary and evaluation. Twin Cities Field Office. Bloomington, MN. 37p.

Zelmar, C.D., and R.S. Currah. 1995. Ceratorhiza pernacutena and Epulorhiza calendulina spp. ov.: mycorrhizal fungi of terrestrial orchids. Canadian Journal of Botany 73(12):1981-1985.