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Proactive Management of Pestiferous Rangeland Grasshopper Habitat of the Northern Plains

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Cover Photograph
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Preface

Pestiferous rangeland grasshopper population outbreaks can be extremely detrimental to the plant resources of a region, which in turn, can have devastating consequences for the livestock that depend on those plants for forage and for the beef producers that depend on the nutrients produced by the forage plants for family income. The information in this report explains what, why, how, and when Northern Plains beef producers and land managers could change traditional grazingland management practices three years before the next grasshopper problem to prevent or reduce the damaging ecological and economical impacts caused by pestiferous rangeland grasshopper population increases. These paradigm changes are proactive long-term land management strategies that are favorable for livestock production and create habitat unfavorable for pest grasshopper production and that are sensible alternatives to the typical reactive short-term chemical insecticide spray treatments implemented after the grasshopper numbers have intensified.

These guidelines for proactive management of pestiferous rangeland grasshopper habitat of the Northern Plains are based on recent discoveries of grasshopper biology and population dynamics and on the latest technologies for activation of the defoliation resistance mechanisms within grass plants and activation of the biogeochemical processes within rangeland ecosystems. The resulting habitat changes in residuum vegetation structure during the growing season inhibit access to direct sunlight that decreases day-degrees of heat reaching the eggs, reducing embryonic development, and delaying hatch date, and that restricts thermoregulation of grasshopper body temperature at optimal high levels, reducing developmental growth rates of nymphs and adults, increasing mortality rates, and reducing population numbers to tolerable densities.

Introduction

Grasshoppers are a natural component of native rangelands and domesticated grasslands of the Northern Plains. Grasshopper population densities ordinarily remain at levels that can be supported by the resources of the ecosystem. At low densities, grasshoppers are not a problem. However, when favorable conditions decrease mortality rates, increase available food plants, and/or increase access to direct sunlight, pestiferous rangeland grasshopper populations can increase to problem densities.

Pestiferous rangeland grasshopper population densities are regulated by the mortality rates caused by natural enemies, by the availability of nutritious food plants, and by the level of access to direct sunlight throughout the day. Grasshoppers living on arid rangelands of the intermountain west region and of the southern short grass region have abundant access to direct sunlight but are limited by the availability of adequate nutritious food plants except during growing seasons with above normal precipitation. Grasshoppers living on rangelands of the Northern Plains have adequate nutritious food plants available even during dry growing seasons but are limited by restricted access to direct sunlight except during growing seasons with high water deficiencies or drought conditions or on heavily grazed, poorly managed, or double used grazinglands with considerable bareground areas and reduced grass plant stature.

Habitat favorable for pestiferous grasshopper production in the Northern Plains has the canopy cover reduced to less than 40% of the ordinary with relatively short stature grass plants and numerous bareground areas. Direct sunlight saturates the majority of the bareground locations during most of the day for the entire growing season.

Grasshoppers are ectothermal (cold blooded), unable to regulate their body temperature metabolically. Grasshoppers must bask on bareground sites in direct sunlight to raise their body temperature to the optimal high levels above 95° F (35° C) and must constantly adjust their exposure in and out of direct sunlight to maintain the body temperature within a few degrees throughout the day. The greater proportion of hours per day that a grasshopper can achieve optimal body temperature, the greater the rate of growth and development because of the accompanying greater rates of metabolism, nutrient assimilation, food plant ingestion, and activity levels; in addition, the grasshopper has greater speed to escape predators. The length of time nymphs are at each instar stage is reduced, a greater percent of the nymphs reach the adult stage, maturation time after adults fledge is reduced, and the quantity of viable eggs produced by each adult female is increased.

All, except one, of the pestiferous rangeland grasshoppers in the Northern Plains deposit egg pods below the soil surface in bareground sites. Bareground areas provide ideal egg pod deposition sites because abundant direct sunlight reaches the soil surface maximizing the day-degrees of heat accumulation by the eggs resulting in increased embryo development rates, earlier hatch initiation, and reduced hatch period duration. The remuneration to the land manager that provides favorable habitat with abundant access to direct sunlight for pestiferous rangeland grasshoppers is the multifold increase in the number of hatchlings produced during the next growing season.

Beef producers that use the old traditional range management concepts to mange the aboveground perennial grass resources for a single primary use as forage for livestock or for the products removed cause spiraling degradation of the ecosystem that results in reduced grass plant density, increased size and number of bareground areas, and decreased grass herbage biomass production creating habitat favorable for pestiferous grasshoppers. Traditional range management has one solution for this common problem; reduced stocking rate.

Fortunately, there are new technologies that can manage grazingland ecosystems as complete systems that include all of the aboveground and belowground components and improve ecosystem functionalities that result in greater grass plant densities, decreased size and number of bareground areas, and increased grass herbage biomass production creating habitat unfavorable for pest grasshopper production.

Rangelands are complex ecosystems consisting of numerous interactive biotic (living) and abiotic (nonliving) components. The biotic components are the plants, soil microorganisms, and large grazing graminivores that have biological and physiological requirements. The abiotic components include the major and minor essential elements that have transformable characteristics between organic and inorganic forms. The major essential elements are carbon, hydrogen, nitrogen, and oxygen and the minor essential elements consist of seven macrominerals and ten microminerals. The abiotic components also include radiant energy from the sun. Numerous biological, geological, chemical, and atmospheric pathways transfer the major essential elements into and out of an ecosystem and numerous pathways transfer the minor essential elements out of an ecosystem. Rangeland ecosystems are functioning units of coacting biotic organisms interacting with the abiotic components and the environment. The complex of mechanisms and processes connected with these extensive interactions are the defoliation resistance mechanisms within and around grass plants and the biogeochemical processes within an ecosystem.

The defoliation resistance mechanisms provide important biological and physiological processes permitting grass plants to produce greater herbage biomass that replaces lost leaf material, to restore disrupted vital processes, and to vegetatively reproduce secondary tillers from axillary buds that increase grass tiller density. The soil microorganisms in the rhizosphere and the biogeochemical processes cycle essential elements between the organic and inorganic forms that permit renewable natural resource ecosystems to be functionally renewable.

A biologically effective grazing management strategy has been developed with two grazing periods in each of the 3 to 6 pastures that have rotation dates coordinated with grass phenological growth stages. Partial defoliation by grazing that removes about 25% to 33% of the aboveground leaf material of grass lead tillers between the 3.5 new leaf stage and the flower stage activates the defoliation resistance mechanisms and the biogeochemical processes that improve ecosystem productivity and create conditions favorable for livestock production and unfavorable for pest grasshopper production.

Grasshopper IPM Program: A Retrospective

Grasshopper populations increased during the 1930's to devastating numbers that infested millions of acres of federal and private lands in 17 western states. The grasshopper outbreaks overwhelmed local control efforts. The United States Congress charged the United States Department of Agriculture in 1934 with the control of grasshoppers on federal land. With authorization from several congressional acts, grasshopper control on federal lands and leadership of large scale regional grasshopper control programs became one of the duties of the USDA Animal and Plant Health Inspection Services (APHIS) (Foster 1996a).

Cooperative control programs for rangeland grasshoppers were undertaken by APHIS during almost every proceeding year in affected parts of the Great Plains and Intermountain West. The standard pest control treatment used was liquid insecticide chemicals. Grasshopper populations increased to devastating numbers again during the 1980's that heavily infested 55 million acres of land in western United States. Following standard pest control treatment guidelines was continued and liquid insecticides were aerially applied in blocks of 10,000 acres or larger resulting in a total of more than 20 million acres treated during 1985-1986 (Foster et al. 2000). These large-scale insecticide treatments generated serious concerns about the effects on nontarget organisms, the environment, and the ecosystems.

The development of the Grasshopper Integrated Pest Management Project was described by Cunningham (2000) which has been summarized for this report. In 1987, APHIS initiated the Grasshopper Integrated Pest Management (GHIPM) Project to develop and demonstrate new integrated pest management (IPM) technologies that included prescribed biological, chemical, and cultural methods to control pest grasshopper populations that were above economic thresholds, refinement of grasshopper phenology information, modeling population dynamics, and development of an integrated expert system for grasshopper management. The overall purpose of the GHIPM Project was to develop tools that would help in predicting outbreaks and to develop a combination of preventive tactics that would reduce reliance upon chemical insecticides for control. The comprehensive research and development component was conducted from 1987 to 1994 at two demonstration sites that were established in northwestern North Dakota and in south central Idaho. The Idaho demonstration site lacked high grasshopper populations during 1988 to 1994, making this site less suitable for demonstrating new IPM control technologies. The results from numerous individual research projects were written in a nonscientific format, compiled over a period from 1995 to 2000, and issued during the summer of 2000 as the Grasshopper Integrated Pest Management User Handbook, USDA, APHIS, Technical Bulletin No. 1809.

The grasshopper control studies conducted at the North Dakota Grasshopper IPM Demonstration Project Site during 1987 to 1993 were described by Quinn et al. (2000) which have been summarized for this report. The results from the protozoan pathogen *Nosema*-bran bait study suggested that this biological control field treatment had little, if any, effects on grasshoppers. The results from the 2% carbaryl-bran bait studies showed short-term reductions in total grasshopper populations at an average of 44.5%. Two applications of carbaryl-bran bait were needed when initial grasshopper populations were at very high densities. These moderate levels of control from carbaryl-bran baits resulted because only some grasshopper species consume litter. The grasshopper species that do not consume litter, do not consume bran bait, and are thus not affected by the insecticide. The aerial and ground applications of malathion sprays and carbaryl sprays were the most efficacious treatments with reductions in total grasshopper populations at an average from 84% to 99%.

The grasshopper IPM studies in North Dakota developed more intensive management methods that conduct thorough grasshopper surveys for adults during late summer and for nymphs during spring to more accurately define areas of grasshopper infestations and treat these grasshopper hotspots with carefully timed applications of either malathion or carbaryl insecticidal sprays. The expected outcome from implementation of the grasshopper control techniques developed during the IPM project was great reductions in the costs of grasshopper control treatments and in the amounts of insecticides applied to rangelands compared to the standard treatment of large-scale aerial application of insecticidal sprays to regional grasshopper outbreaks. The conclusion of this report (Quinn et al. 2000) was that the grasshopper control technologies developed during the North Dakota demonstration project should be incorporated into the national grasshopper IPM programs.

A few changes have been made since the printing of Technical Bulletin No. 1809. During the Grasshopper IPM Project, carbaryl bran baits were found not to be particularly effective against high densities of diverse grasshopper assemblages (Foster and Onsager 1996a). Since then, commercial bait products containing carbaryl have no longer been registered for use on rangeland.

The registration for use of the chemical insecticide acephate on grazed or cut for hay rangeland was not renewed. Between the first year of registration in 1982 and the last year of registration, acephate was rarely used for grasshopper control because of the undesirable mixing (Foster and Onsager 1996b). Acephate is still registered for insect control on noncropland areas not grazed or cut for hay. Both carbaryl bran baits and the chemical insecticide acephate have been removed as treatments used during cooperative rangeland grasshopper control programs (APHIS 2002).

An insect growth regulator, dimilin (diflubenzuron), that inhibits chitin formation in immature insects was registered as a restricted use pesticide (RUP) by the US Environmental Protection Agency (EPA) for rangeland grasshopper control. In order to effectively prevent immature grasshoppers from forming their chitinous exoskeleton, dimilin must be applied early in the season when nymphs compose almost the entire population (Foster and Reuter 1996).

During the Grasshopper IPM Project, reduced rates of chemical insecticide sprays were tested with some results showing enough success to continue the research (Reuter and Foster 1996). During 1995 to 2003, reduced chemical research was conducted by University of Wyoming and USDA scientists on a chemical control method referred to as Reduced Area and Agent Treatments (RAATs) where the insecticide rates were reduced below traditional blanket treatment rates and treated swaths alternated with untreated swaths (Lockwood and Schell 1997, Lockwood et al. 2000, Foster et al. 2000, Lockwood et al. 2001, Lockwood and Latchininsky 2004). Both the insect growth regulator dimilin and the chemical control method Reduced Area and Agent Treatments (RAATs) have been added as treatments used during cooperative rangeland control programs (APHIS 2002).

Cultural control of rangeland grasshoppers by manipulation of habitat by livestock grazing practices was studied at the North Dakota Grasshopper IPM Demonstration Project Site during 1993 and 1994. The research was conducted as a joint project between the Range Research Laboratory at the NDSU, Dickinson Research Extension Center, Dickinson, North Dakota and the Rangeland Insect Laboratory, USDA-ARS, Bozeman, Montana. The range laboratory team was responsible for the grazing management treatments and the vegetation parameter data and the insect laboratory team was responsible for the grasshopper identification and population density data. This study was conducted with the cooperation of the USDA Forest Service and the McKenzie County Grazing Association. From 1995 through 1998, the cultural control study was conducted as two independent projects without funding from APHIS. Preliminary reports were included in USDA/APHIS Project Annual Reports (Manske 1993, 1994a, 1994b). Project reports were included in the Grasshopper IPM User Handbook (Onsager 1996, Manske 1996b). Summary project reports were presented to the National Grasshopper Management Board and included in the proceedings (Manske and Onsager 1996, 1997; Onsager 1998). Manske (1999a) explained the adaptive tolerance mechanisms that had coevolved among the soil organisms, grass plants, and grazing livestock interactions and described how management of grazing livestock can be used to manipulate these mechanisms and change rangeland habitat to be unfavorable for pestiferous rangeland grasshoppers. Onsager (2000) documented the occurrence of a grasshopper outbreak on rangeland managed by seasonlong grazing and the prevention of the grasshopper outbreak on rangeland managed by the twice-over rotation grazing strategy and explained how the grazing system changes in habitat caused differences in grasshopper population dynamics. Unfortunately, the results from these two separate but collaborative projects were not reported jointly. The objective of this report is to explain how cultural management can be used to reduce pestiferous grasshopper outbreaks by connecting the relationships of grasshopper life cycle growth and development biology with the unfavorable habitat changes resulting from grazing manipulation of rangeland ecosystem biogeochemical processes.

Even though research on cultural control of grasshoppers was include among the numerous projects during the Grasshopper IPM Project, cultural management practices will not be included as treatments used during cooperative rangeland grasshopper control programs. APHIS lacks land management authority. The responsibility of APHIS is to directly intervene and suppress grasshopper populations only when requested and only when those grasshopper populations on a large region or on a hotspot reach levels that can cause economic damage to rangeland forage and/or adjacent cropland (APHIS 2002). Implementation of the actual cultural practices, such as grazing management strategies, that are intended to prevent grasshopper outbreaks are the responsibility of the livestock producers and land managers rather than APHIS. This report will assist in the development and operation of grasshopper cultural management practices.

Grasshopper Mortality: Pathogens, Parasites, and Predators

Grasshopper population numbers are a balance between fecundity and mortality. Mortality of grasshoppers by natural enemies; pathogens, parasites, and predators is high. Grasshoppers have numerous natural enemies. Most grasshopper species have high fecundity levels and can replace themselves several times over. Most female grasshoppers that survive to the adult stage typically produce 100 to 200 fertile eggs. Without the activities of the natural enemies, grasshoppers would be a perpetual serious annual problem.

The incidence of parasites and predators tends to increase proportionally with the increase in grasshopper densities. The increased mortality rate from natural enemies would be expected to cause reductions in the longevity of individual grasshoppers that are members of populations with greater densities (Hewitt and Onsager 1983). Even though the complex of natural enemies can cause high mortality rates in grasshopper populations, none of the individual natural enemies are technically biological control agents. None of the natural enemies are known to reduce the grasshopper populations severe enough to prevent periodic outbreaks.

Grasshopper species have affinities to several grassland biomes resulting in diverse combinations of grasshopper assemblages in different habitats. Grasshopper natural enemies also have affinities to several grassland biomes that results in the development of different combinations of pathogens, parasites, and predators in the various grassland habitats. The combinations of grasshopper species present vs. the combination of natural enemies present will be extremely variable in the numerous different grassland habitats.

Pathogens

Pathogens are microorganisms that cause diseases. It is uncommon for grasshoppers to be affected by diseases caused by viruses and bacteria. Two types of viruses have been isolated from grasshoppers; entomopoxvirus and crystalline array viruses (Hostetter and Streett 1994) (table 1). As of yet, no bacteria have been found to effectively increase mortality of grasshoppers under field conditions (Hostetter and Streett 1994). Understanding the roles of viruses and bacteria causing grasshopper mortality is still at rudimentary stages.

Protozoa are unicellular microorganisms. Only one genius, *Nosema*, is known to affect at least 90 species of grasshoppers. Three species of *Nosema* have been isolated: *N. locustae*, *N. acridophagus*, and *N. cuneatum* (table 1). Grasshoppers are infected with *Nosema* by consuming the spore stage on food items or by eating infected cadavers. The ingested spores enter the epithelial cells of the midgut, reproduce asexually, and then attack the fat bodies, and the pericardial and neural tissue of the host. Some grasshopper species can overcome the protozoan disease by encapsulating the mobile sporozoan. Infection levels can be acute, causing death in several days, and can be chronic, showing no outward symptoms. Microsporidia are passed to the next generation through eggs laid by infected females (Watts et al. 1989, Streett 1994, Hildreth et al. 1994, Vaughn et al. 1994, Hostetter and Streett 1994).

A few fungi infect grasshoppers. Fungi spores are not infectious when ingested by grasshoppers. Fungi spores that come in contact with the exoskeleton of a grasshopper, attachs with external mycelial on the surface of the grasshopper, and then develops a tube that penetrates the body wall releasing a protoplast which has a single nucleus capable of asexual reproduction in the body cavity of the host. The fungus grows rapidly inside of the host, killing the grasshopper. The fungus grows back through the body wall, forms vegetative stalks that produce primary spores, conidia, that are discharged into the atmosphere capable of infecting some of the grasshopper species it comes in contact (Watts et al. 1989, Hostetter and Streett 1994, Bidochka and Roberts 1994).

There are two groups of fungi that are pathogenic to grasshoppers. The deuteromycota fungi are facultative and do not require a grasshopper host to live. An infection of *Beauveria bassiana* is characterized by white mycelial and the conidia are globose, globelike. An infection of *Metarhizium anisopliae* is characterized by green mycelial and the conidia are rod shaped. An infection of *Aspergillus flavus* is characterized by green mycelial and the conidia are spherical (Bidochka and Roberts 1994) (table 1).

The zygomycota fungi are obligate and require a grasshopper host to live. The pathogenic fungi are a complex of *Entomophaga grylli* comprised of pathotypes which have recently been separated into species. *Entomophaga maclead* (pathotype I) infect bandwinged grasshoppers of the Oedipodinae subfamily. *Entomophaga calopteni* (pathotype II) infect spurthroated grasshoppers of the Melanoplinae subfamily. *Entomophaga praxibuli* (pathotype III) infect slantfaced grasshoppers of the Gomphocerinae subfamily, spurthroated grasshoppers of the Melanoplinae subfamily, and bandwinged grasshoppers of the Oedipodinae subfamily (Hostetter and Streett 1994, Bidochka and Roberts 1994) (table 1). Epizootic infections of fungal diseases require high relative humidity associated with microhabitats in relatively tall dense vegetation. *Entomophaga* decreases or ceases to exist in dry habitats. In humid environments, the highest mortality rate usually occurs before the nymphs complete the third instar. During the advanced stages of infection from *Entomophaga* pathotypes, the infected grasshoppers crawl to the tops of plants, wrap their legs around the plant stalk, and die with head up (Bidochka and Roberts 1994).

Invertebrate Parasites and Predators

Numerous insects, arachinids, and nematodes are parasites on or in grasshoppers or predators of grasshoppers. Not all of the listed parasites and predators occur on all rangeland ecosystems, however, more than one natural enemy would be expected to be active at some level on all grasshopper habitats. The inverbetrate natural enemies of grasshoppers are considered to be nontarget species but are susceptible to the chemical insecticides used to control grasshopper infestations.

The larvae of 26 species of blister beetles (Meloidae) consume and destroy grasshopper egg pods. The female blister beetle lays 100 to 200 eggs in a chamber she has dug into the soil. After hatching, the larvae are quite mobile and search for food in the soil. When they find a grasshopper egg pod, they feed on the eggs, and transform into a fat white grub. Completion of larvae development may require more than one grasshopper egg pod (Munro 1939, Dysart 1994) (table 1).

The larvae of numerous species of ground beetles (Carabidae) consume and destroy grasshopper egg pods (Dysart 1994) (table 1).

The larvae of an anthomyiid fly (Anthomyiidae) are endoparasites of nymph and adult grasshoppers. The gravid female fly captures a grasshopper, chews a hole in the grasshopper exoskeleton with her rasping mouth parts, and feeds upon the body fluids of the host, then she inserts her ovipositor through the hole and lays eggs inside the host body cavity. The eggs hatch within 48 hours. Twenty to seventy larvae feed on the host and complete 3 instars in 16 to 20 days. Mature larvae emerge from the host, enter the soil, and pupate. The process reduces grasshopper feeding, prevents reproduction, and with larvae emergence, kills the host grasshopper (Watts et al. 1989, Hostetter 1994) (table 1).

The adults of 26 species of robber flies (Asilidae) are large enough to capture nymph and adult grasshoppers. The robber fly sucks out the internal contents and leaves an empty grasshopper shell. Under some conditions, robber flies can reduce grasshopper populations by 11% to 15% (Watts et al. 1989, Hostetter 1994) (table 1).

The larvae of 13 genera of bee flies (Bombyliidae) are predators of grasshopper egg pods. Bee fly eggs are deposited in soil cracks near ovipositing grasshoppers. The bee fly eggs hatch after a brief incubation period and the larvae wander through the soil in search for food, randomly locating the nearby egg pods. Bee fly larvae consume and destroy one to three egg pods to complete development. The fully developed larvae moves near the soil surface and pupates (Munro 1939, Dysart 1994) (table 1).

The larvae of 2 species of tangleveined flies (Nemestrinidae) are endoparasites of late instar nymphs and adult grasshoppers. The tangleveined flies overwinter in the soil as mature larvae, pupate and emerge as adults in the spring. Gravid female flies deposit thousands of eggs on dead vegetation or fenceposts at heights of 3 to 40 feet above the ground. The eggs hatch in 8 to 10 days and the small larva are distributed by the wind. The fly larva makes random contact with a grasshopper host and penetrates the body wall within 30 minutes. The larva develops a spiral respiratory tube that opens to the outside of the hosts body wall. The larva feeds on the host's fat and reproductive tissue, completing 4 instars. The large larva emerges, then burrows into the soil. The process reduces grasshopper feeding, prevents reproduction, and with larva emergence, kills the host grasshopper (Watts et al. 1989, Hostetter 1994) (table 1).

The larvae of 21 to 23 species of flesh flies (Sarcophagidae) are endoparasites of nymph and adult grasshoppers. Flesh flies are ovoviviparous, the eggs develop and hatch in the female fly uterus. The female fly captures a grasshopper in the air or on the ground and deposits live larvae in or on the host. The larvae deposited on a grasshopper quickly penetrates the host body wall. The fly larvae feed on the hosts body fluids and tissue, and continue feeding through the completion of 3 instars in 6 to 9 days. The mature larva exits the host and pupates in the soil. The process reduces grasshopper feeding, prevents reproduction, and with larva emergence, kills the host grasshopper (Watts et al. 1989, Hostetter 1994) (table 1).

The larvae of 3 species of tachinid flies (Tachinidae) are endoparasites of nymph and adult grasshoppers. The female fly deposits their eggs on the surface of the host grasshopper. The egg hatches, the larva burrows into the host, and feeds on body fluids and tissue. The larva completes 3 instars, emerges from the host, and pupates in the soil. The process reduces grasshopper feeding, prevents reproduction, and with larva emergence, kills the host grasshopper (Watts et al. 1989, Hostetter 1994) (table 1).

Rangeland ants (Formicidae) are opportunistic predators of hatchling grasshoppers. The hatchling grasshoppers wriggle to the soil surface from the egg pod. They are covered by an embryonic membrane called the serosa. This membrane prevents the hatchlings from standing upright and jumping away from predatory ants. Shedding the serosa requires a few minutes of squirming by the hatchling on its side or back. After the serosa has been shed, they can stand up and jump away from the ants. The number of hatchlings captured by rangeland ants has little effect on grasshopper populations (Wheeler and Wheeler 1963, Watts et al. 1989, Hostetter 1994, Pfadt 1994) (table 1).

The larvae of 2 genera and 21 species of the minute scelionid wasps (Scelionidae) are parasites of grasshopper eggs. The adult female wasp locates grasshopper egg pods by some chemical attraction to the pod froth. The female wasp chews a passage through the froth plug to the grasshopper eggs. She extends her long ovipositor into the egg pod and lays one wasp egg per grasshopper egg. The wasp egg hatches, the larva feeds internally on the grasshopper embryo. When the wasp larva matures, it pupates within the host egg shell and emerges as an adult during summer (Dysart 1994) (table 1).

The larvae of 29 species of solitary wasps (Sphecidae) are parasites of living paralyzed adult grasshoppers. The female digger wasp catches an adult grasshopper, paralyzes it, caches it in a burrow in the soil, and deposits an egg on the live grasshopper. After the egg hatches, the wasp larva consumes the live grasshopper. These threadwaisted wasps are usually rare in most rangeland grasshopper habitat (Watts et al. 1989, Hostetter 1994) (table 1).

Adult spiders of 9 species have been reported as predators of nymph and adult grasshoppers. The food preferences of rangeland spiders is difficult to collect. Most spiders are opportunistic and consume anything they can catch, including grasshoppers. The large nonweb building wolf spiders (Lycosidae) and jumping spiders (Salticidae) are abundant on rangelands and prey on grasshoppers. The cobweb building black widow spiders (Theridiidae) consume the grasshoppers that hop into their web (Watts et al. 1989, Hostetter 1994, Oedekoven and Joern 2000) (table 1).

The larvae of 2 species of red mite (Trombidiidae) are ectoparasites of adult grasshoppers, and at least 1 species of mite prey on grasshopper eggs at the nymph and adult stages. The mite larvae attach to the external surface of adult grasshoppers and suck blood (hemolymph). The larvae of the common species of mite attaches to the adult grasshopper at the base of the wings. The larvae of an unnamed recently found species of mite attaches to the grasshopper on the legs and antennae. The mite larvae remain feeding on the grasshopper until fully engorged. The mite larva drops off the host, burrows into the soil, and transforms into an eight legged immature nymph. The mite nymph finds grasshopper egg pods and feeds on the eggs. Each mite nymph requires more than two grasshopper eggs to become an adult. Adult male mites require three grasshopper eggs to mature and become reproductive. Adult female mites require seven to eight grasshopper eggs to mature and become reproductive. The adult mites mate while in the grasshopper egg pods. The female mite lays 300 to 700 eggs per cell. Mite larvae emerge in 28 to 30 days and attach themselves to the exoskeleton of an adult grasshopper (Watts et al. 1989, Belovsky et al. 1994, Hostetter 1994) (table 1).

The larvae of 3 species of nematodes (Mermithidae) are endoparasites of nymph grasshoppers. The nymph grasshopper becomes infected when it consumes a nematode egg that had been deposited on a grass leaf or when a hatched nematode larva penetrates the exoskeleton. The nematode larva moves to the grasshopper's body cavity and feeds on the blood (hemolymph) for 4 to 10 weeks. The mature larva exits the host grasshopper**,** overwinters in the soil, and molts into an adult nematode in the spring. The process kills the host grasshopper (Belovsky et al. 1994, Hostetter 1994) (table 1).

The second stage terrestrial larvae of horsehair worms (Gordiacea) are incidental endoparasites of nymph and adult grasshoppers. Adult horsehair worms are free living in aquatic habitats. The female worm lays thousands of eggs in long strings in the water. The eggs hatch and the first larvae stage is endoparasitic of an aquatic insect host. The second larvae stage is endoparastic of a terrestrial insect host, frequently the terrestrial host is a grasshopper (Hostetter 1994). When the mature horsehair worm, which has eaten most of the insides of the host and is, by then, several times the length of the grasshoppers' body, is ready to exit the host and return to an aquatic habitat, the parasite produces two proteins that are similar to insect type proteins and injects these proteins into the brain of the host. The proteins manipulate the host to look for water and to jump in. The worm leaves the insect, enters into the aquatic habitat, and soon develops to sexual maturity. The grasshopper is a poor swimmer and drowns (Wade 2005) (table 1).

Table 1. Rangeland grasshopper invertebrate natural enemies: pathogens, parasites, and predators.

Pathogen - a disease producing microorganism including viruses, bacteria, protozoans, and fungi.

Viruses. uncommon in grasshoppers under natural conditions.
two types found in grasshoppers.
entomopoxvirus.
crystalline array viruses.

Protozoan. unicellular animal organisms.
grasshoppers consume spore stage or eat infected cadaver.
Family: Microsporida.
Nosema locustae. attacks fat bodies, pericardial and neural tissue.
Nosema acridophagus. has potential, needs additional research.
Nosema cuneatum. has potential, needs additional research.

Fungi.

Deuteromycota. facultative, does not need grasshopper host to live.
most common.
Beauveria bassiana. white mycelial, globose conidia.
Metarhizium anisopliae. green mycelial, rod shaped conidia.
Aspergillus flavus. green mycelial, spherical conidia.

Zygomycota. obligate, needs grasshopper to live.
Entomophaga grylli. complex.
Entomophaga macleod. pathotype I.
infects Oedipodinae.
Entomophaga calopteni. pathotype II.
infects Melanoplinae.
Entomophaga praxibuli. pathotype III.
infects Gomphocerinae, Melanoplinae, and Oedipodinae.

Table 1 cont. Rangeland grasshopper invertebrate natural enemies: pathogens, parasites, and predators.

Parasites and Predators

Parasite - an organism living on (ectoparasitism) or in (endoparasitism) the body of another (host) from which the parasite obtains nutrients and contributes nothing to host.

Parasitoid - an organism that is alternately parasitic and free living, during the parasitic stage the host is consumed and killed.

Predator - an organism that hunts, captures, and kills another (prey) for food.

Phylum: Arthropoda.

Subphylum: Hexapoda.

Class: Insecta.

Order: Coleoptera (beetles).

Family: Meloidae (blister beetles). egg pod predators.
26 species.
larvae of blister beetles consume and destroy about 9% of egg pods.

Family: Carabidae (ground beetles). egg pod predators.
numerous species.
larvae of ground beetles consume and destroy about 3% of egg pods.

Order: Diptera (flies).

Family: Anthomyiidae (anthomyiid flies). endoparasite of nymphs and adults.
Acridomyia canadensis.
female fly oviposits eggs inside host body, larvae consume grasshopper.

Family: Asilidae (robber flies). predators of nymphs and adults.
26 species. can reduce grasshopper population 11% to 15%.
Northern Plains species.
Stenopogon coyote
Stenopogon neglectus
Stenopogon picticornis

Family: Bombyliidae (bee flies). egg pod predator.
13 genera.
larvae of bee flies consume and destroy about 6% of egg pods.

Family: Nemestrinidae (tangleveined flies). endoparasites of nymphs and adults.
Neorhynchocephalus sackenii
Trichopidea clausa
larvae distributed by wind, locate host, feeds inside on fat and reproductive tissue.
parasitism rates at 30% to 95% of grasshopper population.

Table 1 cont. Rangeland grasshopper invertebrate natural enemies: pathogens, parasites, and predators.

Family: Sarcophagidae (flesh flies). endoparasites of nymphs and adults.
21 to 23 species.
Prominent species.
Acridophaga aculeata
Kellymyia kellyi:
Opsophyta opifera
Protodexia hunteri
Protodexia reversa
female fly deposits larvae on or in host, larvae feed on grasshopper body fluids.
parasitism rates at 1% to 50% of grasshopper population.

Family: Tachinidae (tachinid flies). endoparasites of nymphs and adults.
Acemyia tibialis parasitism rates at 16% to 65% of grasshopper population.
Ceracia dentata parasitism rates at 1% to 5% of grasshopper population.
Hemithrixion oestriforme parasitism rates at 1% to 5% of grasshopper population.

Order: Hymenoptera (ants, wasps, bees).

Family: Formicidae (ants). predators of helpless hatchlings.
rangeland ant species.
Formica rufa obscuripes
Formica obtusopilosa
Myrmica sabuletti americana
Solenopsia molesta validiuscula
opportunistic predation of hatchlings has little effect on grasshopper population.

Family: Scelionidae (minute scelionid wasps). egg parasites.
2 genera, 21 species.
one wasp egg oviposited per grasshopper egg, wasp larvae consume grasshopper embryo.
parasitism rates destroy about 5% to 15% of egg pods.

Family: Sphecidae (solitary wasps). parasites of adults.
Subfamily: Sphecinae (threadwaisted wasp). Tribe: Ammobiini.
Prionyx parkeri
paralyzed living grasshopper placed in wasp nest with wasp egg, wasp larvae consume live grasshopper.
these wasps are generally rare in grasshopper habitat

Table 1 cont. Rangeland grasshopper invertebrate natural enemies: pathogens, parasites, and predators.

Subphylum: Chelicerata.

Class: Arachnida

Order: Araneida (spiders).

Family: Lycosidae (wolf spiders). predators of nymphs and adults.
Schizocosa sp.

Family: Salticidae (jumping spiders). predators of nymphs and adults.
Pellenes sp.

Family: Theridiidae (cobweb spiders). predators of nymphs and adults.
Latrodectus sp. (black widow spiders)

Order: Acarina (mites).

Family: Trombidiidae (velvet mites). ecotoparasites of adults.
Eutrombidium locustarum (red mites) on wings.
unnamed recently found mite (different red mite) on legs.
mite larvae stage attaches to grasshopper exoskeleton and sucks blood (hemolymph) until larvae is engorged.

Phylum: Nematoda (roundworms).

Family: Mermithidae (nematodes). endoparasites of nymphs.
Agamermis decaudata
Agamospirura melanopli
Mermis nigrescens
grasshopper nymphs consume nematode eggs on vegetation, nematode larvae consumes grasshopper.

Family: Gordiacea (horsehair worms). incidental endoparasites for nymphs and adults.
second stage terrestrial larvae seeks second host, feeds from inside grasshopper.

Vertebrate Predators

Grasshoppers provide nutritious food for rangeland amphibians, reptiles, birds, and small mammals. Grasshoppers have high energy value and contain 50% to 70% crude protein. The relatively large size of grasshoppers provides greater nutrient quantity than the amount of nutrients that small rangeland predators expend during the capture of grasshopper food (Belovsky et al. 1990).

The rangeland amphibians that prey on grasshoppers for food are adult frogs, toads, and salamanders (table 2). The rangeland reptiles that prey on grasshoppers for food are skinks, lizards, snakes, and terrestrial turtles (Over 1923, Wheeler and Wheeler 1966) (table 2).

Several rangeland birds use grasshoppers as a significant source of high quality nutrients. Nestlings and chicks must go through a period of rapid development and growth to survive their juvenile stage. Grasshoppers are important for the successful raising of young birds (Watts et al. 1989, McEwen et al. 1994). Pheasants, turkeys, prairie grouse, harriers, cooper's hawks, swainson's hawks, kestrels, plovers, sandpipers, gulls, cuckoos, shorteared owls, burrowing owls, shrikes, horned larks, bluebirds, catbirds, thrashers, grassland sparrows, dickcissels, bobolinks, and meadowlarks consume grasshoppers during the growing season for a great proportion of the juvenile food and for 30% to 90% of the adult staple diet (Jackson 1926, Bent 1968) (table 2).

Nonmigratory gallinaceous birds, notably prairie chickens and sharptailed grouse, have learned how to search and find dried grasshoppers during each month of the nongrowing season in the stacks of hay stored as livestock feed. The high crude protein content of dried grasshoppers contribute a substantial portion of the nutrients needed for the winter survival of these grouse (Manske unpublished data).

Several small rangeland mammals use grasshoppers as an important portion of their regular diet. Opossums, shrews, ground squirrels, grassland mice, raccoons, and skunks consume substantial quantities of grasshoppers when they are available (Jones et al. 1983, Chapman and Feldhamer 1992) (table 2). Predation by amphibians, reptiles, birds, and small mammals on rangeland grasshoppers has the potential force to stabilize grasshopper populations (Watts et al. 1989, Fowler et al. 1991).

Grasshoppers that have completed the morning basking period and raised their body temperature can escape predators by jumping away. Their enormous hind legs can propel a grasshopper distances of 20 times their body length. The grasshoppers' explosive jump is possible because the powerful energy force of the large muscles in the femur is stored in the elastic fibers of a semilunar crescent organ located in the knee. When a predator approaches, the released energy catapults the grasshopper away from danger (Davidowitz 2013).

Grasshoppers have numerous patterns of cryptic coloration that permit them to blend in with the background colors and textures of their habitat. These natural camouflage colorations improve the chances for individual grasshoppers to avoid being caught and eaten by predators (Anonymous 2013). Many slantfaced, Gomphocerinae, grasshoppers have horizontal light and dark bands that run most of the length of their bodies that help them mimic grass blades when they set vertically within a clump of grass. Many bandwinged, Oedipodinae, grasshoppers have cryptic coloration with the addition of deceptive escape strategies. During the short escape flight, the bandwinged grasshopper flashes the brightly colored wings and produces crepitation noises to attract attention from the predators; then upon landing the cryptic coloration hides the grasshopper, while the predator is still looking for a colorful noisy meal (Johnson 2001, Davidowitz 2013).

Table 2. Amphibian, reptilian, avian, and small mammalian predators of rangeland grasshoppers in the Northern Plains.

Class: Amphibia	Amphibians
Order: Anura	
Family: Ranidae	Frogs
Rana pipiens	Leopard Frog
Family: Bufonidae	Toads
Bufo americanus	American Toad
Bufo cognatus	Great Plains Toad
Bufo hemiophrys	Canadian or Dakota Toad
Bufo woodhousei	Woodhouse’s Toad
Family: Ambystomatidae	Salamanders
Ambystoma tigrinum	Tiger Salamander
Class: Reptilia	Reptiles
Order: Squamata	
Family: Scincidae	Skinks
Eumeces obsoletus	Great Plains Skink
Eumeces septentrionalis	Prairie Skink
Family: Iguanidae	Lizards
Holbrookia maculata	Lesser Earless Lizard
Phrynosoma douglassi	Short Horned Lizard
Sceloporus graciosus	Sagebrush Lizard
Sceloporus undulatus	Northern Prairie Lizard
Family: Colubridae	Snakes
Coluber constrictor	Racer
Heterodon nasicus	Hognosed Snake
Opheodrys vernalis	Smooth Green Grass Snake
Thamnophis radix	Plains Garter Snake
Thamnophis sirtalis	Redsided Garter Snake
Family: Emydidae	Box Turtles
Terrapene ornata	Western Box Turtle
Class: Aves	Birds
Order: Galliformes	
Family: Phasianidae	Grouse
Phasianus colchicus	Ringnecked Pheasant
Meleagris gallopavo	Wild Turkey
Tympanuchus cupido	Greater Prairie Chicken
Tympanuchus phasianellus	Sharptailed Grouse
Centrocercus urophasianus	Greater Sage Grouse

Table 2 cont. Amphibian, reptilian, avian, and small mammalian predators of rangeland grasshoppers in the Northern Plains.

Order: Falconiformes	
Family: Accipitridae	Hawks
Circus cyaneus	Northern Harrier
Accipiter cooperii	Cooper's Hawk
Buteo swainsoni	Swainson's Hawk
Family: Falconidae	Falcons
Falco sparverius	American Kestrel
Order: Charadriiformes	
Family: Charadriidae	Plovers
Charadrius vociferus	Killdeer
Family: Scolopacidae	Sandpipers
Limosa fedoa	Marbled Godwit
Bartramia longicauda	Upland Sandpiper
Family: Laridae	Gulls
Larus pipixcan	Franklin's Gull
Chlidonias niger	Black Tern
Order: Cuculiformes	
Family: Cuculidae	Cuckoos
Coccyzus americanus	Yellowbilled Cuckoo
Coccyzus erythropthalmus	Blackbilled Cuckoo
Order: Strigiformes	
Family: Strigidae	Owls
Asio flammeus	Shorteared Owl
Athene cunicularia	Burrowing Owl
Order: Passeriformes	
Family: Laniidae	Shrikes
Lanius ludovicianus	Loggerhead Shrike
Family: Alaudidae	Larks
Eremophila alpestris	Horned Lark
Family: Turdidae	Thrushes
Sialia sialis	Bluebird
Sialia currucoides	Mountain Bluebird

Table 2 cont. Amphibian, reptilian, avian, and small mammalian predators of rangeland grasshoppers in the Northern Plains.

Family: Mimidae	Mockingbirds
Dumetella carolinensis	Gray Catbird
Toxostoma rufum	Brown Thrasher
Family: Emberizidae	Sparrows
Spizella pusilla	Field Sparrow
Spizella breweri	Brewer's Sparrow
Chondestes grammacus	Lark Sparrow
Ammodramus savannarum	Grasshopper Sparrow
Ammodramus bairdii	Baird's Sparrow
Calamospiza melanocorys	Lark Bunting
Passerculus sandwichensis	Savannah Sparrow
Pooecetes gramineus	Vesper Sparrow
Calcarius ornatus	Chestnut Collared Longspur
Calcarius mccownii	McCown's Longspur
Family: Cardinalidae	Cardinals
Spiza americana	Dickcissel
Family: Icteridae	Blackbirds
Dolichonyx oryzivorus	Bobolink
Sturnella neglecta	Meadowlark
Class: Mammalia	Mammals
Order: Marsupialia	
Family: Didelphidae	Opossums
Didelphis virginiana	Virginia Opossum
Order: Insectivora	
Family: Soricidae	Shrews
Sorex arcticus	Arctic Shrew
Sorex cinereus	Masked Shrew
Order: Rodentia	
Family: Sciuridae	Squirrels
Spermophilus franklinii	Franklin's Ground Squirrel
Spermophilus richardsonii	Richardson's Ground Squirrel
Spermophilus tridecemlineatus	Thirteenlined Ground Squirrel
Family: Cricetidae	Mice
Peromyscus maniculatus	Deer Mouse
Onychomys leaucogaster	Grasshopper Mouse
Order: Carnivora	
Family: Procyonidae	Raccoons
Procyon lotor	Raccoon
Family: Mustelidae	Weasels
Mephitis mephitis	Striped Skunk

Grasshopper Life Cycle

Grasshoppers in the Northern Plains have a one year life cycle with an active period that occurs, during most years, from early May to mid October. The grasshopper active period is exactly the same 5.5 month period of active grass growth of native upland sedges and native perennial cool and warm season grasses.

Most grasshopper species spend the 6.5 month inactive period through the winter as a partially developed embryo stage in an egg. Grasshoppers transition by simple metamorphosis through three life stages; egg, nymph, and adult. The majority of grasshoppers' life cycle is egg-nymph-adult-egg. A few grasshopper species spend the winter period as an hibernating mid to late stage nymph. Their life cycle is nymph-adult-egg-nymph.

Egg survival during the winter months depends upon the amount of standing vegetation and snow cover that insulates the soil temperatures from low air temperatures. Without insulation, long periods of subzero air temperatures can greatly reduce the soil temperatures decreasing embryo survival. Munro (1939) found high survival rates of *Melanoplus sanguinipes* eggs collected during early May in eastern North Dakota with an egg viability of 94%. However, when the soil was dried, the eggs did not survive.

Grasshopper egg hatch in the Northern Plains usually occurs from early May to late July. Eggs of grasshopper species tend to hatch during the same periods each year. In the Northern Plains, *Aeropedellus clavatus* is one of the first grasshoppers to hatch and *Phoetaliotes nebrascenis* is among the last grasshoppers to hatch, that overwinter as an egg (Hewitt and Onsager 1983, Watts et al. 1989). The grasshoppers that overwinter as a nymph usually hatch a month later than the late hatching grasshoppers. These seasonal hatch periods of grasshopper species have been categorized into five hatching groups. The **very early hatch** occurs from late April to early May; the **early hatch** occurs from mid to late May; the **intermediate hatch** occurs from early to mid June; the **late hatch** occurs from mid to late June; and the grasshoppers that overwinter in the nymph stage have a **very late hatch** that occurs from mid to late July. The actual time of hatch can vary from year to year. The hatch time mainly depends on the total amount of accumulated heat units received by the eggs. The quantity of heat units varies with the depth of egg deposition; eggs at shallow depths accumulate heat units more rapidly than eggs at deep depths (Cushing 1993, 1996; Pfadt 1994; Cushing et al. 1996).

The air temperatures of the preceding autumn effect the quantity of heat units accumulated by the egg pods prior to diapause. Soil temperature and soil moisture of the soil around the egg pods effects the winter survival of the eggs (Watts et al. 1989). The spring air temperatures effect the rate of heat unit accumulation, the rate of embryonic development, and thus the egg hatch date (Fisher et al. 1996a). The duration of egg hatch for most grasshopper species is around 4 weeks with a range of 2 to 6 weeks (Pfadt 1994).

Embryonic development begins immediately after egg deposition. The embryos receive nourishment from the yolk (Pfadt 1994). The rate of embryonic development depends on receiving sufficient heat units measured in day-degrees. Day-degrees (DD) are the accumulation of degrees each day that are above the threshold temperatures of 50° or 55° F (10° or 13° C). Grasshopper eggs require about 400 DD day-degrees of heat by fall in order for development to reach embryo stage 19, which is 50% developed. Most grasshopper species cease embryonic development at stage 19 (50%); some grasshopper species cease development at stage 24 (80%), and begin diapause (Pfadt 1994). At the onset of diapause, the growth hormones are shutdown, growth and metabolic activity cease, some physiological activity continues, and resistance to environmental extremes increases (Fisher et al. 1996a). Diapause is an evolutionary adaptation that functions to prevent completion of embryonic development and hatching of nymphs during the inclement weather of late fall or winter, when the nymphs would have a low chance for survival (Fisher et al. 1996a). Cold soil temperatures of winter end diapause and the embryos enter into a dormant state until spring warmup (Watts et al. 1989).

Eggs that do not receive sufficient day-degrees of heat between deposition and diapause, do not reach the necessary advanced embryonic development stage of the species and these embryos have reduced survivability and hatchability (Pfadt 1994).

During the next spring when soil temperatures reach the threshold temperatures of 50° or 55° F (10° or 13° C), the embryos resume their development (Fisher et al. 1996a). An additional 150 DD day-degrees of heat are required for the embryos to reach stage 27 (100%). A total of 500 to 600 DD day-degrees of heat are required for complete development from embryonic stage 1 to stage 27. About 400 DD of heat are required during the summer of egg deposition for embryonic development to stage 19 (50%) and about an additional 150 DD of heat are required the following spring to complete embryonic development to stage 27 and hatching (Pfadt 1994).

The rate at which the day-degrees of heat are accumulated determines the rate of embryonic development. Egg hatch is accelerated by moist soil and by temperatures above 50° F (10° C). Grassland canopy cover that has been reduced through low precipitation, heavy grazing, or mowing provides unobstructed access to the soil increasing the quantity of incident solar radiation resulting in elevated air and soil temperatures and an accelerated rate of accumulation of heat units causing increased rates of embryo development and earlier hatch dates. Egg hatch is delayed by dry soil and by temperatures below 50° F (10° C). Biologically managed moderately tall grassland canopy cover shade the soil surface reducing the quantity of incident solar radiation and lowering the grass canopy air and soil temperatures that cause slower accumulation of heat units and reduced rates of embryo development delaying the hatch date.

The embryos of a single egg pod hatch together within several minutes. The nymphs wiggle to the soil surface, still covered with an embryonic membrane, the serosa. The nymphs are unable to stand upright and they cannot jump away from predators until they squirm out of the serosa (Pfadt 1994). Newly hatched nymphs look like small adult grasshoppers except they lack wings, they have fewer antenna segments, and their genitalia are only rudimentary (Pfadt 1994).

The timing of egg hatch in the spring is important to grasshopper growth and development, and survival. Grasshoppers are cold blooded (old term: Poikilothermal; new term: Ectothermal). Grasshoppers are unable to regulate their body temperature metabolically. Their body temperature varies with the surrounding environment. In order to increase their body temperature above ambient temperature, grasshoppers absorb heat by basking in direct sunlight. In order to reduce their body temperature, grasshoppers elevate their body above the soil on the shady side of vegetation and hyperventilate to increase the volume of air moving in and out of their tracheae causing evaporative cooling (Carruthers et al. 1992). The evaporative cooling process would have physiological limitations to prevent desiccation.

The rate of nymphal development is determined by the nutritional quality of the food plants and by the amount of time the nymphs can raise their body temperatures to optimal levels through basking in unobstructed direct sunlight. The nymphs grow and develop; at intervals they molt (ecdysis) their old exoskeleton and change structure, form, and size. A diet high in crude protein is required to develop each new exoskeleton. The stage between molts is referred to as an instar. Most grasshopper species develop through five instar stages (Watts et al. 1989, Fisher et al. 1996a). The males of some grasshopper species develop through four instar stages. The females of a few large grasshopper species develop through six instar stages. Under typical environmental conditions, most grasshopper species develop from hatchling to adult stage in 30 to 50 days, at a rate of 7 to 10 days per instar. However, under cool, cloudy conditions, or if the grassland canopy cover shades the sun for long portions of the day, nymphal development rate is greatly extended. When the air temperature of the grassland microhabitat is below 65° to 68° F (18° to 20° C), the nymphs do not feed. If the period of low air temperatures is prolonged, nymphal mortality greatly increases (Campbell et al. 2006).

The grasshopper nymph becomes an adult, or imago, with the fifth or last instar molt. The new fledgling adult has fully functional wings, however, the reproductive organs are not fully developed. The young grasshoppers require a period of time, usually 1 to 3 weeks, to increase in weight and to complete maturation of reproductive organs (Pfadt 1994).

Grasshopper daily activities start shortly after dawn and are closely linked with the air and soil temperatures, wind speed, and light intensity. During the night, the grasshoppers body temperature is the same temperature as the environment (Parker 1982). The grasshopper crawls on the ground to an open spot that receives unobstructed direct radiant rays from the sun. The common basking position is to turn its side perpendicular to the sun rays and lower the associated hindleg, which exposes the abdomen. Periodically, they turn around and expose the opposite side and sometimes they expose their back (Carruthers et al. 1992).

Grasshoppers use incident solar radiation to raise their internal body temperatures above ambient levels. Grasshoppers can increase their body temperatures 25° to 28° F (14° to 16° C) above the air temperature, when they bask on open ground and are exposed to both the direct rays from the sun plus the rays reflected from the ground. Grasshoppers basking from a perch in vegetation can increase their body temperature only 15°to 18° F (8°to 10° C) above ambient temperature (Onsager 1998). The preferred optimal body temperature for rangeland grasshoppers is 95° to 104° F (35° to 40° C) (Parker 1982, Carruthers et al. 1992). Maintenance of body temperatures above ambient air temperatures requires the daily behavioral rhythm to be constantly connected with thermoregulation and all activity movements need to be related to solar position. Maintaining body temperature at high optimal levels increases metabolic rates, increases developmental rates, increases activity levels, and increases the speed of escape from predators (Joern et al. 1996). Maintaining body temperature at 104° F (40° C) can delay or reduce the impacts of infectious diseases from *Entomophaga* and *Nosema* (Carruthers et al. 1992).

The morning basking period usually lasts 1 to 2 hours on sunny days. Grasshopper daily activities begin after the air temperature has reached 81° F (27° C) (Jech 1996). Several rangeland grasshoppers feed on grass leaves from the ground. The grass leaves are severed from the plant, then consumed while sitting on the ground. Some grasshopper species feed by climbing onto the grass or forb plant with head up or head down and consume the leaves while still on the plant. Some grasshoppers climb onto the plant, cut off a leaf and let it drop to the ground, then climb down and consume the cut leaf while sitting on the ground. Feeding continues long enough to fill the grasshoppers crop and the feeding sessions stop until the crop is empty. While the crop empties, the grasshopper walks around aimlessly; this behavior is called pottering. The grasshoppers repeat the cycle of feeding sessions and pottering (Jech 1996).

Most grasshopper species are extremely discriminating when selecting food plants. The grasshopper approaches a potential food plant, lowers their antennae to the leaf surface and then drum or tap on the leaf with their maxillary and labial palpi. These sensory organs can separate the properties of plant chemicals into attractants or repellents. The grasshopper rejects the unfavorable plants and chooses the favorable host plants. If the first test has inconclusive results, the grasshopper may take a small bit to taste the leaf for an additional test (Pfadt 1994).

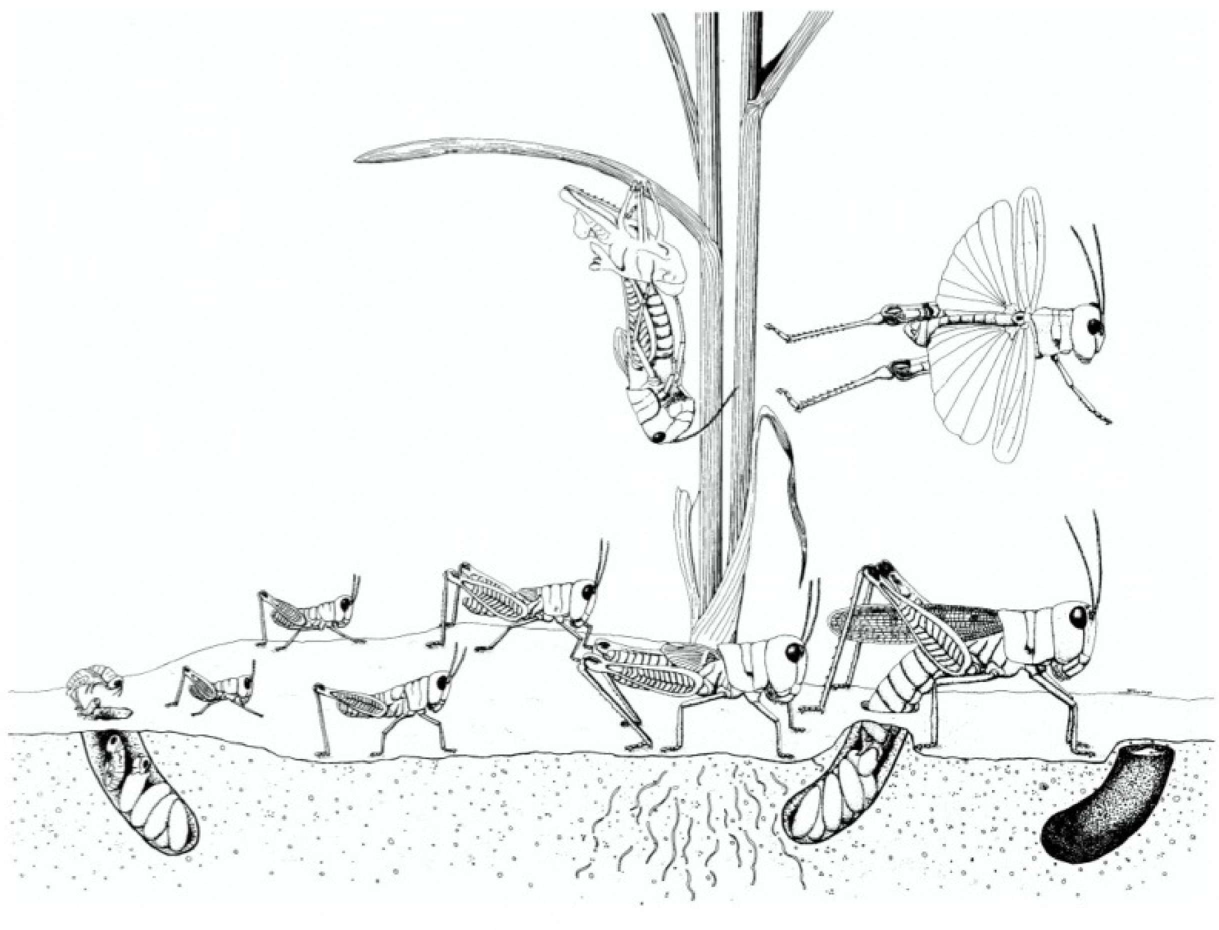
Grasshoppers remain active throughout the day as long as the air temperatures remain between 81° to 90 ° F (27° to 32° C) (Jech 1996). As the air temperature rises from 90° to 95° F (32° to 35°C), grasshoppers on the ground will stilt. They raise up on their legs to increase the distance between their body and the soil surface. With continued increases of the air and soil temperature, the stilting grasshoppers move stiff legged into the shade of vegetation. As soil temperatures approach 120° F (49° C), all other activities cease and the grasshoppers climb up grass stems or other vegetation, some species climb to a height of around 2 inches (5 cm), while other species climb to a height of 5 to 12 inches (13 to 30 cm) or even higher (Pfadt 1994). Grasshoppers perch on the shady side of the vegetation in a vertical position with the head up to avoid excessive heat. If the air temperature drops below 90° F (32° C) while there is still daylight, the grasshoppers will resume the cycle of active feeding and pottering. When the air temperature drops below 81° F (27° C), the evening basking period takes place until sundown. Daily activities are interrupted and the grasshoppers generally remain sheltered and inactive when air temperatures are below 68° F (20° C), the wind speed is greater than 15 mph (24 km/hr), the sky is overcast, or it is drizzling or raining (Jech 1996).

Female grasshoppers require a preoviposition period of one to two weeks between fledging and laying the first cluster of eggs in order to increase in weight and to fully develop their reproductive organs. The male grasshoppers usually hatch a little ahead of the females and are then fully mature when the females are completely developed (Pfadt 1994). Males actively search for mature females. The courtship varies with species. Grasshoppers are able to identify other members of its species. Grasshoppers communicate through visual and audible signals (Pfadt 1994). The bandwinged males court the females with short flights that flash their brightly colored wings and produce distinct crepitation sounds by snapping their wings (Gomez et al. 2012). The slantfaced males court the females with a species specific stridulation song that is produced by rapidly moving the hind femur, which has a row of small pegs on the inner surface, up and down against the tegmen, which is the leathery forewing (Davidowitz 2013). If she is enamored by his songs, they mate, otherwise, she ignores him or literally kicks him out. The male spurthroated grasshoppers do not produce distinct crepitation sounds or specific stridulation songs to count the females and little else is known about the courtship of melanopline (Pfadt 1994, Johnson 2002).

Following mating, the females require a period for egg development. The gravid female grasshopper deposits a clutch of eggs in a hole in the soil. The female may probe the soil several times to collect information on the physical and chemical properties of the soil. The selection of a favorable egg laying site is influenced by soil texture, temperature, moisture level, acidity, salt content, size of bare area, and type of vegetation (Pfadt 1994). Some grasshopper species select loose soil that is sandy or gravelly, however, most species select compact loamy soils. At a favorable site, the female digs a hole in the soil about 0.5 to 1.5 inches (1 to 4 cm) deep with her ovipositor. The female has three pairs of digging and egg laying structures at the end of the abdomen. The sides of the hole in the soil are lined with a secreted froth that becomes the egg pod (Davidowitz 2013). The clutch of eggs is deposited at the bottom of the pod. Many grasshopper species secrete a frothy glue between and surrounding the eggs, and some species do not. Additional froth is placed above the egg clutch at the top of the pod to act as a plug. Then the female places particles of soil on top of the plug with her hind legs (Fisher et al. 1996a). Each species has a uniquely shaped egg pod, and the number of eggs per clutch varies among species. A female grasshopper deposits a clutch of eggs about every 2 or 3 days. Most females are able to produce 4 to 25 egg pods with 1 to 90 eggs per clutch. The larger the clutch of eggs, the fewer the number of egg pods. The typical maximum number of eggs produced by one female is around 100 to 200 eggs. A few more fecund species, the *Melanoplus bivittatus* and *Melanoplus differentialis* are capable of producing 400 to 600 eggs per female (Pfadt 1994).

Embryonic development begins immediately after egg deposition. The rate of development of the embryo depends on the rate of accumulation of heat units. Eggs deposited at shallow depths, just below the soil surface, accumulate greater day-degrees of heat more rapidly than the egg pods deposited at medium and deep depths. The embryo must develop to at least stage 19 (50%) before diapause stops growth (Pfadt 1994). Thus, the one year life cycle of egg-nymph-adult-egg continues.

A few grasshopper species, such as *Eritettix simplex*, spend the winter as a late instar nymph. The nymphs become active in early spring when the air temperature and incident solar radiation permits sufficient elevation of their body temperature. The adults fledge in late April or May. Females oviposit eggs in early summer. The eggs hatch and the nymphs emerge in June and July. The partially grown nymphs hibernate under vegetation litter in late September or October. The grasshopper species that overwinter as a nymph, are the first grasshoppers to feed on young developing grass tillers before they reach the three and a half new leaf stage (Watts et al. 1989).



Grasshopper Life Cycle
from Pfadt 1994

Pestiferous Rangeland Grasshoppers

There are about 600 grasshopper species (Hewitt and Onsager 1982b) in North America, nearly 400 grasshopper species inhabit the western portion, of which, 70 of these species are common (Pfadt 1994), and 200 of these grasshopper species exist on rangelands (Onsager 1987); 25 rangeland grasshopper species regularly reach densities that cause economic damage (Hewitt and Onsager 1983), 12 rangeland grasshopper species frequently occur in high densities, and another 12 species occasionally occur in high densities (Hewitt and Onsager 1983). In spite of these specific numbers, a definitive list in which grasshopper species were characterized as frequently pestiferous, occasionally pestiferous, sometimes pestiferous, potentially pestiferous, and nonpestiferous was not located. However, numerous regional lists compiled by entomologists from various states and provinces identified the problem grasshopper species in the Northern Plains, albeit, placing them into several different severity categories (Watts et al. 1989, Cushing 1993, Pfadt 1994, Dysart 1996, Foster 1996b, Onsager 2000, Calpas and Johnson 2003, Schell et al. 2004, Campbell et al. 2006) (table 3).

The most commonly used category to distinguish pestiferous rangeland grasshoppers was any harmful grasshopper species that had increased its population to infestation levels and consumed or destroyed sufficient quantities of livestock forage to cause economic damage (Johnson 2001, 2002, 2003; APHIS 2002, Campbell et al. 2006, Brust et al. 2008). The various degrees of ecosystem deterioration caused by grasshopper species has had little scientific attention. Some grasshopper species have the ability to seriously injure young growing grass tillers and cause ecosystem degradation before their densities reach threshold outbreak levels. For the purposes of this report, grasshopper species that cause ecological degradation to rangeland ecosystems will also be accepted as pestiferous. Thus, the included list of pestiferous rangeland grasshopper species in the Northern Plains is a divergent concession with no pretense of being resolute (table 4).

The Northern Plains is comprised of all or parts of the states of Montana, Nebraska, North Dakota, South Dakota, and Wyoming, and the provinces of Alberta, Manitoba, and Saskatchewan (figure 1). The distribution of the pestiferous rangeland grasshoppers is throughout the Northern Plains. All the pest grasshoppers occur in each state and province, except three pest grasshoppers do not occur in one of the prairie provinces each (Pfadt 1994) (table 5).

Eight (35%) of the pestiferous rangeland grasshoppers are small size grasshoppers; 6 (75%) are members of the Gomphocerinae (slantfaced) subfamily, 1 (12.5%) is a member of the Melanophinae (spurthroated) subfamily, and 1 (12.5%) is a member of the Oedipodinae (bandwinged) subfamily. The average small size adult male grasshopper has a live weight of 119.4 mg and a body length of 16.5 mm. The average small size adult female grasshopper has a live weight of 255.9 mg and a body length of 20.6 mm (table 6).

Eleven (48%) of the pestiferous rangeland grasshoppers are medium size grasshoppers; 3 (27%) are members of the Gomphocerinae (slantfaced) subfamily, 6 (55%) are members of the Melanophinae (spurthroated) subfamily, and 2 (18%) are members of the Oedipodinae (bandwinged) subfamily. The average medium size adult male grasshopper has a live weight of 235.7 mg and a body length of 19.0 mm. The average medium size adult female grasshopper has a live weight of 460.2 mg and a body length of 23.3 mm (table 6).

Four (17%) of the pestiferous rangeland grasshoppers are large size grasshoppers; 3 (75%) are members of the Melanophinae (spurthroated) subfamily, and 1 (25%) is a member of the Oedipodinae (bandwinged) subfamily. The average large size adult male grasshopper has a live weight of 471.3 mg and a body length of 27.3 mm. The average large size adult female grasshopper has a live weight of 851.0 mg and a body length of 33.9 mm (table 6).

Table 3. Identification of pestiferous rangeland grasshoppers in the Northern Plains.

Pestiferous Rangeland Grasshoppers	A NP	B ND	C NA	D NA	MT	NE	E ND	SD	WY	F ND	G AB	H NE
Aer cla	X	X	X	32			X					
Age deo	X	X	X	5	X	X	X	X	X	X		X
Amp col	X	X	X	8	X		X	X	X			X
Aul ell	X	X	X	2	X		X	X	X			X
Aul fem	X			12					X	X		X
Cam pel	X	X	X	3	X		X		X		X	
Cor occ	X		X	15					X	X		X
Enc cos	X			34						X		
Eri sim	X			26		X	X				X	
Mel biv		X	X	4	X				X		X	
Mel con		X		48			X					
Mel dif			X	10					X	X		
Mel fem		X	X	7		X		X	X	X		
Mel gla		X		21		X				X		
Mel inf	X	X	X	13	X		X	X	X	X	X	
Mel occ				18					X			
Mel pac		X	X	6	X				X		X	
Mel san	X	X	X	1	X		X	X	X	X	X	X
Met par		X	X	25								
Ope obs	X			14		X	X	X	X	X		
Phl qua	X	X	X	9	X	X	X	X	X			X
Pho neb	X			16		X		X		X		X
Tra kio	X	X	X	11	X		X	X	X	X		X

A. Watts et al. 1989; B. Cushing 1993; C. Pfadt 1994; D. Dysart 1996; E. Foster 1996b, and Schell et al. 2004; F. Onsager 2000; G. Calpas and Johnson 2003; H. Campbell et al. 2006.

Table 4. Pestiferous rangeland grasshoppers in the Northern Plains.

Aer cla	*Aeropedellus clavatus*	(Thomas)	Clubhorned Grasshopper
Age deo	*Ageneotettix deorum*	(Scudder)	Whitewhiskered Grasshopper
Amp col	*Amphitornus coloradus*	(Thomas)	Striped Grasshopper
Aul ell	*Aulocara elliotti*	(Thomas)	Bigheaded Grasshopper
Aul fem	*Aulocara femoratum*	(Scudder)	Whitecrossed Grasshopper
Cam pel	*Camnula pellucida*	(Scudder)	Clearwinged Grasshopper
Cor occ	*Cordillacris occipitalis*	(Thomas)	Spottedwinged Grasshopper
Enc cos	*Encoptolophus costalis*	(Scudder)	Dusky Grasshopper
Eri sim	*Eritettix simplex*	(Scudder)	Velvetstriped Grasshopper
Mel biv	*Melanoplus bivittatus*	(Say)	Twostriped Grasshopper
Mel con	*Melanoplus confusus*	(Scudder)	Pasture Grasshopper
Mel dif	*Melanoplus differentialis*	(Thomas)	Differential Grasshopper
Mel fem	*Melanoplus femurrubrum*	(DeGeer)	Redlegged Grasshopper
Mel gla	*Melanoplus gladstoni*	(Scudder)	Gladston Grasshopper
Mel inf	*Melanoplus infantilis*	(Scudder)	Little Spurthroated Grasshopper
Mel occ	*Melanoplus occidentalis*	(Thomas)	Flabellate Grasshopper
Mel pac	*Melanoplus packardii*	(Scudder)	Packard Grasshopper
Mel san	*Melanoplus sanguinipes*	(Fabricius)	Migratory Grasshopper
Met par	*Metator pardalinus*	(Saussure)	Bluelegged Grasshopper
Ope obs	*Opeia obscura*	(Thomas)	Obscure Grasshopper
Phl qua	*Phlibostroma quadrimaculatum*	(Thomas)	Fourspotted Grasshopper
Pho neb	*Phoetaliotes nebrascensis*	(Thomas)	Largeheaded Grasshopper
Tra kio	*Trachyrhachys kiowa*	(Thomas)	Kiowa Grasshopper

Table 5. Distribution of pesiferous rangeland grasshoppers in the Northern Plains.

Pestiferous Rangeland Grasshoppers	Montana	Nebraska	North Dakota	South Dakota	Wyoming	Alberta	Manitoba	Saskatchewan
	MT	NE	ND	SD	WY	AB	MB	SK
Aer cla	X	X	X	X	X	X	X	X
Age deo	X	X	X	X	X	X	X	X
Amp col	X	X	X	X	X	X	X	X
Aul ell	X	X	X	X	X	X	X	X
Aul fem	X	X	X	X	X	X		X
Cam pel	X	X	X	X	X	X	X	X
Cor occ	X	X	X	X	X	X	X	X
Enc cos	X	X	X	X	X	X	X	X
Eri sim	X	X	X	X	X	X		X
Mel biv	X	X	X	X	X	X	X	X
Mel con	X	X	X	X	X	X	X	X
Mel dif	X	X	X	X	X		X	X
Mel fem	X	X	X	X	X	X	X	X
Mel gla	X	X	X	X	X	X	X	X
Mel inf	X	X	X	X	X	X	X	X
Mel occ	X	X	X	X	X	X	X	X
Mel pac	X	X	X	X	X	X	X	X
Mel san	X	X	X	X	X	X	X	X
Met par	X	X	X	X	X	X	X	X
Ope obs	X	X	X	X	X	X	X	X
Phl qua	X	X	X	X	X	X	X	X
Pho neb	X	X	X	X	X	X	X	X
Tra kio	X	X	X	X	X	X	X	X

Information from geographic range maps developed by Pfadt 1994.

Table 6. Live weight and body length of adult pestiferous rangeland grasshoppers.

Pestiferous Rangeland Grasshoppers	Sex	Adult Live Weight mg	Adult Body Length mm
Small size grasshoppers			
Aeropedellus clavatus	male		17.0-17.5
	female		19.5-21.0
Ageneotettix deorum	male	110	15.5-16.2
	female	310	21.0-24.0
Amphitornus coloradus	male	144	17.8-20.3
	female	275	21.5-25.0
Cordillacris occipitalis	male	101	16.5-18.5
	female	224	21.0-23.5
Melanoplus infantilis	male	157	16.5-17.0
	female	236	16.0-19.0
Opeia obscura	male	66	13.5-15.0
	female	143	18.0-19.7
Phlibostroma quadrimaculatum	male	110	14.5-15.0
	female	300	18.5-21.5
Trachyrhachys kiowa	male	148	15.0-18.0
	female	303	17.0-24.0

Table 6 cont. Live weight and body length of adult pestiferous rangeland grasshoppers.

Pestiferous Rangeland Grasshoppers	Sex	Adult Live Weight mg	Adult Body Length mm
Medium size grasshoppers			
Aulocara elliotti	male	180	17.0-20.0
	female	474	20.5-25.0
Aulocara femoratum	male	141	15.1-17.0
	female	460	20.0-25.0
Camnula pellucida	male	201	19.5-21.5
	female	605	22.0-25.0
Encoptolophus costalis	male	168	15.0-18.5
	female	468	21.5-25.5
Eritettix simplex	male	108	15.0-16.5
	female	269	22.0-23.5
Melanoplus confusus	male		18.0-19.0
	female		23.0-24.0
Melanoplus femurrubrum	male	289	17.5-23.0
	female	389	24.0-28.0
Melanoplus gladstoni	male	446	19.0-22.5
	female	509	20.1-25.2
Melanoplus occidentalis	male	280	19.2-21.0
	female	567	22.0-24.0
Melanoplus sanguinipes	male	338	20.0-26.0
	female	442	20.0-29.0
Phoetaliotes nebrascensis	male	206	17.8-19.4
	female	419	20.5-22.5

Table 6 cont. Live weight and body length of adult pestiferous rangeland grasshoppers.

Pestiferous Rangeland Grasshoppers	Sex	Adult Live Weight mg	Adult Body Length mm
Large size grasshoppers			
Melanoplus bivittatus	male	549	28.0-30.0
	female	1,086	36.0-41.0
Melanoplus differentialis	male		22.0-32.0
	female		30.0-33.0
Melanoplus packardii	male	571	27.0-32.0
	female	639	32.0-35.5
Metator pardalinus	male	294	22.0-25.0
	female	828	30.0-34.0

Live weight and body length of adult male and female from Pfadt 1994.

Life History of the clubhorned grasshopper

Aeropedellus clavatus (Thomas) (Aer cla), the clubhorned grasshopper, is a frequent dominant pest on rangelands, primarily in the prairie provinces and in North Dakota on sand prairie and it can be injurious to grassland ecosystems because it is able to consume substantial quantities of leaves from young native grass tillers prior to the 3.5 new leaf stage, and it is a subdominant pest on croplands. The clubhorned grasshopper has wide distribution in western North America and it inhabits the rangelands of the Northern Plains. It is a member of the Gomphocerinae subfamily of slantfaced grasshoppers. The adults are small sized grasshoppers. Body length of the males is 0.67 to 0.69 in (17.0 to 17.5 mm) and the females is 0.77 to 0.83 in (19.5 to 21.0 mm).

The hatching period is with the very early group starting about early May and lasting 3 to 4 weeks. The nymphs develop rapidly through 4 instar stages in about 30 days. The fledgling adults require a period for growth and maturation after they appear. The males court the females with an intraspecific stridulation song. Females require a period for egg development after mating. Gravid females deposit 5 to 8 eggs per clutch in a pod that is 0.39 to 0.51 in (10 to 13 mm) long and 0.14 to 0.16 in (3.5 to 4.0 mm) in diameter placed vertically into the bare soil near the roots of grasses or sedges. The eggs develop rapidly to stage 26 (95%), then enter diapause; the following spring, the embryos complete development to stage 27 and emerge very early.

The clubhorned grasshopper is graminivorous and feeds on grasses and sedges. In the mixed grass prairie, the main food plants are western wheatgrass, prairie junegrass, sandberg bluegrass, needle and thread, threadleaf sedge, needleleaf sedge, and kentucky bluegrass. Small amounts of grass seeds, forbs, fungi, pollen, and arthropod parts are consumed.

Typical densities on rangeland are 1 to 2 adults/yd^2 (1.2 to 2.4/m^2). The clubhorned grasshopper is geophilous and spends most of the time on the ground. The adults remain in the same area that they hatched. The females have short wings and do not fly. The males can have either short or long wings. Males with long wings frequently take short flights but do not go far from the females. *Aeropedellus clavatus* is one of the preferred hosts of the endoparasite *Neorhynchocephalus sackenii* (tangleveined fly); the fly larvae consume the grasshopper from inside.

The clubhorned grasshopper has been the dominant species increasing to adult densities of 20/yd^2 (24/m^2) during outbreaks in the sand prairies of the prairie provinces of Canada and southeastern North Dakota. During infestations in Montana, North Dakota, and Saskatchewan on rangelands that have less favorable silty or clayey soil types, the clubhorned grasshopper frequently was abundant in the grasshopper assemblages as a codominant and contributed at a reduced level to the severe damage caused to forage grasses and to cereal grain plants in nearby fields.

This summary life history of the clubhorned grasshopper was based primarily from the work of Pfadt 1994 with additional information from Mulkern et al. 1969, Watts et al. 1989, and Hostetter 1994.

Life History of the whitewhiskered grasshopper

Ageneotettix deorum (Scudder) (Age deo), the whitewhiskered grasshopper, is a frequent serious dominant pest on rangelands, primarily in the mixed grass prairie and it is a pest on crested wheatgrass pastures in western North Dakota. It requires dry upland native prairie with short grasses and open bare areas. The whitewhiskered grasshopper has wide distribution in North America and it inhabits the rangelands of the Northern Plains. It is a member of the Gomphocerinae subfamily of slantfaced grasshoppers. The adults are small sized grasshoppers. Live weight of the males average 110 mg and the females average 310 mg. Body length of the males is 0.61 to 0.64 in (15.5 to 16.2 mm) and the females is 0.83 to 0.94 in (21.0 to 24.0 mm).

The hatching period is with the early group starting about mid May and lasting 4 to 6 weeks. The nymphs usually develop through 5 instar stages in 40 to 48 days, however, some males require only 4 instars and some females require 6 instars. The fledgling adults require a period for growth and maturation after they appear. Females have a preoviposition period of 14 days between fledging and ovipositing the first clutch of eggs. The males court the females with visual signals of raising and lowering the hind femurs and its antennae. Females require a period for egg development after mating. Gravid females deposit 3 to 5 eggs per clutch in a tough curved pod that is 0.39 to 0.47 in (10 to 12 mm) long and 0.16 in (4 mm) in diameter placed at a shallow depth horizontally just below the surface into bare ground or near blue grama or buffalograss. The eggs begin embryonic growth in the summer of deposition and continue until they attain 50% development (stage 19), then enter obligatory diapause; the following spring, the embryos complete development to stage 27 and emerge.

The whitewhiskered grasshopper is graminivorous and feeds on grasses and sedges. The main food plants are blue grama, western wheatgrass, needle and thread, threadleaf sedge, needleleaf sedge, sandberg bluegrass, and kentucky bluegrass. Preferentially, they feed from the ground, they reach up, sever the grass leaves from the plant, then eat the leaf while sitting on the ground. Adults sometimes cling to grass plants and feed on the leaves in a head down position while remaining on the plant. Small amounts of forbs, grass seeds, felled leaf parts, dry plant litter, cattle dung, and arthropod parts are also consumed from the soil surface.

At typical low densities, the adults remain in the same area that they hatched. They are diurnal, active during the day and inactive at night. The whitewhiskered grasshopper is geophilous and spends most of the day and all of the night on the ground. After sunrise and before sunset, they bask on the ground by resting perpendicular to the rays of the sun and by hugging the ground surface. Adults perform normal activities of mating, egg laying, feeding, and pottering (walking around aimlessly). The percent time engaged in daily activities was 81.8% basking, 13.0% pottering, and 4.4% feeding. During the afternoons that the soil temperatures become too hot at 120° F (49° C), individuals seek the shade of small shrubs and rest on the bare ground or litter. *Ageneotettix deorum* is one of the preferred hosts of the endoparasite *Neorhynchocephalus sackenii* (tangleveined fly); the fly larvae consumes the grasshopper from inside.

The whitewhiskered grasshopper has frequently been the dominant species in grasshopper assemblages infesting the mixed grass prairie. The population numbers commonly increase gradually at 1.5 to 3 fold annually for about 4 years and then with a sudden increase of 6 fold that causes an outbreak with an adult population of around $50/yd^2$ ($60/m^2$). The high densities usually remain for 3 to 5 years before the population crashes back to low levels. Usually the whitewhiskered grasshopper contributes 50% of the high density. The remaining assemblage can include bigheaded, spottedwinged, striped, and kiowa grasshoppers.

This summary life history of the whitewhiskered grasshopper was based primarily from the work of Pfadt 1994 with additional information from Mulkern et al. 1969, Heidorn and Joern 1984, Watts et al. 1989, Belovsky et al. 1990, Hostetter 1994, Jech 1996, Joern 1996c, Fisher et al. 1996a, and Onsager 2000.

Life History of the striped grasshopper

Amphitornus coloradus (Thomas) (Amp col), the striped grasshopper, is a common codominant pest on rangelands with increased economic importance on western mid and short grass rangelands. The striped grasshopper has wide distribution in western North America and it inhabits the rangelands of the Northern Plains. It is a member of the Gomphocerinae subfamily of slantfaced grasshoppers. The adults are small sized grasshoppers. Live weight of the males average 144 mg and the females average 275 mg. Body length of the males is 0.70 to 0.80 in (17.8 to 20.3 mm) and the females is 0.85 to 0.98 in (21.5 to 25.0 mm).

The hatching period is with the early group starting about mid to late May and lasting 4 to 5 weeks. The nymphs develop slowly through 5 instar stages in 50 to 56 days. The fledgling adults require a period for growth and maturation after they appear. The males court the females with a brief intraspecific stridulation song. Females require a period for egg development after mating. Gravid females deposit 4 eggs per clutch in a tough, thimbleshaped pod that is 0.28 to 0.32 in (7 to 8 mm) long and 0.12 to 0.16 in (3 to 4 mm) in diameter placed below the soil surface at the center of the crown of needle and thread or threadleaf sedge. The eggs begin embryonic growth in the summer of deposition, continue until stage 19 (50%), then enter diapause; the following spring, the embryos complete development to stage 27 and emerge.

The striped grasshopper is graminivorous and feeds mostly on grasses and sedges. The main food plants are blue grama, needle and thread, threadleaf sedge, and needleleaf sedge; sometimes they feed on western wheatgrass, prairie junegrass, sandberg bluegrass, and sand dropseed. Preferentially, they feed from the ground, they reach up, sever the grass leaves from the plant, then eat the leaf while sitting on the ground. Sometimes, the grasshopper climbs on the grass plant to feed. The striped grasshopper spend the nonfeeding periods within clumps of grass on a stem or leaf in the upright position. Its cryptic body markings make it difficult for predators to find. Rarely they will feed on the ground and consume small amounts of forbs, arthropod parts, and fungi. This grasshopper does not eat dry litter.

Typical low densities on rangeland are 0.1 to 0.8/yd^2 (0.12 to 1.0/m^2). The adults have long wings and the power of strong flights, however, most adults remain in the same area that they hatched. They spend part of the day on vegetation and part on the ground; and they spend all of the night inactive on the ground. After sunrise and before sunset, they bask on the ground by exposing their side or back to the rays of the sun and by hugging the ground. Adults perform normal activities of mating, feeding, and pottering (walking around aimlessly). The percent time engaged in daily activities was 77.4% basking, 8.4% pottering, and 14.2% feeding. During summer afternoons that the air temperatures rise above 90° F (32° C), the adults climb small shrubs and rest head up 2 to 8 inches (5.1 to 20.3 cm) above the ground in the shade to reduce body temperature through evaporative cooling by hyperventilation.

The population density of the striped grasshopper may remain low for long periods of up to 9 years. The population density usually grow gradually at 2 fold annually for about 3 to 4 years and then increase at 3 or 4 fold that causes an outbreak with an adult striped grasshopper density that generally exceeds 8/yd^2 (9.6/m^2). The striped grasshopper is rarely the dominant species during the outbreak. The other grasshoppers of the outbreak assemblage are the bigheaded, whitewhiskered, and spottedwinged grasshoppers that had parallel population growth reaching combined densities of 20 to 40/yd^2 (24 to 48/m^2). All of the assemblage grasshoppers contribute to the economical damage to the rangelands.

This summary life history of the striped grasshopper was based primarily from the work of Pfadt 1994 with additional information from Mulkern et al. 1969, Watts et al. 1989, Belovsky et al. 1990, Carruthers et al. 1992, and Jech 1996.

Life History of the bigheaded grasshopper

Aulocara elliotti (Thomas) (Aul ell), the bigheaded grasshopper, is a serious major dominant pest and is among the most damaging species on rangelands, primarily in the mixed and short grass prairies and it can be injurious to grassland ecosystems because it is able to consume substantial quantities of leaves from young native grass tillers prior to the 3.5 new leaf stage. It prefers arid grassland habitat of short grasses with open bare ground between plant clumps. The bigheaded grasshopper has wide distribution in western North America and it inhabits the rangelands of the Northern Plains. It is a member of the Gomphocerinae subfamily of slantfaced grasshoppers. The adults are medium sized grasshoppers. Live weight of the males average 180 mg and the females average 474 mg. Body length of the males is 0.67 to 0.79 in (17.0 to 20.0 mm) and the females is 0.81 to 0.98 in (20.5 to 25.0 mm).

The hatching period is with the early group starting about mid May and lasting 3 to 4 weeks. The nymphs complete development in 36 to 42 days; the males with usually 4 instar stages and the females with 5 instar stages. The fledgling adults require a period for 6 to 8 days for growth and maturation after they appear. The males court the females with visual cues by tipping the hind femur and waving their antennae. Females require a period for egg development after mating. Gravid females deposit 7 to 9 eggs per clutch in a tough slightly curved pod that is 0.5 to 0.63 in (12.7 to 15.9 mm) long and 0.19 in (4.8 mm) in diameter placed horizontally into bare ground at a shallow depth of 0.5 in (12.7 mm) just below the surface. The eggs begin embryonic growth in the summer of deposition, continue until stage 19 (50%), then enter obligatory diapause; the following spring, the embryos resume development at the base soil temperature of 50° F (10° C) and complete development to stage 27 after 450 DD (degree days) of heat and emerge.

The bigheaded grasshopper is graminivorous and feeds mainly on the green leaves of grasses and sedges. The main food plants are blue grama, western wheatgrass, needle and thread, threadleaf sedge, needleleaf sedge, and crested wheatgrass. The grasshopper climbs up a leaf blade, turns around head down and chews on the leaf; frequently the chewing cuts through the leaf and the above portion drops to the ground while the grasshopper continues feeding on the lower portions of the leaf. Sometimes they feed on the ground and consume small amounts of dropped grass leaves, seeds, dry plant litter, and arthropod parts.

The adults have fully developed wings and are able to fly. During the typical low densities, the adults remain in the same area that they hatched. The bigheaded grasshopper is geophilous and spends most of the day and all of the night on the ground. After sunrise and before sunset, they bask on the ground by resting with their side exposed to the rays of the sun and by hugging the ground. When soil temperatures are 95° F (35° C) or greater, and air temperatures are 70° F (21° C) or greater, the adults perform normal activities of mating, egg laying, feeding, and pottering (walking around aimlessly). The percent time engaged in daily activities was 69.5% basking, 17.2% pottering, and 13.2% feeding. During summer afternoons when the soil temperatures rise to 120° F (49° C), individuals stilt by raising up on their legs and hold their bodies off the ground, then they seek the shade of small shrubs and rest on the bare soil or litter.

Populations of the bigheaded grasshopper irrupt frequently in the mixed grass prairie. The population numbers commonly increase gradually at 2 fold annually for 3 to 4 years, and then in 1 year the density increases at 3 or 4 fold that causes an outbreak with an adult population of around $20/yd^2$ ($24/m^2$). The high population densities usually remain for 5 or more years before the population crashes. The high densities of grasshoppers can destroy rangeland in one area causing them to move to another area. The bigheaded grasshopper is often the dominant species of an outbreak assemblage along with spottedwinged, whitewhiskered, striped, and kiowa grasshoppers.

This summary life history of the bigheaded grasshopper was based primarily from the work of Pfadt 1994 with additional information from Mulkern et al. 1969, Hewitt, Burleson, and Onsager 1976, Watts et al. 1989, Jech 1996, Fisher et al. 1996a, and Onsager 2000.

Life History of the whitecrossed grasshopper

Aulocara femoratum (Scudder) (Aul fem), the whitecrossed grasshopper, is an important codominant pest on rangelands, primarily in the mixed grass prairie on areas with abundant short grasses and it is a major pest in Nebraska. It prefers grassland habitat of short grasses with open bare ground between plant clumps. The whitecrossed grasshopper has wide distribution in western North America and it inhabits the rangelands of the Northern Plains that have abundant western wheatgrass, needle and thread, and blue grama. It is a member of the Gomphocerinae subfamily of slantfaced grasshoppers. The adults are medium sized grasshoppers. Live weight of the males average 141 mg and the females average 460 mg. Body length of the males is 0.59 to 0.67 in (15.1 to 17.0 mm) and the females is 0.79 to 0.98 in (20.0 to 25.0 mm).

The hatching period is with the intermediate group starting early June and lasting 2 weeks. The male nymphs develop through 4 instar stages in 30 or more days. The female nymphs develop through 5 instar stages in 42 or more days. The females are 3 times the size of the males. The adults appear during the first and second weeks of July and mature in about 3 weeks. The males court the females with stridulation movements, however, no humans have heard the song. Females require a period for egg development after mating. Gravid females deposit 9 to 11 eggs per clutch in a strong thick walled pod that is 0.56 to 0.63 in (14.3 to 15.9 mm) long and 0.25 in (6.4 mm) in diameter placed into bare ground at a depth of 0.75 in (19.1 mm). The bare soil egg laying site is usually surrounded by blue grama or other short grasses. Accumulation of heat units is slowed because of the relatively deep deposition of the eggs. The eggs begin embryonic growth in the summer of deposition and continue until they enter diapause; the following spring, the embryos complete development and emerge.

The whitecrossed grasshopper is graminivorous and feeds on grasses and sedges. The main food plants are western wheatgrass, needle and thread, blue grama, prairie junegrass, and needleleaf sedge. The diets of males and females are different. The males ingest larger amounts of short grasses and sedges and the females ingest more mid grasses. The grasshopper climbs up a leaf blade, turns around head down, and feeds on the blade edge leaving a narrow strip on the opposite side. The males walk extensively on the ground searching for females and come in contact mostly with short grasses. The females are more sedentary and usually climb and feed on mid grasses.

Adults have relatively short wings but have the capacity to fly and disperse. During typical low densities of 0.1 to 2/yd^2 (0.12 to 2.4/m^2), the adults remain in the same area that they hatched. The whitecrossed grasshopper is geophilous and spends most of the day and all of the night on the ground. At night, both nymphs and adults rest on bare soil interspersed among grassy vegetation. After sunrise and before sunset, they bask on the ground by resting with their side exposed to the rays of the sun. During the morning basking period, the soil temperatures range from 60° to 90°F (16° to 32° C) and air temperatures are from 61° to 82°F (16° to 28° C). When soil temperatures are 90° F (32° C) or greater and air temperatures are 82° F (28° C) or greater, the adults perform normal activities of courting, mating, feeding, and pottering. On summer afternoons when the soil temperatures rise; individuals stilt by raising up on their legs and hold their bodies off the hot ground, then they may crawl onto a short grass or sedge plant and rest facing the sun, or they may climb stems of mid grasses to heights of 2 to 7 inches (5.1 to 17.8 cm) and reduce their body temperature through evaporative cooling by hyperventilation.

Populations of the whitecrossed grasshopper can increase from low to high densities of 8 to 13/yd^2 (9.6 to 15.6/m^2) in 1 year. The whitecrossed grasshopper is usually a codominent member of an outbreak assemblage in which bigheaded and bluelegged grasshoppers are more numerous with combined densities of 20 to 25/yd^2 (24 to 30/m^2).

This summary life history of the whitecrossed grasshopper was based primarily from the work of Pfadt 1994 with additional information from Watts et al. 1989, and Carruthers et al. 1992.

Life History of the clearwinged grasshopper

Camnula pellucida (Scudder) (Cam pel), the clearwinged grasshopper, is a severe dominant pest on rangelands, primarily in the northern mixed grass prairie and it is a major pest on croplands. It has adapted to cropland agricultural practices and can damage or destroy cereal grain and vegetable crops during outbreaks. The clearwinged grasshopper has wide distribution across North America and it inhabits the rangelands of the Northern Plains. It is a member of the Oedipodinae subfamily of bandwinged grasshoppers. The adults are medium sized grasshoppers. Live weight of the males average 201 mg and the females average 605 mg. Body length of the males is 0.77 to 0.85 in (19.5 to 21.5 mm) and the females is 0.87 to 0.98 in (22.0 to 25.0 mm).

The hatching period is with the early group starting about mid to late May in egg beds on native sod and lasting 2 to 5 weeks. The nymphs quickly develop through 5 instar stages in 26 to 40 days. The adults appear first as dark colored. The fledgling adults require a period for growth and maturation after they appear; male requires 5 to 7 days and females require 7 to 10 days. As they mature they turn bright yellow. The males court the females with an intraspecific stridulation song, and the males hold their antennae in an upright V-shape. The males usually remain on the egg beds during the courtship period. The females move between the feeding ground and the egg beds. The egg beds are on grass sod, usually the same area of native sod that was used the previous year. Females require a period for egg development after mating. Gravid females deposit 10 to 38 eggs per clutch in a short stout slightly curved pod that is 0.63 in (15.9 mm) long and 0.19 in (4.8 mm) in diameter placed into bare ground in the top inch (2.5 cm) of soil near grass roots. The eggs begin embryonic growth in the summer of deposition, continue development to stage 19 (50%) after 400 DD (degree days) of heat, then enter diapause until low soil temperatures during winter break diapause; the following spring, the embryos resume development at the base soil temperature of 55° F (12.8° C) and complete development to stage 27 after 150 DD (degree days) of heat and, at the soil temperature of 80°F (26.7°C), the nymphs emerge.

The clearwinged grasshopper is graminivorous and feeds mainly on grasses. The wide variety of food plants include idaho fescue, red fescue, sandberg bluegrass, western wheatgrass, intermediate wheatgrass, slender hairgrass, kentucky bluegrass, crested wheatgrass, smooth bromegrass, downy brome, and soft brome. Generally, they climb in or on the grass plant to feed. Sometimes they consume small amounts of forbs.

The clearwinged grasshopper populations can remain on rangeland at low densities for 5 to 10 years. They are diurnal, active during the day and inactive at night. The clearwinged grasshopper is geophilous and spends most of the time on the ground. At night, they seek warm stones and sheltered places. After sunrise and before sunset, they bask by resting on bare ground, earth clods, or dried cattle dung with their sides exposed to the rays of the sun. During the day, they move about and feed while the ground temperature range from 95° to 102° F (35° to 39° C) and air temperatures are around 67° to 75°F (19° to 24° C). During the summer afternoons when the soil temperatures rise to 107° F (42° C), individuals move to shade and climb 2 inches (5.1 cm) up plant stems and reduce their body temperatures through evaporative cooling by hyperventilation. *Camnula pellucida* is one of the preferred hosts of the endoparasite *Neorhynchocephalus sackenii* (tangleveined fly); the fly larvae consumes the grasshopper from inside.

Populations of clearwinged grasshopper increase gradually over 3 to 4 years. The outbreaks consist almost entirely of only 1 species. The young nymphs move away from the egg beds as food plants are depleted. The older instars march in cohesive bands to green vegetation. The adults have fully developed long wings and can migrate long distances to grain fields and vegetable crops. When egg laying begins, migration ceases. If the previous egg bed is a short distance from the feeding ground, the males remain on the enlarged egg bed and the females fly back and forth. If the previous egg bed is a long distance from the new feeding ground, a grass sod area near the feeding ground will be used during the outbreak. The outbreak densities increase and remain high for 2 or 3 years, then the population crashes as a result of high or total mortality over the expanded distribution area. Between outbreaks, clearwinged grasshoppers survive on rangeland habitats.

This summary life history of the clearwinged grasshopper was based primarily from the work of Pfadt 1994 with additional information from Watts et al. 1989, Belovsky et al. 1990, and Carruthers et al. 1992.

Life History of the spottedwinged grasshopper

Cordillacris occipitalis (Thomas) (Cor occ), the spottedwinged grasshopper, is a serious dominant pest on rangelands, primarily in the mixed grass prairie with sandy loam soils and it can be injurious to grassland ecosystems because it is able to consume substantial quantities of leaves from young native grass tillers prior to the 3.5 new leaf stage. The spottedwinged grasshopper has wide distribution in western North America and it inhabits the rangelands of the Northern Plains. It is a member of the Gomphocerinae subfamily of slantfaced grasshoppers. The adults are small sized grasshoppers. Live weight of the males average 101 mg and the females average 224 mg. Body length of the males is 0.65 to 0.73 in (16.5 to 18.5 mm) and the females is 0.83 to 0.93 in (21.0 to 23.5 mm).

The hatching period is with the early group starting about mid May and lasting 4 weeks. The nymphs develop through 5 instar stages in 36 to 41 days. The fledgling adults require a period of 1 to 2 weeks for growth and maturation after they appear. The males court the females with an intraspecific stridulation song and the male also sends visual signals by raising and lowering his antennae and tipping his hind legs. Females require a period for egg development after mating. Gravid females deposit 2 to 3 eggs per clutch in a straight cylinder shaped pod that is 0.38 in (9.5 mm) long and 0.13 in (3.2 mm) in diameter placed vertically at a shallow depth of 0.5 in (12.7 mm) into bare ground. The eggs begin embryonic growth in the summer of deposition, continue until stage 19 (50%), then enter diapause; the following spring, the embryos complete development to stage 27 and emerge.

The spottedwinged grasshopper is graminivorous and feeds on the green leaves of grasses and sedges. The main food plants are blue grama, needle and thread, western wheatgrass, sand dropseed, downy brome, threadleaf sedge, and needleleaf sedge. The grasshopper climbs up a leaf blade, turns around head down and chews on the leaf; sometimes the chewing cuts through the leaf and parts fall to the ground. Only rarely do they eat from a horizontal position on the ground, by holding a cut leaf with the front tarsi and consume all of the leaf. They rarely consume small amounts of forbs, dropped leaves, and arthropods parts. This grasshopper does not eat litter.

The adults have long wings and can make lengthy flights. During typical light densities of 0.2 to 0.5/yd^2 (0.24 to 0.6/m^2), the adults remain in the same area that they hatched. They spend part of the day on the ground and part in vegetation. At night, they rest either on vegetation or on the ground. After sunrise and before sunset, they bask by resting with their side exposed to the rays of the sun and by hugging the ground. They perform normal activities of mating, egg laying, feeding, and pottering while the air temperatures are from 70° to 82°F (21° to 28° C). The percent time engaged in daily activities was 81.0% basking, 9.1% pottering, and 9.8% feeding. During the afternoons when the soil temperatures rise above 120° F (49° C), individuals climb small shrubs, like fringed sagebrush, and rest head up in the shade 2 to 8 inches (5.1 to 20.3 cm) above the ground and reduce their body temperature through evaporative cooling by hyperventilation.

Populations of the spottedwinged grasshopper can increase as the dominant species on rangeland with sandy loam soils. The population increases gradually at 2 fold annually for 3 years, and then increases 3 to 4 fold the following year at outbreak numbers of 20/yd^2 (24/m^2). The other members of the outbreak assemblage increase at parallel rates. Densities of whitewhiskered reach 9/yd^2 (10.8/m^2), bigheaded reach 7/yd^2 (8.4/m^2), and striped reach 7/yd^2 (8.4/m^2).

This summary life history of the spottedwinged grasshopper was based primarily from the work of Pfadt 1994 with additional information from Mulkern et al. 1969, Watts et al. 1989, Carruthers et al. 1992, and Jech 1996.

Life History of the dusky grasshopper

Encoptolophus costalis (Scudder) (Enc cos), the dusky grasshopper, is usually considered to be a subdominant pest on rangelands and, thus, its biology has not been studied intensively, however, it has considerable abundance in the northern mixed grass prairie where it has been associated with a local outbreak in western North Dakota and it has had high population densities in Saskatchewan, and it has been considered to be a pest on alfalfa and winter wheat croplands. The dusky grasshopper has wide distribution in the central region of North America and it inhabits the rangelands of the Northern Plains. It is a member of the Oedipodinae subfamily of bandwinged grasshoppers. The adults are medium sized grasshoppers. Live weight of the males average 168 mg and the females average 468 mg. Body length of the males is 0.59 to 0.73 in (15.0 to 18.5 mm) and the females is 0.85 to 1.0 in (21.5 to 25.5 mm).

The hatching period is with the intermediate group starting about early to mid June and lasting 6 to 8 weeks. The nymphs develop through 5 instar stages over a relatively long period from 56 to 66 days. The adults appear between 8 and 14 August in the Northern Plains. Fledgling adults require a period of 2 to 3 weeks for growth and maturation. Males court the females with an intraspecific stridulation song. A receptive female lowers the hind femur closest to the male and turns her genitalia toward the courting male. Females require a period for egg development after mating. Gravid females deposit 14 to 20 eggs per clutch in a pod that is 0.75 in (19.1 mm) long and slightly curved placed into bare ground, preferably of clay soils, interspersed among native grasses. Little is known about embryo development. The eggs begin embryonic growth in the summer of deposition and continue development until they enter diapause; the following spring, the embryos complete development to stage 27 and emerge.

The dusky grasshopper is graminivorous and feeds on native grasses and sedges. The main food plants are western wheatgrass and needleleaf sedge, and they also feed on northern wheatgrass, needle and thread, green needlegrass, and blue grama. On occasions, they move into cropland and eat alfalfa, winter wheat, and some forbs. The adults feed on grass leaves by climbing onto a leaf head up beginning halfway up the leaf, cuts through it, holds onto the cut section with the front tarsi, consumes it to the dry tip, and drops the tip; or by consuming leaves of short grasses from the horizontal position on the ground, cutting through the leaf and eating the cut section to the dry tip. They appear to be thrifty feeders; they consume the entire green portion of each leaf cut from a plant.

The adults have fully developed long wings, strong thoracic muscles, and are able to disperse and migrate by flight. During typical low densities, the adults remain in the same area that they hatched. The dusky grasshopper is geophilous and spends almost all of the time on the ground. After sunrise and before sunset, they bask on bare ground by turning a side perpendicular to the rays of the sun. After 2 to 3 hours of basking, they become active and perform normal feeding, walking, and sometimes flying while the ground temperatures range from 76° to 120°F (24° to 49° C) and air temperatures are 66° to 79°F (19° to 26° C). During the afternoons when the soil temperatures rise to 125° F (52° C) and higher, the grasshoppers avoid overheating by moving into partial or full shade, climbing on grass 1 inch (2.5 cm) above the ground and face the sun to expose the least body surface.

Populations of the dusky grasshopper are usually low with around 2.5 adults/yd^2 (3.0/m^2). When the species inhabits rangeland areas of fine sandy loam, the populations remain subdominant at around 0.1 to 1.0 adults/yd^2 (0.12 to 1.2/m^2). Under more favorable conditions in rangeland sites of heavy clay soil with wheatgrasses and needlegrasses, the populations increase to densities of 10 to 12 adults/yd^2 (12 to 14.4/m^2) and remain at high dominant levels for 2 or more years. Population declines have been attributed to decreased soil temperatures that resulted from vegetation shading. These unfavorable conditions delayed the development and maturation of the dusky grasshopper and decreased egg production.

This summary life history of the dusky grasshopper was based primarily from the work of Pfadt 1994 with additional information from Mulkern et al. 1969, Watts et al. 1989, and Onsager 2000.

Life History of the velvetstriped grasshopper

Eritettix simplex (Scudder) (Eri sim), the velvetstriped grasshopper, over winters in the nymphal stage and is seldom abundant on most rangelands, however, it has been associated with outbreaks in eastern North Dakota on sand prairie and it can be injurious to grassland ecosystems because it is able to consume substantial quantities of leaves from young native grass tillers prior to the 3.5 new leaf stage. The velvetstriped grasshopper has a wide distribution in the central region of North America and it inhabits the rangelands of the Northern Plains; it has a smaller distribution center along the eastern slopes of the Appalachian Mountains. It prefers grassland habitat of short and mid grasses at a diminished condition with some weeds. It is a member of the Gomphocerinae subfamily of slantfaced grasshoppers. The adults are medium sized grasshoppers. Live weight of the males average 108 mg and the females average 269 mg. Body length of the males is 0.59 to 0.65 in (15.0 to 16.5 mm) and the females is 0.87 to 0.93 in (22.0 to 23.5 mm).

The hatching period is with the very late group, as are all grasshoppers that overwinter as a nymph, starting about mid to late July and lasting 4 weeks. The nymphs develop and grow for about 100 days. Nymphs at the third and fourth instar stages overwinter under the cover of ground litter. Nymphs are cold tolerant and can survive temperatures as low as 5°F (-15° C). The following spring, as temperatures increase and daily photoperiods lengthen, the nymphs crawl out from their winter cover and complete development in April and May. The fledgling adults require some time for growth and maturation. Males follow females and, when near, the male rocks from side to side and courts the females with an intraspecific stridulation song. Females require a period for egg development after mating. Gravid females oviposit into bare ground. A clutch contains about 18 eggs in a fragile pod that is 1 in (25.4 mm) long and 0.13 in (3.2 mm) in diameter. There have been no studies on embryo development. The embryos require favorable incubation temperatures to develop completely to stage 27 and hatch during the same summer they were laid.

The velvetstriped grasshopper is graminivorous and feeds on grasses and sedges. During the summer and fall, the new generation of nymphs feed almost exclusively on blue grama. The next spring, the nymphs feed on cool season grasses and sedges. The adults preferentially feed on blue grama. Velvetstriped grasshoppers feed on grass leaves from the ground raising itself up by its hind legs beginning about 1 inch (2.5 cm) above ground level or by climbing onto the grass plant beginning near the middle. They cut narrow leaves, hold onto the cut section with their front tarsi, and consume the cut leaf to the dry tip, or they feed on wide leaves to the midrib leaving the other half of the leaf attached and standing. Feeding is usually conducted with head up and body vertical or diagonal.

The adults have fully developed wings and are able to disperse by flight. During typical low densities, the adults remain in the same area that they hatched. The velvetstriped grasshopper is geophilous and spends most of the time on the ground. The nymphs are exposed to cold temperatures during the fall and spring and require favorable microhabitat that allows regulation of body temperatures at tolerable levels. During the winter, the hibernating nymphs require protection under ground litter that insulates their bodies from cold air temperatures. Nymphs crawl out from shelter when soil temperatures reach about 60° F (15.6° C) and bask with their body perpendicular to the rays of the sun or by exposing their backs to the rays of the sun. Adults bask on the ground similarly as nymphs. Adults begin feeding when soil temperatures reach 80° F (27° C) and air temperatures at 55° to 60° F (13° to 16° C).

Populations of the velvetstriped grasshopper are usually low on most rangeland habitat with around 0.1 to 0.6 adults/yd^2 (0.12 to 0.72/m^2). Populations have reached dominant pest status on preferred sand prairie habitats in southeastern North Dakota with densities at 6.7 adults/yd^2 (8.0/m^2).

This summary life history of the velvetstriped grasshopper was based primarily from the work of Pfadt 1994 with additional information from Mulkern et al. 1969 and Watts et al. 1989.

Life History of the twostriped grasshopper

Melanoplus bivittatus (Say) (Mel biv), the twostriped grasshopper, is a major pest on rangelands, primarily in tall grass and wet meadow vegetation and is a major pest on croplands. It has adapted to cropland agricultural practices and has taken advantage of the abundant nutritious weedy plants associated with cropland augmenting this grasshoppers capacity to damage or destroy most types of crops during outbreaks. It prefers deteriorated pastures invaded with weeds. The twostiped grasshopper has extensive distribution across North America and it inhabits the rangelands of the Northern Plains that have lush herbaceous vegetation. It is a member of the Melanoplinae subfamily of the spurthroated grasshoppers. The adults are large sized grasshoppers. Live weight of the males average 549 mg and the females average 1,086 mg. Body length of the males is 1.1 to 1.2 in (28.0 to 30.0 mm) and the females is 1.4 to 1.6 in (36.0 to 41.0 mm).

The hatching period is with the early group starting about mid to late May and lasting 4 to 6 weeks. The nymphs develop through 5 instar stages in about 40 days but may be present in the habitat for as long as 75 days because of the extended hatch period. The fledgling males require a period for growth and maturation after they appear. Females have preoviposition period of 1 to 2 weeks between fledging and ovipositing the first clutch of eggs. A male stealthily approaches a female, leaps and mounts the female, then the male performs a courtship ritual by shaking his hind femurs for 3 or 4 seconds. Gravid females deposit 50 to 108 eggs per clutch in a large curved delicate pod that is 1.13 to 1.5 in (28.6 to 38.1 mm) long and 0.25 in (6.4 mm) in diameter placed into bare ground near roots of grasses or weeds. Grasshoppers that have migrated to cropland do not have to travel back to rangeland to deposit the eggs. The females move to poorly managed cropland borders with south facing slopes and compact drift soil. The egg clutches are deposited near roots of grasses or weeds. The eggs begin embryonic growth in the summer of deposition, continue until stage 20 or 24 (60% to 80%), then enter diapause; the following spring, the embryos complete development to stage 27 and emerge.

The twostriped grasshopper is polyphagous and feeds on many kinds of forbs, grasses, and crops. Nymph diets that contain weeds associated with cropland promote high survival, fast growth, and heavy weights. A twostriped grasshopper feeding on cropland foliage wastes 6 times as much vegetation as it consumes. Generally, they climb in or on the plant to feed.

The grasshoppers that hatch on cropland borders appear to be more successful than grasshoppers that hatch on rangeland. They spend part of the day on the ground and part of the day on vegetation and they spend the nights resting halfway up on vegetation. After sunrise and before sunset, they bask on the ground by resting with their side exposed to the rays of the sun. During the day when soil temperatures are 70° F (21° C) or greater, adults perform normal activities on the ground. When the soil temperatures rise to 112° F (44° C), individuals seek shade and climb up on vegetation stems to reduce their body temperature through evaporative cooling by hyperventilation. *Melanoplus bivittatus* is one of the preferred hosts of two endoparasite flies, *Acridomyia canadensis* (anthomyiid fly) and *Acemyia tibialis* (tachinid fly); both fly larvae consume the grasshopper from inside.

Populations of twostriped grasshoppers increase slowly for 3 or more years in assemblages with the differential grasshopper. Nymphs at the third instar and older move in bands. Adults at high densities develop longer wings and slimmer bodies and can fly long distances in swarms to search for green food and can damage small grains, alfalfa, corn, vegetables, fruit, and shelterbelt trees. During the outbreaks of high densities, the grasshoppers do not need to return to rangeland but can successfully hatch high numbers for 2 to 3 years from cropland border areas that have south facing slopes with compact drift soil. Outbreak assemblages usually comprise differential grasshoppers at about equal numbers. The twostriped grasshopper was one of the major pest species during the severe outbreak of the 1930's in North and South Dakota.

This summary life history of the twostriped grasshopper was based primarily from the work of Pfadt 1994 with additional information from Mulkern et al. 1969, Watts et al. 1989, Belovsky et al. 1990, and Carruthers et al. 1992.

Life History of the pasture grasshopper

Melanoplus confusus (Scudder) (Mel con), the pasture grasshopper, is usually a common subdominant pest on rangelands, however, it has been associated with local outbreaks in Saskatchewan, Wyoming, and North Dakota on rangelands and croplands, and it can be injurious to grassland ecosystems because it is able to consume substantial quantities of leaves from young native grass tillers prior to the 3.5 new leaf stage. The pasture grasshopper has wide distribution across eastern and central North America and it inhabits the rangelands of the Northern Plains. It is a member of the Melanoplinae subfamily of spurthroated grasshoppers. The adults are medium sized grasshoppers. Body length of the males is 0.71 to 0.75 in (18.0 to 19.0 mm) and the females is 0.91 to 0.94 in (23.0 to 24.0 mm).

The hatching period is with the very early group starting about late April to early May and lasting 4 weeks. The nymphs develop through 5 instar stages in about 40 to 46 days. The fledgling adults require a period for growth and maturation after they appear. The male courter approaches a female, when close, he pounces on her and attaches their genitalia. Females require a period for egg development after mating. Gravid females deposit 10 to 15 eggs per clutch in bare ground near buffalograss, blue grama, or other short grass. The eggs are laid deep into the soil about 1.25 in (3.2cm). The pod is 1.0 to 1.13 in (25.4 to 28.6 mm) long and 0.13 in (3.2 mm) in diameter. On top of the eggs is a plug of dried froth 0.5 to 0.75 in (12.7 to 19.1 mm) long. The eggs begin embryonic growth in the summer of deposition and continue until they enter diapause; the following spring, the embryos complete development and emerge very early.

The pasture grasshopper is polyphagous and feeds on both grasses and forbs, and they will consume cereal grains. At typical low densities, the adults remain in the same area that they hatched. They are diurnal, active during the day and inactive at night. The population numbers increase from low densities of less than 0.1 adult/yd^2 to 2.7 adults /yd^2 (0.12/m^2 to 3.2/m^2). The pasture grasshopper remains subdominant in assemblages that include the clubhorned grasshopper when they increase to outbreak levels.

This summary life history of the pasture grasshopper was based primarily from the work of Pfadt 1994 with additional information from Mulkern et al. 1969.

Life History of the differential grasshopper

Melanoplus differentialis (Thomas) (Mel dif), the differential grasshopper, is a major pest on rangelands, primarily on tall grass and wet meadow vegetation and it is a severe destructive pest on croplands and adjacent unmanaged grass areas. It has adapted to cropland agricultural practices and has taken advantage of the abundant nutritious weedy plants associated with cropland augmenting this grasshoppers capacity to damage or destroy most types of crops during outbreaks. It prefers deteriorated pastures with weedy patches. The differential grasshopper has wide distribution across the United States and Mexico and it inhabits the rangelands of the Northern Plains, mostly in moist weedy grassland meadows with taller vegetation. It is a member of the Melanoplinae subfamily of the spurthroated grasshoppers. The adults are large sized grasshoppers. Body length of the males is 0.87 to 1.26 in (22.0 to 32.0 mm) and the females is 1.18 to 1.3 in (30.0 to 33.0 mm).

The hatching period is with the intermediate group starting about mid June and lasting 2 weeks. The nymphs develop rapidly through 5 instar stages in about 32 days. The fledgling adults require a period of several weeks for growth and maturation after they appear. Males and females form mating pairs. Females require a period for egg development after mating. Gravid females deposit 45 to 194 eggs per clutch in a large curved fragile pod that is 1.5 in (38 mm) long and 0.25 in (6.4 mm) in diameter placed in a vertical position in bare ground near roots of grasses or weeds in land with grass sod. The eggs begin embryonic growth in the summer of deposition, continue until development of 54% (between stages 19 and 20), then enter diapause; the following spring, the embryos complete development to stage 27 and emerge.

The differential grasshopper is polyphagous and feeds on many kinds of grasses, forbs, and crops. Diets that contain mainly weedy forbs associated with cropland promote faster growth, larger size, and more eggs.

The grasshoppers that hatch on cropland borders appear to be more successful than grasshoppers that hatch on rangeland. They spend part of the day on the ground and part of the day on vegetation and they spend the nights resting high up on vegetation. After sunrise and before sunset, they bask on the ground by resting with their side exposed to the rays of the sun. During the day while soil temperatures range from 70° F to less than 112° F (21° to 44° C), the adults perform normal activities of mating, laying eggs, and feeding. When the soil temperatures rise to 112° F (44° C), individuals seek shade and climb up on vegetation stems to reduce their body temperature through evaporation cooling by hyperventilation or they may rise in flight. Populations of differential grasshopper can increase to outbreak densities in 1 to 2 years. Nymphs in the third instar and older at high population densities move in the same direction as cohesive bands. Adults at high densities develop longer wings and slimmer bodies and can fly long distances in search for green food. They can damage crops of small grains, corn, soybeans, sunflowers, vegetables, and fruit trees. During the outbreaks of high densities, the grasshoppers do not need to return to rangeland, but can successfully hatch high numbers from unmanaged cropland borders with grass sod. Outbreak assemblages usually comprise twostriped grasshoppers at about equal numbers. The differential grasshopper was one of the major pest species during the severe outbreak of the 1930's in North and South Dakota.

This summary life history of the differential grasshopper was based primarily from the work of Pfadt 1994 with additional information from Mulkern et al. 1969, Watts et al. 1989, and Carruthers et al. 1992.

Life History of the redlegged grasshopper

Melanoplus femurrubrum (De Geer) (Mel fem), the redlegged grasshopper, is a wasteful dominant pest on rangelands primarily in tall grass and meadow vegetation, it is a pest on crested wheatgrass pastures, and it is an extremely destructive major pest on croplands. It has adapted to cropland agricultural practices and the associated unmanged weedy areas and can damage or destroy most types of crops during outbreaks. It prefers deteriorated grassland pastures that have been invaded by weedy plants. The redlegged grasshopper has extensive distribution across North America and is the most abundant grasshopper species in eastern United States and Canada. It inhabits the rangelands of the Northern Plains, mostly in moist weedy grassland meadows with taller vegetation. It is a member of the Melanoplinae subfamily of the spurthroated grasshoppers. The adults are medium sized grasshoppers. Live weight of the males average 289 mg and the females average 389 mg. Body length of the males is 0.69 to 0.91 in (17.5 to 23.0 mm) and the females is 0.94 to 1.1 in (24.0 to 28.0 mm).

The hatching period is with the intermediate group starting about early June and lasting 7 to 8 weeks. The nymphs develop through 5 instar stages in about 40 days. The fledgling males require a period of growth and maturation after they appear. Females have a preoviposition period of 2 weeks or more between fledging and ovipositing. Males and females form mating pairs. Gravid females deposit 20 to 26 eggs per clutch in a distinctly curved pod that is 0.75 to 1.0 in (19.1 to 25.4 mm) long and 0.13 to 0.19 in (3.2 to 4.8 mm) in diameter placed into sod soil with widely variable exposure to sun light. The eggs begin embryonic growth in the summer of deposition and continue until they enter diapause; the following spring, the embryos complete development and emerge.

The redlegged grasshopper is polyphagous and feeds on many kinds of forbs, grasses, and crops. Primarily it feeds on the plants that are available and is known to consume birdsfoot trefoil, white and yellow sweetclover, milkvetches, dandelion, goldenrod, kochia, western ragweed, kentucky bluegrass, smooth bromegrass, japanese brome, timothy, and reed canarygrass. Generally, they climb in or on the plant to feed. The redlegged grasshopper ingests 25% of the foliage removed from food plants and wastes 75%.

Low density periods last from 2 to over 5 years. The adults remain in the same grassland meadows that they hatched. They are active during the day and roost on grasses and weeds at night.

Populations of the redlegged grasshopper can increase within 1 or 2 years to outbreak densities during periods of reduced rainfall and warm temperatures. During years of drought, the adults develop longer wings, fly more, and make lengthy flights with the migratory grasshopper. During the 2 to 3 years at outbreak densities, the assemblages may include the migratory, twostriped, and differential grasshoppers. Following the severe damage to forage grasses of their hatch site, the adults move to cropland and damage or destroy fields of barley, oat, wheat, soybeans, corn, alfalfa, and vegetable crops. The population densities decrease during periods of normal rainfall and cool spring temperatures.

This summary life history of the redlegged grasshopper was based primarily from the work of Pfadt 1994 with additional information from Mulkern et al. 1969, Belovsky et al. 1990, and Onsager 2000.

Life History of the gladston grasshopper

Melanoplus gladstoni (Scudder) (Mel gla), the gladston grasshopper, is a common codominant pest on rangelands, it has been associated with local outbreaks in the short grass and mixed grass prairies, it is a pest on crested wheatgrass pastures, and it has caused destruction on alfalfa and winter wheat croplands. The gladston grasshopper has wide north south distribution through the central region of North America and it inhabits the rangelands of the Northern Plains, primarily the mixed grass prairie. It is a member of the Melanoplinae subfamily of the spurthroated grasshoppers. The adults are medium sized grasshoppers. Live weight of the males average 446 mg and the females average 509 mg. Body length of the males is 0.75 to 0.89 in (19.0 to 22.5 mm) and the females is 0.79 to 0.99 in (20.1 to 25.2 mm).

The hatching period is with the late group starting about mid to late June and lasting 1 to 2 weeks. The nymphs develop through 5 instar stages in about 42 to 70 days. The adults appear from mid August to mid September. Fledgling adults requires about 8 days for growth and maturation. Males and females form mating pairs. Gravid females deposit 16 to 29 eggs per clutch in curved pod that is 1.0 to 1.13 in (25.4 to 28.6 mm) long placed into bare ground. The pod is laid diagonally at relatively shallow depths between 0.31 to 0.63 in (7.9 to 15.9 mm). The eggs begin embryonic growth in the summer of deposition and continue until they enter diapause; the following spring, the embryos complete development and emerge.

The gladston grasshopper is polyphagous and feeds on numerous forbs, grasses, sedges, and dry litter. Food items from grasshopper crops collected from mixed grass, short grass, and sand prairies have included 43 species of forbs, 11 grasses, and 2 sedges. Adults feed by climbing onto a forb or grass with head up or they feed from the ground in the horizontal position.

The adults have fully developed long wings and are strong fliers. They are capable of dispersal flights and mass migration. At typical low densities, the adults remain in the same area that they hatched. The gladston grasshopper is geophilous and dwells chiefly on the ground. They spend the night horizontally on bare ground or on litter under canopies of short grasses, usually blue grama. After sunrise and before sunset, they bask on bare ground by turning a side perpendicular to the rays of the sun. After 1 or 2 hours of basking, they become active when soil temperatures range from 59° to 103° F (15° to 39° C) and air temperatures from 59° to 76° F (15° to 24° C). They mate, feed, and walk about on the ground. When temperatures rise above tolerance levels, they cease activity and face the sun or face directly away and stilt. When temperatures continue to increase, they climb vegetation to heights of 4 inches (10.2 cm) or more to reduce their body temperature through evaporative cooling by hyperventilation.

Populations of the gladston grasshopper are usually low at less than 1.0 adult/yd^2 (1.2/m^2). In short grass areas of the mixed grass prairie and in the short grass prairie during outbreaks, gladston grasshopper densities can increase to 4 adult/yd^2 (4.8/m^2) and they usually remain as subdominant members of the assemblage.

This summary life history of the gladston grasshopper was based primarily from the work of Pfadt 1994 with additional information from Mulkern et al. 1969, Carruthers et al. 1992, and Onsager 2000.

Life History of the little spurthroated grasshopper

Melanoplus infantilis (Scudder) (Mel inf), the little spurthroated grasshopper, is an important dominant pest on rangelands, primarily in the northern mixed grass prairie in the United States and in the prairie provinces of Canada north to the aspen parkland. It is a pest on crested wheatgrass pastures, and it can be injurious to grassland ecosystems because it is able to consume substantial quantities of leaves from young native grass tillers prior to the 3.5 new leaf stage. The little spurthroated grasshopper has wide distribution in western North America and it inhabits the rangelands of the Northern Plains. It is a member of the Melanoplinae subfamily of spurthroated grasshoppers. The adults are small sized grasshoppers. Live weight of the males average 157 mg and the females average 236 mg. Body length of the males is 0.65 to 0.67 in (16.5 to 17.0 mm) and the females is 0.63 to 0.74 in (16.0 to 19.0 mm).

The hatching period is with the early group starting about late May to mid June and lasting 3 weeks. The nymphs develop most rapidly through 5 instar stages in 27 to 34 days. The fledgling adults require a period of growth and maturation after they appear. Males and females form mating pairs. Females require a period for egg development after mating. Gravid females deposit 10 to 13 eggs per clutch in a curved pod that is 0.88 to 1.0 in (22.2 to 25.4 mm) long placed in bare soil, sometimes near short grass, at depth of 1.0 in (2.5 cm). The eggs begin embryonic growth in the summer of deposition and continue until they enter diapause; the following spring, the embryos complete development and emerge.

The little spurthroated grasshopper feeds on grasses, sedges, and forbs. The food plants include blue grama, western wheatgrass, needle and thread, sand dropseed, idaho fescue, parry oatgrass, sandberg bluegrass, threadleaf sedge, needleleaf sedge, scarlet globemallow, woolly plantain, broom snakeweed, fringed sagebrush, dandelion, and milkvetch. They feed from the ground, cut a section of grass leaf from the plant, hold the cut leaf with their front tarsi, and consume the entire leaf section from the cut end to tip. This process continues until they are satiated. They also eat fallen leaf parts from the ground litter.

At typical low densities of 0.1 to 0.5/yd^2 (0.12 to 0.6/m^2), the adults remain in the same area that they hatched. During the inactive night, they roost on the ground or on small shrubs. After sunrise and before sunset, they bask on bare ground or on the crown of blue grama by exposing their side to the rays of the sun. During the day when the soil temperature is 80° F (27° C) or greater and the air temperature is 68° F (20° C) or greater, adults perform normal activities. During the afternoons that soil temperatures rise to 115° F (46° C), individuals climb grass stems and rest vertically head up 2 inches (5.1 cm) above the soil surface to reduce their body temperature through evaporative cooling by hyperventilation.

Population densities of little spurthroated grasshoppers can increase to outbreak levels of 20 to 40/yd^2 (24 to 48/m^2) during favorable conditions. The outbreak assemblages usually include the bigheaded grasshopper and other species. The little spurthroated grasshopper is sometimes the dominant member.

This summary life history of the little spurthroated grasshopper was based primarily from the work of Pfadt 1994 with additional information from Mulkern et al. 1969, Watts et al. 1989, Carruthers et al. 1992, and Onsager 2000.

Life History of the flabellate grasshopper

Melanoplus occidentalis (Thomas) (Mel occ), the flabellate grasshopper, is a frequent codominant pest on rangelands, primarily in the northern mixed grass prairie and it can be injurious to grassland ecosystems because it is able to consume substantial quantities of leaves from young native grass tillers prior to the 3.5 new leaf stage. The flabellate grasshopper has wide distribution in the central region of North America and it inhabits the rangelands of the Northern Plains. It is a member of the Melanoplinae subfamily of spurthroated grasshoppers. The adults are medium sized grasshoppers. Live weight of the males average 280 mg and the females average 567 mg. Body length of the males is 0.76 to 0.83 in (19.2 to 21.0 mm) and the females is 0.87 to 0.94 in (22.0 to 24.0 mm).

The hatching period is with the early group starting about mid May and lasting 3 to 4 weeks. The nymphs develop through 5 instar stages in about 40 to 45 days. The fledgling adults require a period of growth and maturation after they appear. Males and females form mating pairs. Females require a period for egg development after mating. Gravid females deposit 8 to 10 eggs per clutch in a curved pod that is 1.0 in (25.4 mm) long and 0.13 in (3.2 mm) in diameter placed into bare ground at a depth of about 1.0 in (2.5 cm). The eggs begin embryonic growth in the summer of deposition and continue until they enter diapause; the following spring, the embryos complete development and emerge.

The flabellate grasshopper feeds chiefly on forb leaves but also consumes substantial quantities of grasses and dry litter. The main food plants are scarlet globemallow, wildbuckwheat, milkvetch, blue grama, needle and thread, western wheatgrass, kentucky bluegrass, and needleleaf sedge. Adults feed by climbing onto a forb or grass plant or they feed from the ground.

The adults have fully developed long wings and are strong fliers. They are capable of dispersal flights and appears likely to be able to migrate in mass. At typical low densities, the adults remain in the same area that they hatched. The flabellate grasshopper is geophilous and spends most of the time on the ground. At night, both nymphs and adults rest horizontally on bare ground. After sunrise and before sunset, they bask on bare ground by turning a side perpendicular to the rays of the sun. After about 2 hours of basking, they become active and perform normal mating, egg laying, feeding, and pottering activities while the ground temperatures range from 90° to 100° F (32° to 38° C) and air temperature are around 70° F (21° C). During the afternoons when soil temperatures rise to 130° F (54° C) and air temperatures rise above 90° F (32° C), adults climb small shrubs to heights of 3 to 6 inches (7.6 to 15.2 cm) and rest in the shade.

Populations of flabellate grasshopper are usually low at around 0.1 adult/yd^2 (0.12/m^2) but have increased to 7.3 adult/yd^2 (8.8/m^2) as part of multispecies outbreak assemblages.

This summary life history of the flabellate grasshopper was based primarily from the work of Pfadt 1994 with additional information from Mulkern et al. 1969.

Life History of the packard grasshopper

Melanoplus packardii (Scudder) (Mel pac), the packard grasshopper, is a serious codominant pest on rangelands, primarily in the northern mixed grass prairie, preferring vegetation on loamy or sandy loam soils with scant grass canopy cover. It is also an important pest on croplands and adjacent unmanaged grass areas. It has adapted to cropland agricultural practices and can damage many types of crops during outbreaks. The packard grasshopper has wide distribution in western North America and it inhabits the rangelands of the Northern Plains. It is a member of the Melanoplinae subfamily of spurthroated grasshoppers. The adults are large sized grasshoppers. Live weight of the males average 571 mg and the females average 639 mg. Body length of the males is 1.06 to 1.26 in (27.0 to 32.0 mm) and the females is 1.26 to 1.40 in (32.0 to 35.5 mm).

The hatching period is with the early group starting about mid May to early June and lasting 5 weeks. Nymphs develop through 5 instar stages in 47 to 63 days. The fledgling adult males require a period for growth and maturation after they appear in early July. Females have a preoviposition period of 3 weeks between fledging and ovipositing. Males and females form mating pairs. Gravid females deposit 16 to 29 eggs per clutch in a slightly curved pod that is 1.25 in (3.18 mm) long and 0.19 in (4.8 mm) in diameter placed deep in bare ground. The eggs begin embryonic growth in the summer of deposition, continue until a late stage with greatly advanced development, then enter diapause; the following spring, the embryos complete development of the last few stages and emerge early.

The packard grasshopper is polyphagous and feeds on both forbs and grasses, and they consume numerous types of crops. The food plants include scurfpea, milkvetch, woolly loco, prickly lettuce, western ragweed, sweetclover, blue grama, sand dropseed, needle and thread, and smooth bromegrass. They feed from the ground, reach up, and feed on leaves.

At typical low densities of 0.1 to 0.4/yd^2 (0.12 to 0.48/m^2), most adults remain in the same area that they hatched. The packard grasshopper is geophilous and spends most of the time on the ground. At night, they rest horizontally on bare ground or on litter. After sunrise and before sunset, they bask on bare ground with their side or back exposed to the rays of the sun. During the day when soil temperatures are 80° F (27° C) or greater and air temperatures are 70°F (21° C) or greater, adults perform normal activities. When the soil temperatures rise above 120° F (49° C) and air temperatures are above 90° F (32° C), individuals climb vegetation and rest vertically head up 2 to 10 inches (5.1 to 25.4 cm) above the ground to reduce their body temperature through evaporative cooling by hyperventilation. *Melanoplus packardii* is one of the preferred hosts of the endoparasite *Acridomyia canadensis* (anthomyiid fly); the fly larvae consumes the grasshopper from inside.

Populations of the packard grasshopper can increase to outbreak densities. The assemblages usually include the migratory grasshopper as the dominant, the twostriped grasshopper as the second, and the packard grasshopper as the third. All three species have long wings and are strong fliers. The adults move to cropland and damage or destroy fields of winter wheat, fall rye, barley, alfalfa, and sunflowers. During the outbreak periods, these adapted grasshoppers perform well in the unmanaged grass and weed areas near cropland fields, feeding on nutritious weeds and field crops, and laying eggs in favorable sites of drift soil with south facing slopes.

This summary life history of the packard grasshopper was based primarily from the work of Pfadt 1994 with additional information from Mulkern et al. 1969, Carruthers et al. 1992, and Hostetter 1994.

Life History of the migratory grasshopper

Melanoplus sanguinipes (Fabricius) (Mel san), the migratory grasshopper, is the most damaging and the most widely distributed dominant pest on rangelands and crested wheatgrass pastures. It has successfully adapted to cropland agricultural practices and has caused more damage than any other grasshopper species. It prefers deteriorated grassland pastures invaded with weeds. The migratory grasshopper has extensive distribution across North America and it inhabits the rangelands of the Northern Plains. It is a member of the Melanoplinae subfamily of spurthroated grasshoppers. The adults are medium sized grasshoppers. Live weight of the males average 338 mg and the females average 442 mg. Body length of the males is 0.79 to 1.02 in (20.0 to 26.0 mm) and the females is 0.79 to 1.14 in (20.0 to 29.0 mm).

The hatching period is with the early group starting mid to late May and lasting 3 to 6 weeks depending on soil temperature, soil type, and amount of shading from vegetation. The male nymphs develop through 5 instar stages and the female nymphs usually develop through 6 instar stages in 35 to 55 days depending on air temperatures. The fledgling males require a period for growth and maturation after they appear. The females have a preoviposition period of 2 to 3 weeks between fledging and ovipositing the first clutch. The males court the females by waving his antennae and vibrating his hind femurs. About 6 days after they mate, gravid females deposit 18 to 24 eggs per clutch in a curved pod that is 1.0 in (25.4 mm) long and 0.13 in (3.2 mm) in diameter placed vertically into bare soil with the eggs oriented diagonally among the roots of blue grama or other short grass. On cropland, the egg pods are deposited around the base of crop or weedy plants. The eggs begin embryonic growth in the summer of deposition, continue development to stage 24 (80%) after 422 DD (degree days) of heat, then enter diapause until low soil temperatures during winter break diapause; the following spring, the embryos resume development at the base soil temperature of 50° F (10° C) and complete development to stage 27 after an additional 105 DD (degree day) of heat and emerge. Complete embryonic development of the eggs during the summer and spring requires a total of 527 DD day-degrees of heat above threshold of 50° F (10° C) soil temperature.

The migratory grasshopper is polyphagous and feeds on many kinds of plants both forbs and grasses, and they consume numerous types of crops. The food plants include dandelion, mustards, pepperweed, western ragweed, blue grama, western wheatgrass, sandberg bluegrass, sand dropseed, downy brome, kentucky bluegrass, squirreltail, and stinkgrass. Generally, they climb in or on the plant to feed. They also ingest dry plant litter and cattle manure from the ground.

At typical low densities of 0.1 to 3.0/yd^2 (0.12 to 3.6/m^2), the adults remain on the same rangeland area that they hatched. They are diurnal, active during the day and inactive at night. The migratory grasshopper is geophilous and spends most of the time on the ground. During the night, nymphs and adults rest horizontally on the ground. After sunrise and before sunset, they bask on the ground or on vegetation by exposing their side to the rays of the sun. During the day, adults perform normal activities of mating, laying eggs, feeding, and pottering (walking around aimlessly). As soil temperatures rise, grasshoppers on bare ground stilt. When the soil temperatures rise above 130° F (54° C), individuals climb vegetation, often western wheatgrass, to heights of 2 to 8 inches (5.1 to 20.3 cm) and reduce their body temperature through evaporative cooling by hyperventilation. *Melanoplus sanguinipes* is one of the preferred hosts of the endoparasite *Acemyia tibialis* (tachinid fly); the fly larvae consumes the grasshopper from inside.

The migratory grasshopper has a great capacity to increase its population numbers. A low density at 3/yd^2 (3.6/m^2) can reproduce exponentially in a favorable year so that the next year, the population reaches outbreak densities of 30/yd^2 (36/m^2). Over a period of several favorable years, densities can reach enormous levels of 60 to 140/yd^2 (72 to 168/m^2). The older nymphs travel together in a band at rates of around 0.1 mile per hour (0.16 km/hr) and move distances of less than 5 miles (8 km) to as far as 10 miles (16 km). Adults are highly migratory during their prereproductive stage. Swarming occurs on clear days and move with the wind at speeds of 10 to 12 miles per hour (16 to 19 km/hr). During the afternoon, they alight to feed and rest. At high densities, they can nearly destroy fields of wheat, barley, oat, corn, alfalfa, clover, vegetables, and ornamental plants. They also attack vines, bushes, and trees, feeding on foliage, fruit, and bark. The high density outbreaks can last 2 to 3 years. The large populations develop on the unmanaged grass and weedy areas near cropland fields. The females deposit the egg pods near roots of weedy plants in wind blown drift soil with south facing slopes. The outbreak assemblages are usually dominated by the migratory grasshopper and may include the twostriped, the differential, the redlegged, and/or the packard grasshoppers.

This summary life history of the migratory grasshopper was based primarily from the work of Pfadt 1994 with additional information from Mulkern et al. 1969, Watts et al. 1989, Belovsky et al. 1990, Carruthers et al. 1992, Hostetter 1994, and Onsager 2000.

Life History of the bluelegged grasshopper

Metator pardalinus (Saussure) (Met par), the bluelegged grasshopper, is an important codominant pest on rangelands, primarily in the northern mixed grass prairie, preferentially on areas dominant by western wheatgrass on clay soils. The bluelegged grasshopper has wide distribution in central North America and it inhabits the rangelands of the Northern Plains. It is a member of the Oedipodinae subfamily of bandwinged grasshoppers. The adults are large sized grasshoppers. Live weight of the males average 294 mg and the females average 828 mg. Body length of the males is 0.87 to 0.98 in (22.0 to 25.0 mm) and the females is 1.18 to 1.34 in (30.0 to 34.0 mm).

The hatching period is with the intermediate group starting about early June and lasting as short as 1 week. The nymphs develop through 5 instar stages in about 36 days. The fledgling adults require a period for growth and maturation after they appear. Males and females form mating pairs. Courtship of the bluelegged grasshopper has not been recorded. Females require a period for egg development after mating. Gravid females deposit 14 large eggs per clutch in a pod placed 1 to 2 inches (2.5 to 5.1 cm) deep into bare ground or ground covered with litter among short grasses. The eggs begin embryonic growth in the summer of deposition, development continues to an undetermined stage, then enter diapause; the following spring, the embryos complete development to stages 27 and emerge.

The bluelegged grasshopper is graminivorous and feeds almost exclusively on grasses and sedges. The preferred food plants are western wheatgrass and needleleaf sedge, but will also eat bluebunch wheatgrass, needle and thread, green needlegrass, sand dropseed, prairie junegrass, and blue grama. They also will consume small amounts of licken, green and dry grass litter, and dry cattle dung. The grasshopper climbs the stem of western wheatgrass and cuts a 3 to 4 inch (7.6 to 10.2 cm) section of leaf, which falls to the ground. The grasshopper drops to the ground and recovers the cut leaf section. Holding the cut leaf with its front tarsi, the grasshopper devours the leaf from one end to the other. The grasshopper will consume any green leaf lying on the ground or any low attached leaf that can be reached from the ground.

Typical low densities are 1 to 4/yd^2 (1.2 to 4.8/m^2). The adults have long wings and could disperse to new areas, however, the majority of adults remain in the same area that they hatched. The bluelegged grasshopper is geophilous and spends most of the day and all of the night on the ground. At night, both nymphs and adults sit on the bare ground under canopies of grass or some sit unprotected by grass. After sunrise and before sunset, they bask by resting on bare ground with their side exposed to the rays of the sun. During the day when soil temperatures are 80° F (27° C) or greater and air temperatures are 67°F (19° C) or greater, the adults perform normal activities of seeking a mate, feeding, and walking around. On afternoons when the soil temperatures rise to 120° F (49° C), individuals rest horizontally on the ground in shade of vegetation or they may climb on grass stems to a height of 2 inches (5.1 cm) to reduce their body temperature through evaporative cooling by hyperventilation. Some adults may move into the crowns of grasses and rest diagonally on leaves in the shade. *Metator pardalinus* is one of the preferred hosts of the endoparasite *Neorhynchocephalus sackenii* (tangleveined fly); the fly larva consumes the grasshopper from inside.

Populations of the bluelegged grasshopper can increase to high densities of 10/yd^2(12/m^2) in mesic habitats dominated by western wheatgrass. During outbreak populations, the bluelegged grasshopper is codominant with the bigheaded grasshopper.

This summary life history of the bluelegged grasshopper was based primarily from the work of Pfadt 1994 with additional information from Mulkern et al. 1969, Carruthers et al. 1992, and Hostetter 1994.

Life History of the obscure grasshopper

Opeia obscura (Thomas) (Ope obs), the obscure grasshopper, is an important codominant pest on rangelands, primarily in the short grass vegetation dominated by blue grama. It has been associated with a local outbreak in western North Dakota. The obscure grasshopper has wide distribution in western North America and it inhabits the rangelands of the Northern Plains. It prefers grassland habitat with short grass of blue grama or buffalograss, or heavily grazed mid and tall grasses. It is a member of the Gomphocerinae subfamily of slantfaced grasshoppers. The adults are small sized grasshoppers. Live weight of the males average 66 mg and the females average 143 mg. Body length of the males is 0.53 to 0.59 in (13.5 to 15.0 mm) and the females is 0.71 to 0.78 in (18.0 to 19.7 mm).

The hatching period is with the late group starting about early to late June and lasting 2 to 4 weeks. The nymphs develop through 5 instar stages in about 36 to 50 days. The adults appear from late July to early August. Fledgling adults require a period for growth and maturation after they appear. Males and females form mating pairs. Females require a period for egg development after mating. Gravid females deposit 8 to 10 small eggs per clutch in a pod that is 0.88 in (22.2 mm) long placed into bare ground at a relatively deep depth of 0.63 to 0.88 in (15.9 to 22.2 mm). The eggs begin embryonic growth in the summer of deposition and continue until they enter diapause; the following spring, the embryos complete development and emerge.

The obscure grasshopper is graminivorous and feeds on grasses. It prefers blue grama. The grasshopper consumes the green portion of grass leaves. It sits vertically, head up, on a blue grama leaf, cuts it near the middle, holds the cut portion with the front tarsi, and devours the cut leaf to the dry tip, or it feeds on a blue grama leaf in the horizontal position from the ground.

The adults have wings that nearly reach the end of the abdomen and some have wings that are 0.12 in (3 mm) longer than the abdomen. They have the ability of evasive flight. It is unknown if they have the capacity for dispersion or migration. At typical low densities, adults generally remain in the same area that they hatched. The obscure grasshopper is a phytophilous species, spending most of the day sitting vertically head up on the stems and leaves of grasses about 1 to 2 inches (2.5 to 5.1 cm) above ground. After sunrise and before sunset, both nymphs and adults bask by directly exposing a side or their back to the rays of the sun from a diagonal position on a blue grama plant, on a small mound of bare soil, or on bare ground. During the basking period, the ground temperatures range from 70° to 100° F (21° to 38° C) and air temperatures range from 64° to 83° F (18°to 28° C). Normal activities begin when the ground temperature is 85° F (29° C) or above and air temperature is around 70° F (21° C). During the afternoon when soil temperatures are from 110° to 130° F (43° to 54° C) and air temperatures are 90° F (32° C) or above, the grasshoppers avoid overheating by resting in the shade of canopy vegetation on blue grama above the ground, move to a diagonal position on blue grama facing the sun to expose less body surface, or climb a midgrass stem to a height of up to 4 in (10.2 cm) above the ground to reduce their body temperature through evaporative cooling by hyperventilation.

Population densities of the obscure grasshopper are usually low at around 0.1 to 2.2 adults/yd^2 (0.12 to 2.6/m^2). The population densities generally grow gradually for a couple of years and then increase at 3 to 5 fold in 1 year. The multispecies assemblages that include obscure grasshopper as a subdominant or codominant increase to greater densities on the short grass prairie or on short grass areas on the mixed grass prairie.

This summary life history of the obscure grasshopper was based primarily from the work of Pfadt 1994 with additional information from Mulkern et al. 1969, Watts et al. 1989, Carruthers et al. 1992, and Onsager 2000.

Life History of the fourspotted grasshopper

Phlibostroma quadrimaculatum (Thomas) (Phl qua), the fourspotted grasshopper, is a serious codominant pest on rangelands, primarily in the mixed grass prairie and it can become a major economic pest on dry upland grassland areas that have a dominance of blue grama and other short grasses and mixed in mosaic patches with mid grasses in the short grass and mixed grass prairies. The fourspotted grasshopper has wide distribution in central North America and it inhabits the rangelands of the Northern Plains. It is a member of the Gomphocerinae subfamily of slantfaced grasshoppers. The adults are small sized grasshoppers. Live weight of the males average 110 mg and the females average 300 mg. Body length of the males is 0.57 to 0.59 in (14.5 to 15.0 mm) and the females is 0.73 to 0.85 in (18.5 to 21.5 mm).

The hatching period is with the intermediate group starting about early to mid June and lasting 2 to 3 weeks. The male nymphs usually develop through 4 instar stages, occasionally 5 instar stages. The female nymphs develop through 5 instar stages. Nymphal development lasts 33 to 55 days, with an average of 48 days. The fledgling adults require a period of about 2 weeks for growth and maturation after they appear. The females are nearly 3 times larger than the males. The males chase after moving females, if the female stops, she is courted with an intraspecific stridulation song. The females require a period for egg development after mating. Gravid females deposit 6 to 14 eggs per clutch in a tough pod that is 0.88 to 1.0 in (22.2 to 25.4 cm) long placed into bare ground, near buffalograss, blue grama, or other short grass, at about 1 inch (25 mm) in depth. The eggs begin embryonic growth in the summer of deposition and continue until they enter diapause; the following spring, the embryos complete development and emerge.

The fourspotted grasshopper is graminivorous and feeds almost exclusively on grasses. The preferred food plants are blue grama and buffalograss but will also feed on needle and thread, western wheatgrass, sand dropseed, sideoats grama, and prairie sandreed. Rarely do they feed on upland sedges or forbs. The grasshopper climbs up a green leaf blade, turns around hanging onto adjacent leaves, and feeds on the entire width from about 1 inch (2.5 cm) below the tip toward the base. Sometimes the grasshopper sits horizontally within the grass crown and feeds on green leaves from near the tip to the base. The fourspotted grasshopper is a thrifty feeder and only small amounts of clipped leaf parts fall to the ground and become litter.

Typical low densities on rangeland are 0.2 to 1.5/yd^2 (0.24 to 1.8/m^2). The adults have functional wings, however, most adults remain in the same area that they hatched. The fourspotted grasshopper is geophilous and spends most of the time on the ground. At night, both nymphs and adults rest on areas of bare ground or on litter near blue grama or other short grass. After sunrise and before sunset, they bask horizontally on the ground by exposing their side to the rays of the sun. During the day when the soil temperatures are 70° F (21° C) or greater, adults perform normal activities of mating, feeding, and pottering (walking around aimlessly). The percent time engaged in daily activities was 76.8% basking, 18.4% pottering, and 5.8% feeding. When soil temperatures rise to 100° F (38° C), individuals stilt by raising up on their legs and hold their bodies off the hot ground. When soil temperatures rise to 120° F (49° C), they move into blue grama plants and climb up 0.5 to 4.0 inches (1.3 to 10.2 cm) above the ground and face the sun. Grasshoppers can reduce their body temperature through evaporative cooling by hyperventilation.

Populations of fourspotted grasshoppers increase with other species of the outbreak assemblages. However, they are usually codominant or subdominant. No information is available on how rapidly or under what conditions populations increase to outbreak numbers.

This summary life history of the fourspotted grasshopper was based primarily from the work of Pfadt 1994 with additional information from Mulkern et al. 1969, Watts et al. 1989, Carruthers et al. 1992, Jech 1996, and Joern et al. 1996.

Life History of the largeheaded grasshopper

Phoetaliotes nebrascensis (Thomas) (Pho neb), the largeheaded grasshopper, is a common and often dominant pest on rangelands, primarily on tall lush grass areas in the tall grass and mixed grass prairies, it has been associated with a local outbreak in western North Dakota, it is a pest on crested wheatgrass pastures, and it is considered to be a major pest on winter wheat cropland. The largeheaded grasshopper has wide distribution in the central region of North America and it inhabits the rangelands of the Northern Plains. It is a member of the Melanoplinae subfamily of spurthroated grasshoppers. The adults are medium sized grasshoppers. Live weight of the males average 206 mg and the females average 419 mg. Body length of the males is 0.70 to 0.76 in (17.8 to 19.4 mm) and the females is 0.81 to 0.89 in (20.5 to 22.5 mm).

The hatching period is with the late group starting about mid to late June and lasting 4 or more weeks. The nymphs develop slowly through 5 instar stages in about 55 days. The adults appear between mid July and early August. The fledgling adults require a period of growth and maturation after they appear. Males and females form mating pairs. Because of the males much smaller size, the female's genitalia must curve up to meet the male's curving down. Females require a period for egg development after mating. Gravid females deposit 20 to 28 eggs per clutch in a curved pod that is 1.0 to 1.25 in (25.4 to 31.8 mm) long placed into bare ground at a depth of an inch (25 mm) or more. The eggs begin embryonic growth in the summer of deposition and continue until they enter diapause; the following spring, the embryos complete development and emerge.

The largeheaded grasshopper is graminivorous and feeds almost exclusively on grasses. The main food plants are little bluestem, big bluestem, western wheatgrass, and kentucky bluegrass. The grasshopper feeds either head up or head down and eats the edge of the leaf, creating a long gouge along one side, and leaving a narrow edge of the leaf intact. This grasshopper does not eat litter on the ground.

Most adults have short wings and do not fly but can disperse from dry vegetation to green vegetation or to winter wheat cropland. A few adults have well developed long wings and are strong fliers. At typical low densities, most adults remain in the same area that they hatched. Long winged adults tend to disperse to new areas. The largeheaded grasshopper is phytophilous and spends most of the day on grass stems and leaves. During warm nights, the grasshoppers rest vertically head up on grass leaves at heights of 6 to 12 inches (15.2 to 30.5 cm). During cold nights, the grasshoppers rest close to the ground or under litter. After sunrise and before sunset, they bask by turning a side perpendicular to the rays of the sun while resting vertically head up on tall grasses. In habitats of short or mid grass or grazed tall grass, the grasshoppers bask by sitting horizontally on bare ground.

Population densities of largeheaded grasshoppers are usually 3 to 4 adults/yd^2 (3.6 to 4.8/m^2) and increase to much higher densities during outbreaks. The highest densities are reached in habitats of lush tall grass in the tall grass and mixed grass prairies that provide an abundance of food.

This summary life history of the largeheaded grasshopper was based primarily from the work of Pfadt 1994 with additional information from Mulkern et al. 1969, Watts et al. 1989, and Onsager 2000.

Life History of the kiowa grasshopper

Trachyrhachys kiowa (Thomas) (Tra kio), the kiowa grasshopper, is a injurious codominant pest on rangelands, primarily on short grass areas dominated by blue grama in the mixed grass and tall grass prairies and it is a pest on crested wheatgrass pastures. The kiowa grasshopper has wide distribution across North America and it inhabits the rangelands of the Northern Plains. It is a member of the Oedipodinae subfamily of bandwinged grasshoppers. The adults are small sized grasshoppers. Live weight of the males average 148 mg and the females average 303 mg. Body length of the males is 0.59 to 0.71 in (15.0 to 18.0 mm) and the females is 0.67 to 0.94 in (17.0 to 24.0 mm).

The hatching period is with the intermediate group starting about early to mid June and lasting 2 to 4 weeks. The nymphs develop through 5 instar stages in 37 to 53 days. The fledgling adults require a period for growth and maturation after they appear. The males court the females on the ground with single stridulating strokes of both hind femurs. Females require a period for egg development after mating. Gravid females deposit 8 to 10 eggs per clutch in a fragile pod that is 1.13 to 1.25 inches (28.6 to 31.8 mm) long placed into bare ground near short grasses. The eggs begin embryonic growth in the summer of deposition and continue until they enter diapause; the following spring, the embryos complete development and emerge.

The kiowa grasshopper is graminivorous and feeds almost exclusively on grasses and sedges. The preferred food plant is blue grama but will also feed on western wheatgrass, needle and thread, threadleaf sedge, needleleaf sedge, sunsedge, and kentucky bluegrass. The grasshopper feeds on the green leaf blades from the tip to the base. Sometimes, they may climb into a grass crown and feed head down on leaf blades. Preferentially, they remain on the ground, raise up on the hindlegs, hold a cut leaf blade with the front tarsi, and consume the leaf from tip to base. They do not eat litter from the ground.

Typical low densities on rangeland are 0.1 to 2.0/yd^2 (0.12 to 2.4/m^2). The adults have very long wings and have moved as migratory swarms. However, the majority of adults remain in the same area that they hatched. The kiowa grasshopper is geophilous and spends most of the time on the ground. At night, both nymphs and adults rest on the ground in bare areas without a grass canopy overhead. After sunrise and before sunset, they bask on the ground by exposing their side or back to the rays of the sun. During the day when soil temperatures are less than 90° F (32° C) and air temperatures are less than 80° F (27° C), the grasshoppers spend most of the time on the ground. The percent time engaged in daily activities was 36.8% basking, 31.4% pottering, and 31.7% feeding. When soil temperatures rise to 130° F (54° C), individuals climb grasses and forbs to rest 0.5 to 1.0 inch (1.3 to 2.5 cm) above ground level, or they may remain on the ground but move to areas shaded by vegetation.

Populations of kiowa grasshopper may remain at low densities for 5 or more years. Under favorable conditions the population can increase 3 to 7 fold in 1 year. The increase to outbreak densities occurs in assemblages that include the bigheaded and the whitewhiskered grasshoppers. The kiowa grasshopper usually remains a codominant in the outbreak assemblage.

This summary life history of the kiowa grasshopper was based primarily from the work of Pfadt 1994 with additional information from Mulkern et al. 1969, Watts et al. 1989, Belovsky et al. 1990, Jech 1996, and Onsager 2000.

Grasshopper Habitat

Most grasshopper species are able to successfully occupy a wide variety of prairie types throughout North America (Onsager 1998). The pestiferous rangeland grasshopper species of the Northern Plains have extensive distribution across the regions grassland prairies; with 100% of the species inhabiting the mixed grass prairie, 91% of the species inhabiting the short grass prairie, 70% of the species inhabiting the tall grass prairie, 70% of the species inhabiting the sandhills prairie, and 61% of the species inhabiting the bunch grass prairie.

The grassland conditions in which a grasshopper species performs best and develops the highest population densities is considered to be the preferred habitat. Nine (39%) of the pestiferous rangeland grasshoppers prefer habitat with short grass areas mixed amongst many open bareground patches. The short grass areas can be located on dry upland sites dominated by blue grama and upland sedges or sites with mid and tall grass species heavily grazed to a short stature. Ten (43%) of the pestiferous rangeland grasshoppers prefer habitat with areas that have a mixture of mid and short grasses interspersed among numerous bareground patches. Four (17%) of the pestiferous rangeland grasshoppers prefer habitat with deteriorated mid and tall vegetation on moist meadows, invaded by weeds, and containing many open bareground patches. All of these preferred grassland habitat conditions are abundantly present within all of the regions prairie types.

The universally important habitat characteristic is the numerous open bareground patches. Pestiferous grasshoppers need the bareground patches for egg pod deposition sites and for basking in unobstructed sunlight to raise their body temperatures to optimal levels. Twenty two (96%) of the pestiferous rangeland grasshoppers deposit their egg pods in bareground patches (table 7). Only one (4%) of the grasshoppers deposit their egg pods into vegetation crowns.

The depth of deposition of the egg pods is a characteristic of a grasshopper species. Three (13%) of the pestiferous rangeland grasshoppers deposit their egg pods at shallow depths. Nine (39%) and eleven (48%) of the pestiferous rangeland grasshoppers deposit their egg pods at medium and deep depths, respectively (table 7). The egg pods deposited at shallow depths should have the advantage of location and accumulate degree days of heat more rapidly than the egg pods deposited at deeper depths; thus the shallow deposited egg pods should have more rapid embryonic development and earlier hatch. The three grasshopper species that deposit their egg pods at shallow depths hatch with the early group during mid to late May. Three grasshopper species that deposit their egg pods at medium depths and four grasshopper species that deposit their egg pods at deep depths also hatch with the early group (table 7). Two grasshopper species that deposit their egg pods at a medium depth and a deep depth, respectively, hatch with the very early group during late April to early May (table 7). This information indicates that the depth of egg deposition is not the most important factor that determines the rate of embryonic development and when the eggs will hatch.

Twenty (87%) of the pestiferous rangeland grasshoppers of the Northern Plains deposit their egg pods at medium and deep depths (table 7). The deeper depths provide greater protection from cold air temperatures during the winter. The greater protection from cold air temperatures provided by deeper egg pod depths must give northern grasshoppers greater advantages and increased survival rates than the more rapid accumulation of degree days of heat provided by shallow egg pod depths.

Twelve (52%) of the pestiferous rangeland grasshoppers hatch before early June; 2 (9%) hatch very early during late April to early May, and 10 (43%) hatch early during mid to late May. Ten (43%) of the pestiferous rangeland grasshoppers hatch after early June; 7 (30%) hatch intermediate during early to mid June, and 3 (13%) hatch late during mid to late June. One (4%) of the pestiferous rangeland grasshoppers overwinter in a late nymphal stage, deposit egg pods at a medium depth, and hatch very late during mid to late July in the same growing season that they were laid (table 7).

Before the end of a six year study on the effects of grazing management on grasshopper habitat and densities, Onsager (1998) was able to distinguish that the pestiferous grasshopper species that hatched after early June declined from a population at greater rates than the pestiferous rangeland grasshopper species that hatched before early June following the implementation of a biologically effective grazing management practice, the twice-over rotation system, that had reduced the size and number of bareground spaces in their habitat. Onsager (1998) suspected that lower fecundity in the later hatching grasshoppers was of greater importance in the more rapid decline in density than lower survival rates.

Twenty three (100%) of the pestiferous rangeland grasshoppers bask on bareground areas to accumulate thermal heat from unobstructed sunlight and also to take advantage of the additional rays reflected off the nearby bare soil for the purpose of increasing their body temperature to optimal levels. Three (13%) grasshoppers also climb vegetation too heights that receive direct sunlight as another primary basking site (table 8). Basking in vegetation is less effective than basking on bareground.

Twenty three (100%) of the pestiferous rangeland grasshoppers conduct some or most of their daily activities of courting, mating, pottering, and resting on bareground. Nine (39%) grasshoppers also conduct some of their daily activities in vegetation (table 8).

Fourteen (61%) of the pestiferous rangeland grasshoppers are graminivorous and eat mostly grasses, two (9%) grasshoppers are mixed feeders and eat both grasses and forbs, and seven (30%) pestiferous grasshoppers are polyphagus and eat many different kinds of food plants usually in the percentage of abundance. Eleven (48%) of the pestiferous rangeland grasshoppers have also adapted to eating agricultural crops (table 8). Most of the pestiferous rangeland grasshoppers, 16 (70%), prefer to feed by climbing on the food plant. Seven (30%) of the grasshoppers prefer to feed on the food plant from the ground (table 8).

Fifteen (65%) of the pestiferous rangeland grasshoppers are geophilous; they bask and conduct most of their daily and nightly activities on the ground. Two (9%) of the pestiferous rangeland grasshoppers are phytophilous; they bask on the ground and in vegetation and conduct most of their daily and nightly activities on or in vegetation. Six (26%) of the pestiferous rangeland grasshoppers bask on the ground and conduct their daily and nightly activities on the ground or in vegetation.

Reduction of the number and size of the bareground areas in pestiferous rangeland grasshopper habitat reduces the number of days and the hours per day that grasshopper thermoregulation of body temperature reaches or stays at their optimal level. Metabolic rates and processes are reduced, digestion rates are diminished, food intake is decreased, and growth and development are slowed down resulting in higher mortality of juveniles, fewer adults fledge, maturation of adults is lengthened, the time period for egg production is shortened, the quantity of viable eggs deposited is reduced, causing decreased grasshopper densities and lower grasshopper populations (Onsager 1998).

Table 7. Pestiferous rangeland grasshopper egg hatch period, egg pod habitat, and egg pod depth.

Pestiferous Rangeland Grasshoppers	Hatch Group	Hatch Start	Hatch Duration weeks	Egg Pod Site Habitat	Egg Pod Depth mm 7-12 Shallow	13-24 Medium	25-38 Deep
Aer cla	Very Early	E May	3-4	Bareground, near roots		X	
Age deo	Early	M May	4-6	Bareground, near grass	X		
Amp col	Early	M-L May	4-5	In vegetation crown	X		
Aul ell	Early	M May	3-4	Bareground	X		
Aul fem	Intermediate	E Jun	2	Bareground, near grass		X	
Cam pel	Early	M-L May	2-5	Bareground, near roots			X
Cor occ	Early	M May	4	Bareground, near grass			X
Enc cos	Intermediate	E-M Jun	6-8	Bareground, near grass		X	
Eri sim	Very Late	M-L Jul	4	Bareground		X	
Mel biv	Early	M-L May	4-6	Bareground, near roots			X
Mel con	Very Early	L Apr-E May	4	Bareground, near grass			X
Mel dif	Intermediate	M Jun	2	Bareground, near roots			X
Mel fem	Intermediate	E Jun	7-8	Bareground, near sod			X
Mel gla	Late	M-L Jun	1-2	Bareground, near sod		X	
Mel inf	Early	L May-M Jun	3	Bareground, near grass			X
Mel occ	Early	M May	3-4	Bareground		X	
Mel pac	Early	M May-E Jun	5	Bareground		X	
Mel san	Early	M-L May	3-6	Bareground, near roots		X	
Met par	Intermediate	E Jun	1	Bareground, near grass			X
Ope obs	Late	E-L Jun	2-4	Bareground, near grass		X	
Phl qua	Intermediate	E-M Jun	2-3	Bareground, near grass			X
Pho neb	Late	M-L Jun	4+	Bareground, near grass			X
Tra kio	Intermediate	E-M Jun	2-4	Bareground, near grass			X

Information from Cushing 1993, Pfadt 1994.

Table 8. Activity sites and preferred food plants of pestiferous rangeland grasshoppers.

Pestiferous Rangeland Grasshoppers	Basking Site	Daily Activity Site	Feeding Position	Food Plants: Grass	Forbs	Poly	Ag Crop
Aer cla	Bareground	Bareground	Ground	G			X
Age deo	Bareground	Bareground	Ground	G			
Amp col	Bareground	Vegetation/Ground	Ground	G			
Aul ell	Bareground	Bareground	Vegetation	G			
Aul fem	Bareground	Bareground	Ground/Vegetation	G			
Cam pel	Bareground	Bareground	Vegetation	G			X
Cor occ	Bareground	Ground/Vegetation	Vegetation	G			
Enc cos	Bareground	Bareground	Vegetation/Ground	G			X
Eri sim	Bareground	Bareground	Ground	G			
Mel biv	Bareground	Ground/Vegetation	Ground/Vegetation			P	X
Mel con	Bareground	Ground/Vegetation	Ground/Vegetation			P	X
Mel dif	Bareground	Ground/Vegetation	Vegetation/Ground			P	X
Mel fem	Bareground	Ground/Vegetation	Vegetation			P	X
Mel gla	Bareground	Bareground	Vegetation			P	X
Mel inf	Bareground	Ground/Vegetation	Ground	G	F		
Mel occ	Bareground	Bareground	Vegetation	G	F		
Mel pac	Bareground	Bareground	Ground			P	X
Mel san	Ground/Vegetation	Bareground	Vegetation			P	X
Met par	Bareground	Bareground	Ground/Vegetation	G			
Ope obs	Vegetation/Ground	Vegetation/Ground	Vegetation/Ground	G			
Phl qua	Bareground	Bareground	Vegetation	G			
Pho neb	Vegetation/Ground	Vegetation/Ground	Vegetation	G			X
Tra kio	Bareground	Bareground	Ground	G			

Information from Mulkern et al. 1969, Pfadt 1994.

Grasshopper Outbreaks

Insects and the ancestors of grasshoppers have been on earth a long time. Hexapod (six-legged) insects are believed to have split off from aquatic crustaceans during the Silurian period around 410 million years ago (mya). The oldest fossil insect is from the Devonian period around 407 to 396 mya. Insect flight is thought to have developed through several stages of adaptive intermediate steps involving aquatic insects skimming on water with each stage providing less contact with the water until water was no longer needed. The shorthorned grasshoppers (Caelifera) and the longhorned crickets (Ensifera) split from each other near the Permian-Triassic boundary around 251 mya (Anissimov 2013). Flowering plants (Angiosperms) started to evolve during the Mezozoic Era around 120 mya. The modern Acrididae family of grasshoppers started development during the Upper Cretaceous around 99 mya. Fossil grasshoppers from the Cretaceous have external anatomical characteristics similar to modern grasshoppers which is homologous to the phylogenetic pattern followed by cockroaches (Blattaria) from the Cretaceous to modern cockroaches (Manske and Lewis 1990). The Cretaceous "grasshopper" has a retroactive name because they did not live in grassland habitats and did not eat grass food plants which came much later. The grasshopper subfamilies of Gomphocerinae, Melanoplinae, and Oedipodinae developed during 90 to 50 mya. Near the end of the Eocene epoch around 34 mya, the global climate cooled resulting in reduced forest ecosystems and increased open savannah ecosystems that later developed into grasslands (Chintauan-Marquier et al. 2011, Gomez et al. 2012, Anissimor 2013, Anonymous 2013). The major climate change in the Eocene resulted in the development of modern grasses between 30 and 20 mya. The grasses (Poaceae) and orchids (Orchidaceae) are advanced angiosperms that were among the last families to evolve. During the period of 30 to 20 mya, modern native grasses, rhizosphere organisms, large grazing mammalian graminivores, and modern grasshoppers coevolved and developed complex interactive processes that have improved mutual survival on grassland ecosystems.

Grasshoppers evolved as a natural and integral component of rangeland ecosystems. Grasshoppers are an important source as part of the food chain for numerous rangeland birds, small mammals, reptiles, amphibians, arachnids, and other insects (Watts et al. 1989). Grasshopper populations usually remain at densities that can be supported by the ecosystem and, at these low population densities, grasshoppers are not a problem. However, periodically, grasshopper populations increase to outbreak levels. Grasshopper outbreaks greatly reduce the quantity of forage available for livestock causing economic losses due to reduced livestock stocking rates and weight gains and to the additional costs for chemical insecticide treatments (Watts et al. 1989). Ecological losses occur from grasshopper outbreaks by the removal of greater quantities of leaf material than can be tolerated by grass plants resulting in degraded range condition and reduced wildlife habitat.

Changes in grasshopper density have often been speculated to be directly related with changes in weather conditions. Weather variables are correlated with grasshopper population dynamics, however, weather variables are not the direct cause and effect factors that change grasshopper population numbers (Fisher et al. 1996b, Belovsky et al. 1996, Belovsky 2000). The mechanisms that drive grasshopper population numbers are changes in plant production and nutritional quality, changes in grasshopper growth and development rates, and changes in predation, parasitism, and pathogen infection rates. Grasshopper growth and develpment rates are determined by the nutritional quality and quantity of the food plants and by accessibility to thermal heat units from the sun. Grasshopper population numbers are affected by the mortality rate caused by natural enemies. The quantity of predators, parasites, and pathogens are also determined indirectly by environmental conditions and by the abundance of available prey species.

Grasshopper populations in arid regions, as in the intermountain sagebrush-bunchgrass range (Fielding and Brusven 1996a, b) and the southern short grasslands of Arizona and Colorado (Nerney 1958, Nerney and Hamilton 1969, Capinera and Sechrist 1982, Bock et al. 1992, Onsager 1996), are limited by the quantity of available nutritious food plants. The grasshopper populations in these arid areas are usually suppressed during growing seasons with low or normal precipitation, and tend to increase during years with above normal precipitation. Access to radiant heat from the sun is not limiting the grasshopper population growth at any time in these arid regions because of the relatively low vegetation canopy, however, the available food supply usually limits the grasshopper density except during years with greater than normal precipitation and above normal grass herbage production.

Grasshopper populations in the semiarid, subhumid, and humid regions of the Northern Plains are not limited by the quantity of available nutritious food plants but are limited by the accessibility to thermal heat units from the sun because of the shading effect caused by the relatively tall vegetation canopy. Grasshopper populations in the Northern Plains are usually suppressed during growing seasons with normal and above normal precipitation and normal and above normal grass herbage production. The greater quantities of grass herbage biomass produced and the taller vegetation canopy in the Northern Plains, compared to the grass herbage production and vegetation canopy in the intermountain and desert southwest regions, limit access to radiant heat from the sun except when low precipitation or heavy grazing by livestock reduce the vegetation canopy on native grasslands or when double use, such as grazing and haying, during one growing season reduce the vegetation canopy on domesticated grasslands. Generally, grasshopper populations increase when vegetation canopy height decrease and the highest infestations occur when ground cover is reduced to less than 40% of potential (Onsager 1987, 2000).

Pestiferous rangeland grasshopper outbreaks develop through two processes (Belovsky, Lockwood, and Winks 1996, Lockwood, Brewer, and Schell 1996). The **eruptive outbreak** increases rapidly over one to two years in a relatively small area or "hotspot" and then expands outward into larger areas. The **gradient outbreak** starts with low numbers throughout a region, then gradually increases in numbers over several years, which is followed by a growing season of marked increase of 3 to 5 times the previous years density. The extreme increase in grasshopper numbers during the outbreak growing season usually appear to have resulted from greater longevity and thus greater egg production by adults in the preceding year (Pfadt 1977). Grasshopper outbreaks on rangeland consist of 3 to 4 species, and usually not more than 5 different species; only rarely does an assemblage consist of one species. These outbreak grasshoppers species compose most of the population and makeup the dominate, codominate, and subdominate components of the assemblage. Several other grasshopper species also occur in the outbreak area and compose a small portion in the assemblage, however, their population densities do not increase greatly (Belovsky et al. 1996). All of the grasshopper species comprising the assemblage contribute to the economic forage losses and the ecological degradation.

Vegetation canopy reduction or removal increases solar radiation and day degree heat units at the soil surface and increases air flow over the ground, which increases both the soil and air temperatures and decreases relative humidity for grasshoppers. Increased solar radiation to the soil increases day degree heat units that accelerate embryonic development in the egg that results in earlier hatch. Vegetation canopy reduction improves basking sites that hasten body warm up of nymphs and adults that results in increased metabolic rates and increased growth and development rates that shorten instar stages and adult maturation time. Greater solar radiation, higher soil and air temperatures, and lower humidity in grasshopper microhabitat has debilitating effects on pathogens, resulting in lower mortality rates, which increases the number of nymphs reaching adult stage, and increases the longevity of adults that promotes greater egg production.

The crucial factor for successful cultural management of grasshoppers in the Northern Plains is the stimulative manipulation of the abundant herbage biomass production and the maintenance of relatively tall vegetation canopy so that the growth and development rates of grasshopper eggs, nymphs, and adults are greatly inhibited as a result of restricted access to radiant day degree heat units from the sun.

Grasshopper Forage Use

Grasshopper Diet

All grasshoppers are herbivorous and eat herbaceous plants. The grasshoppers that eat grasses are graminivorous. The grasshoppers that eat forbs are forbivorous. Many grasshoppers are mixed feeders and eat both grasses and forbs. Several of the nasty pestiferous grasshoppers are polyphagus and eat many different kinds of food plants including grasses, forbs, and agricultural crops. All of the substances necessary for growth, reproduction, and maintaining life processes in grasshoppers must come from the food plants that they eat.

Grasshoppers require a diet that provides adequate protein, energy, water, minerals, and vitamins. Protein is the most limiting nutrient. Protein makes up 50% of the cuticle of the exoskeleton. Muscle and organ tissue contain protein. Digestive enzymes and hemolymph (body fluid) require protein. Female ovarian growth and egg formation requires large amounts of the protein vitellogenin. Energy is obtained from simple sugars and soluble starches in plants. Grasshoppers do not require energy at the levels required by mammals. Grasshoppers are cold blooded (ectothermal) and do not regulate their body temperature metabolically. Available liquid water may be limiting in arid and semiarid regions that do not have dew in the morning. Water, then, must come from the food plants. The amount of water in the leaves of food plants could influence preference in dry habitats. Green grass leaves usually have high water content at 60% to 80%. The exoskeleton is efficient at conservation of water. Grasshopper requirements for macrominerals, microminerals, and vitamins is not known. The required amounts may vary but the types of vitamins and elemental minerals may be similar to those required by other living creatures. The quantity of nutrient intake and the allocation of ingested nutrients determines growth and development rates and reproductive production (Heidorn and Joern 1984, Joern 1996a, 1996b).

Grasshopper Digestive Tract

The digestive tract of grasshoppers is separated into three sections. The foregut (stomodaeum) consists of the mouth region. The maxillary and labial palpi are sensory organs that separate plant chemicals into attractants or repellants before the leaf is bitten. The manible cuts the leaf into bit size pieces and starts mechanical digestion.

The salivary glands secrete chemical enzymes that digest carbohydrates.

The midgut (mesenteron) consists of the thorax and anterior segments of the abdomen region. The pharynx and esophagus are located in the buccal cavity and lead to the crop that holds food and starts protein digestion. The gizzard has hard tooth-like features that break up food. The stomach mixes chemical enzymes with the food to break it down. The gastric caecum surrounds the stomach, secretes digestive enzymes, protease, lipase, amylase, invertase, and several others, and absorbs amino acids. The peritrophic membrane continuously produces protein/chitin complex.

The hindgut (protodaeum) consists of the posterior segments of the abdomen region. The ileum section of the intestine continues food digestion and absorbs soluble food matter and water. The malpighian tubules excrete uric acid, urea, and amino acids into the rectum section of the intestine where dry pellets are formed from the food residue and waste products that are then disposed of through the anus (Joern 1996a, 1996b; Anonymous 2013).

Forage Nutritional Quality

Crude protein levels of cool season native range grasses are closely related to the phenological stages of growth and development, which are triggered primarily by the length of daylight. The length of daylight increases during the growing season between mid April and mid June (21 June) and then decreases. Lead tillers contain the highest levels of crude protein during the early stages of development. Cool season grasses are long day plants and the lead tillers usually reach the flower phenological stage before 21 June. Crude protein levels remain above 9.6% at flower stage but decrease rapidly during seed development and seed mature stages, dropping below 7.8% by early August and below 6.2% in late August (Whitman et al. 1951, Manske 2008a). Crude protein levels of cool season secondary tillers increase above 9.6% during July and August to 13.2% in early September, decrease during September, and drop below 9.6% in early to mid October (Sedivec 1999, Manske 2008a). Phosphorus levels of lead tillers drop below 0.18% in late July, when plants reach the mature seed stage (Whitman et al. 1951, Manske 2008b).

Crude protein levels of warm season native range grasses are closely related to the phenological stages of growth and development, which are triggered primarily by the length of daylight. Lead tillers contain the highest levels of crude protein during the early stages of development. Warm season grasses are short day plants and the lead tillers usually reach the flower phenological stage after 21 June. Crude protein levels remain above 9.6% at flower stage but decrease rapidly during seed development and seed mature stages, dropping below 9.6% in late July, and below 6.2% in early September (Whitman et al. 1951, Manske 2008a). Crude protein levels of warm season secondary tillers increase above 9.0% during August to 10.0% in early September, decrease during September, and drop below 9.6% in late September (Sedivec 1999, Manske 2008a). Phosphorus levels of lead tillers drop below 0.18% in late August, when plants reach the mature seed stage (Whitman et al. 1951, Manske 2008b).

Crude protein levels of upland sedges do not follow the same relationships with phenological growth stages as do the crude protein levels of cool and warm season grasses. Upland sedges contain the highest levels of crude protein during the early stages of development. Crude protein levels remain high through flower and seed mature stages and decrease with increases in senescence. Upland sedges grow very early and produce seed heads in late April to early May. Crude protein levels remain above 9.6% after seed mature stage, until mid July. Crude protein levels decrease below 7.8% in early August but do not fall below 6.2% for the remainder of the growing season (Whitman et al. 1951, Manske 2008a). Phosphorus levels drop below 0.18% in mid May, when plants reach the mature seed stage (Whitman et al. 1951, Manske 2008b).

The quality of grass forage available to grasshoppers on rangelands of the Northern Plains is above 9.6% crude protein in the lead tillers of the cool and warm season grasses during mid May to late July. Upland sedges have crude protein levels above 9.6% during early May to mid July. The secondary tillers of the cool and warm season grasses have crude protein levels above 9.6% during mid July to late September or mid October. All the grasses have adequate levels of energy throughout the growing season. Grasshoppers should be able to select a diet with adequate crude protein, energy, and water during early May through mid October from the upland sedges and the lead and secondary tillers of the cool and warm season grasses on the rangelands of the Northern Plains.

Grasshopper Forage Loss

All rangeland grasshoppers consume forage and reduce the quantity available for grazing livestock. Throughout western North America, grasshoppers annually destroy an estimated 21% to 23% of the available range forage (Hewitt and Onsager 1983, Onsager 1987). Only about 12% to 21% of the forage that grasshoppers clip from plants is consumed, the rest is discarded and permitted to drop to the ground as litter (Onsager 1987). The amount of forage consumed and destroyed by the typical low density grasshopper populations have automatically been incorporated into traditional regional stocking rates (Onsager 2000). These traditional stocking rate concessions are crude and grasshopper populations fluctuate with changes in management practices. The understanding of grasshopper biology has made great advancements and methods to calculate grasshopper forage loss have been developed (table 9). It is possible to determine the quantity of forage loss in specific rangeland pastures and to adjust the stocking rate appropriately. The quantity of rangeland forage loss caused by grasshoppers can be determined from the grasshopper species average dry weight and their density.

The regional APHIS cooperative control programs for rangeland grasshoppers traditionally required an average density of $8/yd^2$ ($9.6/m^2$) as the guideline to activate liquid insecticide control treatments. Some of the treatment costs were greater than the value of the forage saved (Onsager 1984). The density count of the grasshopper population alone does not give a valid number for the quantity of forage losses (Hewitt, Burleson, and Onsager 1976). A quantitative assessment of grasshopper caused forage losses needed to be developed to determine the amount of forage destroyed, both the forage consumed along with the forage clipped and let fall to the ground, by each individual grasshopper species (Hewitt, Burleson, and Onsager 1976). The quantity of forage consumed and destroyed by grasshoppers is difficult to determine and is highly variable because of grasshopper species composition, stage of development, and rate of survival (Onsager 1984).

The standard amount of forage destroyed (consumed and wasted) by nymphs was determined from field data collected for *Amphitorus coloradus* and *Camnula pellucida* nymphs from hatching to the adult stage. The total quantity of forage destroyed by the nymphs was divided by the mean total adult dry weight to obtain a nymphal feeding ratio of 4.5 (Hewitt and Onsager 1982a). The standard amount of forage destroyed per day by adults was determined from field data collected for *Melanoplus sanguinipe*s, *Melanoplus infantilis*, *Melanoplus foedus*, and *Aulocara elliotti*. The quantity of forage destroyed per day by the adults was divided by the average dry weight of the adults to obtain the mean adult feeding ratio of 0.65 (Hewitt and Onsager 1982a).

Forage losses (consumed and destroyed) are directly proportional to grasshopper size (Hewitt and Onsager 1982a). Grasshopper species can be divided into 3 size classes using two criteria: the **small size** grasshopper has mean male-female dry weight at less than 65 mg, and female dry weight at less than 100 mg; the **medium size** grasshopper has mean male-female dry weight between 66 mg and 120 mg, and female dry weight from 100 mg to 200 mg; and the **large size** grasshopper has mean male-female dry weight at greater than 120 mg, and female dry weight at greater than 200 mg.

Grasshoppers have 6 stages of development with 5 nymphal instar stages and the adult stage. Because of differences in size, each of the development stages consumes and destroys different amounts of forage. Each immature instar stage requires 7 to 10 days for development; with 5 instar stages, the nymphal period is usually 35 to 50 days long. The first 3 instar stages are responsible for about 15%-20% of the total forage loss caused by a generation of grasshoppers (Onsager 1984). The greatest forage loss occurs during the 4th and 5th instar stages and the adult stage (Hewitt and Onsager 1982a). The period of development during the 4th and 5th instar stages has usually been 7 days each (Hewitt and Onsager 1982a, 1983; Onsager 1987). After fledging, the adult grasshoppers become sexually mature in 10 to 14 days (Hewitt and Onsager 1983). The average life span of a grasshopper is 46 days (Hewitt and Onsager 1982a). The longevity of adult grasshoppers is highly variable from 32 days (Hewitt and Onsager 1982a), to 77 days (Hewitt and Onsager 1983), and up to 90 days (Onsager 1983, 1984). The maximum grasshopper longevity from hatch to death can be 109 days (Onsager 1983), 112 days (Hewitt and Onsager 1983), or 135 days (Onsager 1984).

Grasshopper species within multispecies populations have different mortality rates (Onsager 1987). Grasshoppers with daily survival rates between 0.95 and 0.96 will be able to maintain populations with only slight changes from season to season. Grasshoppers with survival rates of 0.93 or lower would have sharp reductions in their populations. Grasshoppers with daily survival rates of 0.97 or greater would have population growth and could reach outbreak levels within a minimum of two generations (Onsager 1983). The mortality rates for grasshopper species per year in natural populations have wide ranges from 2% to 13% for nymphs and from 3% to 40% for adults (Onsager 1987).

The quantity of grasshopper caused forage loss can be determined for each species from the dry weights of the 4th and 5th instar stages and the mean male-female dry weight of the adult stage (Hewitt and Onsager 1982a), or by the separate adult dry weight of the males and the females. A method that calculates forage losses caused by grasshoppers has been developed by Hewitt and Onsager (1982a). The method determines the forage loss during the 4th and 5th instar stages for 7 days each and during the adult stage for 32 days. The total forage loss for 46 days or the mean forage loss per day (mg/d) are the methods products. An addition step can be performed that converts the forage loss per day (mg/d) into pounds of forage loss per acre per month (lbs/ac/mo) for one grasshopper per square yard ($1/yd^2$) over one acre (table 9).

Forage loss caused by the pestiferous rangeland grasshoppers in the Northern Plains in milligrams per day (mg/d) and pounds per acre per month (lbs/ac/mo) have been determined (table 10). The mean milligrams per day forage loss was 27.4 mg/d, 53.11 mg/d, and 99.76 mg/d for the small, medium, and large grasshoppers, respectively (table 10). The mean pounds per acre per month forage loss was 8.92 lbs/ac/mo, 17.28 lbs/ac/mo, and 32.46 lbs/ac/mo for the small, medium, and large grasshoppers, respectively (table 10).

The forage loss amount in pounds per acre per month (lbs/ac/mo) for each grasshopper species from table 10 can be multiplied by various grasshopper densities to determine the greater quantities of forage losses as the population increases. In addition, the mean forage loss per day (mg/d) for the adults of each grasshopper species (step C, table 9) can be converted into pounds of forage loss per acre per month (lbs/ac/mo) (step E). This forage loss in pounds per acre per month for just the adults can be added to the forage loss for the 4th and 5th instar stages and the adult stage to determine the combined total forage loss during 2 or 3 months (61 days or 92 days) for a grasshopper density of one per square yard over one acre. To determine the greater quantities of forage losses as the population increases, the 2 and 3 month forage loss values for 1 grasshopper can be multiplied by various other grasshopper densities.

Rather than make these forage loss calculations for each of the 400 rangeland grasshopper species in North America, rangeland entomologists have chosen to develop a theoretical average rangeland grasshopper (Hewitt and Onsager 1982a, 1983; Onsager 1984, 1987). The quantity of forage losses caused by the theoretical average grasshopper can be used to estimate the economic significance of any grasshopper infestation, of any density, on any grasshopper habitat (Onsager 1987).

The average rangeland grasshopper infestation has been comprised of 40% small size, 55% medium size, and 5% large size grasshoppers (Hewitt and Onsager 1982a). A composite average grasshopper was developed with the data from the small size grasshoppers, *Ageneotettix deorum* and *Melanoplus infantilis*; the medium size grasshoppers, *Aulocara elliotti* and *Melanoplus sanguinipes*; and the large size grasshopper, *Melanoplus bivittatus* (Onsager 1984).

The composited theoretical average rangeland grasshopper consists of 40% small size, 55% medium size, and 5% large size grasshopper. The average dry weight of the 4th instar, 5th instar, and mean male-female adult is 19.2 mg, 45.3 mg, and 81.6 mg, respectively, and the quantity of forage consumed and destroyed is 9 mg, 22 mg, and 53 mg per day, respectively (Onsager 1984). The amount of forage consumed and wasted by grasshoppers tends to increase with the increasing stages of development (Hewitt and Onsager 1983). The daily rate of forage loss per average grasshopper increases 2.42 times with each successive instar (Onsager 1983).

The forage loss (consumed and destroyed) caused by the average rangeland grasshopper can be calculated by the steps of the forage loss method developed by Hewitt and Onsager (1982a) and explained in detail by Onsager (1983, 1984, 1987) (table 9). The average grasshopper 4th instar stage dry weight is 19.2 mg and in 7 days it destroys 79.49 mg of forage (step A). The average grasshopper 5th instar stage dry weight is 45.3 mg and in 7 days it destroys 156.96 mg of forage (step B). The average grasshopper adult stage dry weight is 81.6 mg and in 32 days it destroys 1697.28 mg of forage at a rate of 53 mg/d (step C). The average grasshopper destroys 79.49 mg as a 4th instar, destroys 156.96 mg as a 5th instar, and destroys 1697.28 mg as an adult for a total of 1933.73 mg of forage destroyed in 46 days at an average rate of 42.04 mg of forage loss per day (step D). The average forage loss of 42.04 mg/d converts into an average forage loss of 13.7 lbs/ac/mo (step E). Which means that one grasshopper at a density of $1/yd^2$ over 1 acre destroys an average of 13.7 pounds of forage per acre per month. Economic value of the annual forage loss caused by grasshoppers is used to determine cost-benefit ratio for the chemical insecticide treatment costs.

The average adult grasshopper can live for 1 or 2 additional months (Onsager 1983, 1984). The forage loss during these 1 or 2 additional months can be calculated from the average adult grasshopper forage loss of 53 mg/d. The average forage loss of 53 mg/d converts into an average forage loss of 17.25 lbs/ac/mo (step E). The average rangeland grasshopper destroys forage during the first month at 13.7 lbs/ac/mo, destroys forage during the second month at 17.25 lbs/ac/mo, and destroys forage during the third month at 17.25 lbs/ac/mo with the total quantity of forage destroyed after two months of 30.95 lbs/ac, and with the total quantity of forage destroyed after three months of 48.2 lbs/ac by 1 grasshopper per square yard on one acre. The greater quantities of forage loss caused by increasing populations can be determined by multiplying the forage loss in lbs/ac/mo for $1/yd^2$ density by other grasshopper densities. The average grasshopper at densities of $4/yd^2$ causes forage losses of 123.8 lbs/ac after two months and 192.8 lbs/ac after three months. The average grasshopper at densities of $8/yd^2$ causes forage losses of 247.6 lbs/ac after two months and 385.6 lbs/ac after three months. Rangeland forage allocation for a 1000 pound cow with a calf is 793 pounds per month.

Grasshopper Ecosystem Degradation

The losses caused by grasshopper feeding should not be evaluated only in terms of the quantity of forage consumed and destroyed. The green leaf material cut and discarded by feeding grasshoppers is not beneficial litter; the loss of this photosynthetically active tissue causes debilitating changes in growing grass tillers. Grasshopper defoliation adversely affects grass plant growth and development. The reductions of grass photosynthetic area decreases herbage biomass production causing reductions in total weight of the leaves, crowns, roots, and rhizomes, decreasing the root depth, and greatly reducing the number of secondary tillers produced (Burleson and Hewitt 1982).

The severity of the detrimental effects on grass plants from grasshopper defoliation will depend on the degree of foliage removal and the phenological growth stage of the grass tillers. The primary period of growth in grass leaf and flower stalk height and the accumulation in aboveground herbage weight occurs during the remarkably short period of May, June, and July, which coincides with the period of greatest precipitation, at 51% of the annual quantity. Cool season grasses complete 100% of their growth in leaf and flower stalk height by 30 July. Warm season grasses complete 100% of their growth in leaf height and 91% of their growth in flower stalk height by 30 July; a small amount of flower stalk elongation continues until 30 August (Goetz 1963). Peak aboveground herbage biomass is reached during the last 10 days of July. After the end of July, herbage weight decreases because the rate of senescence of the grass leaves exceeds the rate of growth (Manske 2000a).

Grass plants that have flowered and reached their maximum leaf and flower stalk height can tolerate removal of up to 50% of the aboveground plant material. Severe defoliation by large grasshopper infestations that remove greater than 50% of the leaf material results in insufficient leaf area retained on the tiller for even partial foliage recovery using current photosynthetic assimilates. Tillers with 50% or more of the aboveground leaf material removed reduce root growth, root respiration, and root nutrient absorption (Crider 1955). Root mortality and decomposition begin within 2 days of severe leaf defoliation (Oswalt et al. 1959). There is a high biological cost to the tiller when the photosynthetic system needs to be replaced from stored carbohydrates (Briske and Richards 1995). This reduction in efficiency results in reduced root growth, decreased tiller development, and low growth rates causing decreased tiller numbers, reduced total basal area, and reduced quantites of herbage biomass produced (Coyne et al. 1995).

Prior to peak herbage biomass, grass plants cannot tolerate defoliation of 50% of the aboveground herbage biomass because removal of that much leaf material deprives tillers of foliage needed for photosynthesis. Grass tillers at phenological growth between the 3.5 new leaf stage and flower (anthesis) stage do well with partial defoliation that removes 25% to 33% of the leaf material. Defoliation that removes 50% of the leaf material after the 3.5 new leaf stage and before the flower stage suppresses secondary tiller development 52.9% below nondefoliated tillers (Manske 2003) and replacement leaf weight is 29.2% less than the weight of the leaf material removed (Manske 2000b).

Grasshopper defoliation of grass tillers prior to the 3.5 new leaf stage is devastating to grass tiller growth and development. Spring growth of grass tillers depends both on carbohydrate reserves and on photosynthetic products from the portions of previous years leaves that overwintered without cell wall rupture and regreened with chlorophyll. Grass growth requires that the tiller maintains adequate leaf area with a combination of carryover leaves and new leaves to provide photosynthetic product for growth of sequential new leaves until the tiller produces 3.5 new leaves. Little spring leaf growth is produced from stored nonstructural carbohydrates because most of the reserves are reduced during the winter respiration period (Coyne et al. 1995). After the 3.5 new leaf stage, the new leaves provide adequate photosynthetic product for subsequent new leaf growth (Manske 2011b).

The critical grass tiller development period prior to the 3.5 new leaf stage for cool and warm season native grasses occurs during 15 May to 21 June. Native grass species do not reach the 3.5 new leaf stage at the same time. Some early native cool season grasses produce the 3.5 new leaf by early June and most native warm season grasses produce the 3.5 new leaf by 21 June.

Several rangeland grasshoppers of the Northern Plains have developmental phenology that overlap with the critical grass tiller development period (table 11). The hatching period of these ecosystem degrading pestiferous grasshoppers is with the very early and early groups starting in late April to mid May. All of these grasshoppers have fledged into the adult stage before the end of the critical grass tiller period (table 11).

During the 38 day critical grass tiller period, the 4th and 5th instar and adult stages of these pestiferous grasshoppers, at densities of 1/yd^2 over 1 acre, consume and destroy an average of 9.5 lbs/ac of grass leaves (table 12). At densities of 8/yd^2 over 1 acre, these grasshoppers would consume and destroy an average of 76.2 lbs/ac of grass leaves.

Premature grasshopper defoliation of grass tillers before production of the 3.5 new leaf could result in greatly reduced growth rates of herbage production (Coyne et al. 1995) causing decreased peak herbage biomass late in the growing season with possible reductions of 45% to more than 75% of the potential herbage biomass (Campbell 1952, Rogler et al. 1962, Manske 2000b).

Ecosystem degradation does not occur instantaneously and usually does not show significant differences for 2 to 3 years after initiation. Grasshoppers that increase to moderate outbreak levels, hatch very early and early, and develop through the 4th and 5th instar stages and adult stage during periods when grass growth is rapid and when soils usually have adequate water consume and destroy leaves of grass tillers before they develop 3.5 new leaves cause ecosystem degradation. Ecosystem degradation results in long term economic losses.

Table 9. Methods to determine forage loss from pestiferous rangeland grasshoppers.

The forage loss methods were developed by Hewitt and Onsager 1982a.

The quantity of forage loss as milligrams per day (mg/d) and pounds per acre per month (lbs/ac/mo) caused by 1 grasshopper is based on mean grasshopper dry weight in milligrams (mg) at the 4^{th} instar for 7 days, the 5^{th} instar for 7 days, and the adult stage of male, female, or mean of both for 32 days.

A. Grasshopper 4^{th} instar dry weight (mg) X 4.5 feeding ratio X 0.92 mortality rate = forage loss (mg) for 7 days.

B. Grasshopper 5^{th} instar dry weight (mg) X 4.5 feeding ratio X 0.77 mortality rate = forage loss (mg) for 7 days.

C. Adult grasshopper dry weight (mg) for male, female, or mean of both X 0.65 feeding ratio = forage loss (mg) per day X 32 days = total forage loss from adult for 32 days.

D. 4^{th} instar forage loss for 7 days + 5^{th} instar forage loss for 7 days + adult forage loss for 32 days = total forage loss by 1 grasshopper for 46 days ÷ 46 days = mean forage loss by 1 grasshopper for 1 day in milligrams per day (mg/d).

Conversion of forage loss from 1 grasshopper in milligrams per day (mg/d) into forage loss in pounds per acre per month (lbs/ac/mo) from a population density of 1 grasshopper per square yard ($1/yd^2$) over an area of 1 acre for a period of 1 month with 30.5 days.

E. Forage loss in mg/d from 1 grasshopper X 4840.0 yd^2/ac ÷ 1000 mg/g X 0.03527 oz/g X 0.0625 oz/lb X 30.5 d/mo = forage loss from 1 grasshopper per square yard per acre ($1/yd^2/ac$) in pounds per acer per month (lb/ac/mo).

Methods from Hewitt and Onsager 1982a, Onsager 1983, 1984, 1987.
30.5 days per grazing season month from Manske 2012a.

Table 10. Forage loss from pestiferous rangeland grasshoppers (one/yd^2) in mg/d and lbs/ac/mo based on mean grasshopper dry weight (mg).

Pestiferous Rangeland Grasshoppers	Sex	Mean dry weight (mg) for one grasshopper			Forage consumed & destroyed by one grasshopper/yd^2	
		4th instar	5th instar	Adult	mg/d	lbs/ac/mo
Small size grasshoppers with females at < 100 mg						
Aeropedellus clavatus	mean	10.7	22.2	45.8	23.34	7.60
Ageneotettix deorum	mean	11.8	27.4	60.0	30.26	9.85
	male			31.0	17.14	5.58
	female			89.0	43.37	14.11
Amphitornus coloradus	mean	19.3	38.0	60.5	31.96	10.40
	male			41.0	22.85	7.44
	female			80.0	40.77	13.27
Cordillacris occipitalis	mean	10.6	12.7	48.5	23.84	7.76
	male			30.0	15.48	5.04
	female			67.0	32.21	10.48
Melanoplus infantilis	mean	12.5	28.1	58.0	29.47	9.59
	male			53.0	27.21	8.85
	female			63.0	31.72	10.32
Opeia obscura	mean	10.6	12.7	34.5	17.51	5.70
	male			21.0	11.41	3.71
	female			48.0	23.62	7.69
Phlibostroma quadrimaculatum	mean	14.0	20.6	62.5	31.07	10.11
	male			35.0	18.64	6.07
	female			90.0	43.51	14.16
Trachyrhachys kiowa	mean	18.8	26.7	62.0	31.74	10.33
	male			44.0	23.60	7.68
	female			80.0	39.88	12.98

Table 10 cont. Forage loss from pestiferous rangeland grasshoppers (one/yd^2) in mg/d and lbs/ac/mo based on mean grasshopper dry weight (mg).

Pestiferous Rangeland Grasshoppers	Sex	Mean dry weight (mg) for one grasshopper			Forage consumed & destroyed by one grasshopper/yd^2	
		4th instar	5th instar	Adult	mg/d	lbs/ac/mo
Medium size grasshoppers with females at 100 mg to 200 mg						
Aulocara elliotti	mean	20.4	45.6	98.0	49.58	16.13
	male			52.0	28.78	9.37
	female			144.0	70.38	22.90
Aulocara femoratum	mean	20.4	45.6	89.5	45.74	14.88
	male			42.0	24.26	7.89
	female			137.0	67.22	21.87
Camnula pellucida	mean	20.4	45.6	80.0	41.44	13.48
	male			55.0	30.14	9.81
	female			105.0	52.75	17.17
Encoptolophus costalis	mean	22.9	67.9	92.5	49.00	15.95
	male			50.0	29.78	9.69
	female			135.0	68.22	22.20
Eritettix simplex	mean	20.4	45.6	71.5	37.60	12.24
	male			33.0	20.19	6.57
	female			110.0	55.01	17.90
Melanoplus confusus	mean	18.4	37.6	117.2	57.48	18.70
Melanoplus femurrubrum	mean	22.7	83.7	106.5	56.50	18.39
	male			87.0	47.69	15.52
	female			126.0	65.32	21.26
Melanoplus gladstoni	mean	36.1	62.0	130.5	66.93	21.78
	male			127.0	65.35	21.27
	female			134.0	68.51	22.29

Table 10 cont. Forage loss from pestiferous rangeland grasshoppers (one/yd^2) in mg/d and lbs/ac/mo based on mean grasshopper dry weight (mg).

Pestiferous Rangeland Grasshoppers	Sex	Mean dry weight (mg) for one grasshopper			Forage consumed & destroyed by one grasshopper/yd^2	
		4th instar	5th instar	Adult	mg/d	lbs/ac/mo
Melanoplus occidentalis	mean	19.2	31.8	130.0	62.91	20.47
	male			86.0	43.01	14.00
	female			174.0	82.80	26.94
Melanoplus sanguinipes	mean	22.9	52.0	131.5	65.44	21.29
	male			112.0	56.62	18.42
	female			151.0	74.26	24.16
Phoetaliotes nebrascensis	mean	23.8	56.4	100.0	51.61	16.79
	male			63.0	34.88	11.35
	female			137.0	68.34	22.24
Large size grasshoppers with females at > 200 mg						
Melanoplus bivittatus	mean	47.6	147.2	253.5	129.99	42.30
	male			166.0	90.43	29.43
	female			341.0	169.56	55.18
Melanoplus differentialis	mean			no data		
Melanoplus packardii	mean	35.4	93.1	174.5	89.10	28.99
	male			141.0	73.96	24.07
	female			208.0	104.25	33.92
Metator pardalinus	mean	22.4	38.7	166.5	80.20	26.10
	male			97.0	48.78	15.87
	female			236.0	111.63	36.33

Dry weight of 4th and 5th instar from Hewitt and Onsager 1982a.
Dry weight of adult male and female from Pfadt 1994.
Methods follow Hewitt and Onsager 1982a and shown in table 9.

Table 11. Pestiferous rangeland grasshopper developmental phenology overlap with cool and warm season grass critical development period prior to 3.5 new leaf stage during 15 May to 21 June.

Pestiferous Rangeland Grasshoppers	Grasshopper Developmental Phenology
Aeropedellus clavatus, Clubhorned Grasshopper,	hatch in early May, develop rapidly through the 3rd instar stage, are in the 4th/5th instar stage for 7 days, and are in the adult stage for 23 days during the critical grass period.
Aulocara elliotti, Bigheaded Grasshopper,	hatch in mid May, develop through the 1st, 2nd, and 3rd instar stages, are in the 4th/5th instar stage for 10 days, and are in the adult stage for 6 days during the critical grass period.
Cordillacris occipitalis, Spottedwinged Grasshopper,	hatch in mid May, develop through the 1st, 2nd, and 3rd instar stages, are in the 4th instar stage for 7 days, are in the 5th instar stage for 7 days, and are in the adult stage for 2 days during the critical grass period.
Eritettix simplex, Velvetstriped Grasshopper,	overwinter in a late instar stage and are in the adult stage for 38 days during the critical grass period.
Melanoplus confusus, Pasture Grasshopper,	hatch in late April, are in the late 4th instar stage for 4 days, are in the 5th instar stage for 7 days, and are in the adult stage for 27 days during the critical grass period.
Melanoplus infantilis, Little Spurthroated Grasshopper,	hatch in late May, develop rapidly through the 1st, 2nd, and 3rd instar stages, are in the 4th instar stage for 5 days, are in the 5th instar stage for 5 days, and are in the adult stage for 8 days during the critical grass period.
Melanoplus occidentalis, Flabellate Grasshopper,	hatch in mid May, develop through the 1st, 2nd, and 3rd instar stages, are in the 4th instar stage for 7 days, are in the 5th instar stage for 7 days, and are in the adult stage for 2 days during the critical grass period.

Table 12. Leaf weight loss (mg and lb/ac) during the critial 38 day period, 15 May to 21 June, of grass tiller development prior to 3.5 new leaf stage from pestiferous rangeland grasshoppers at a density of one/yd^2.

Pestiferous Rangeland Grasshoppers		4th instar		5th instar	Adult	Total	lb/ac/d
Aeropedellus clavatus	days		7		23	30	
	dry wt		22.2		45.8		
	mg		76.92		684.71	761.63	
	lb/ac		0.82		7.31	8.13	0.27
Aulocara elliotti	days		10		6	16	
	dry wt		33.0		98.0		
	mg		126.23		382.20	508.43	
	lb/ac		1.35		4.08	5.43	0.39
Cordillacris occipitalis	days	7		7	2	16	
	dry wt	10.6		12.7	48.5		
	mg	43.88		44.01	63.05	150.94	
	lb/ac	0.47		0.47	0.67	1.61	0.10
Eritettix simplex	days				38	38	
	dry wt				71.5		
	mg				1766.05	1766.05	
	lb/ac				18.84	18.84	0.50
Melanoplus confusus	days	4		7	27	38	
	dry wt	18.4		37.6	117.2		
	mg	63.76		130.28	2056.86	2250.90	
	lb/ac	0.68		1.39	21.94	24.01	0.63
Melanoplus infantilis	days	5		5	8	18	
	dry wt	12.5		28.1	58.0		
	mg	51.75		97.37	301.60	450.72	
	lb/ac	0.55		1.04	3.22	4.81	0.27
Melanoplus occidentalis	days	7		7	2	16	
	dry wt	19.2		31.8	130.0		
	mg	79.49		110.19	169.00	358.68	
	lb/ac	0.85		1.18	1.80	3.83	0.24

Dry weight of 4th and 5th instar from Hewitt and Onsager 1982a.
Dry weight of mean adult from Pfadt 1994.
Methods follow Hewitt and Onsager 1982a and shown in table 9.

Native Vegetation of the Northern Plains

The Northern Plains are part of the North American Interior Plains that extend from the foot of the Rocky Mountains eastward to the Canadian Shield and Appalachian Provinces and extend from the Athabasca River on the Alberta Plateau southward to the Gulf Coastal Plains (Fenneman 1931, 1946; Hunt 1974; Goodin and Northington 1985). The Interior Plains are divided east and west into the Great Plains and the Central Lowland Physiographic Provinces (Fenneman 1931, 1946). The Northern Plains are separated from the Southern Plains by the North Platte-Platte-Missouri River Valleys (Raisz 1957). The portions of the Great Plains and Central Lowland Provinces that exist in the Northern Plains are separated in North and South Dakota and Saskatchewan by an eroded east facing escarpment at the eastern extent of the Tertiary sedimentary deposits of material eroded from the Rocky Mountains that form a fluvial plain overlaying the Cretaceous bedrock (Hunt 1974). The surface landform feature that shows the location of this boundary is the east escarpment of the Missouri Coteau (Finneman 1931). In eastern Nebraska, the separation of the Great Plains and Central Lowland Provinces is the western limit of older pre-Wisconsin glacial drift which has a mantle of loess (wind deposited silt) (Fenneman 1931).

The Northern Plains has a continental climate with cold winters and hot summers. Mean air temperatures increase from north to south changing from about 35° - 40° F (1.7° - 4.4° C) in the north to about 48° - 51° F (8.9° - 10.6° C) in the south. Most of the precipitation occurs during the early portion of the growing season. Total annual precipitation fluctuates greatly from year to year. Periods of water deficiency during the growing season occur more frequently than growing seasons without deficiencies. Drought conditions are common. Mean annual precipitation increases from west to east and increases from north to south. In the northern portion, precipitation ranges from about 12 inches (304.8 mm) in the west to about 24 inches (609.6 mm) in the east. In the southern portion, precipitation ranges from about 14 inches (355.6 mm) in the west to about 32 inches (812.8 mm) in the east.

Evapotranspiration affects the quantity of moisture in the soil and the duration infiltrated water remains available for plant growth. The potential evapotranspiration for most of the Northern Plains is greater than annual precipitation. Potential evapotranspiration demand increases from north to south, and increases from east to west. Along the eastern edge of the Northern Plains, the precipitation is greater than potential evapotranspiration during most years. The region also has several local areas where the combination of stored soil water, precipitation, plus water runin is greater than evapotranspiration. Subirrigated soils where the rooting zone is moist for most of the growing season would be comparable to conditions with greater precipitation than evapotranspiration.

Soil development is effected by climate, parent material, topography, living organisms, and time (Brady 1974). The main climatic factors that affect soil development are temperature and precipitation. Climate determines the type and rate of weathering that occurs. The rates of biogeochemical processes in soil are effected by soil temperature and soil moisture. Climate determines the type of native vegetation and the quantity of biomass production. There is a relationship between the type of native vegetation and the kind of soil that develops. Increases in soil moisture, increase the biomass production and tend to increase organic content of soils. Increases in soil temperature, increase the rate of decomposition and tend to decrease organic content of soils (Brady 1974).

Classification of soils into principal suborders is based on differences caused by climate and associated native vegetation. The biological processes in soil are effected by soil temperature and soil moisture. The different climatic characteristics important in soil development are separated into specific soil temperature regimes and soil moisture regimes.

The Northern Plains has two soil temperature regimes based on mean annual soil temperature. The mean annual soil temperature is considered to be the mean annual air temperature plus 1.8° F (1° C) (Soil Survey Staff 1975). The Frigid soil temperature regime has mean annual soil temperatures of less than 47° F (8° C). The Mesic soil temperature regime has mean annual soil temperatures higher than 47° F (8° C) and lower than 59° F (15° C) (Soil Survey Staff 1975). The separation between the Frigid and Mesic soil temperature regimes occurs along a wide irregular belt that extends eastward from central Wyoming along its north border with Montana and continues to north central South Dakota just south of its north border with North Dakota, then extends at a southeasterly diagonal to about the center of South Dakota's east border with Minnesota, and then extends at a northeasterly angle to the boundary of the Oak Forest.

Soil moisture regimes are based on the soil moisture conditions in the soil. The Northern Plains has four north-south zones of soil moisture regimes that increase in soil moisture from west to east. The soils in the Aridic and Torric soil moisture regime, typically of arid climates, are dry in all parts for more than half the time and the soils are never moist for as long as 90 days during the growing season (Soil Survey Staff 1975). The soils in the Ustic soil moisture regime, typically of semi arid climates, are dry in some or all parts for 90 or more days in most years, but not dry in all parts for more than half the time, and are not dry for as long as 45 days during the 4 months that follow the summer solstice in 6 or more years out of 10 years (Soil Survey Staff 1975). The soils in the Udic soil moisture regime, typically of sub humid climates, are not dry for as long as 90 days. During the summer, the amount of stored moisture plus rainfall is approximately equal to or exceeds the amount of evapotranspiration (Soil Survey Staff 1975). The soils in the Perudic soil moisture regime, typically of humid climates, are rarely dry. During the summer, the precipitation is greater than the evapotranspiration (Soil Survey Staff 1975).

The combination of four soil moisture regimes (Aridic, Ustic, Udic, and Perudic) and two soil temperature regimes (Frigid and Mesic) results in eight distinct soil moisture-temperature regimes in the Northern Plains. The soils in the Aridic-Frigid soil moisture-temperature regime are primarily Aridic Borolls (arid cool Mollisols) and Torriorthents (hot dry recently eroded medium to fine textured Entisols) and support vegetation of short grasses with some mid grasses. The soils in the Ustic-Frigid soil moisture-temperature regime are primarily Typic Borolls (semi arid cool Mollisols) and support vegetation of mid and short grasses. The soils in the Udic-Frigid soil moisture-temperature regime are primarily Udic Borolls (sub humid cool Mollisols) and support vegetation of mid grasses with some tall grasses. The soils in the Perudic-Frigid soil moisture-temperature regime are primarily Aquolls (humid cool Mollisols that are saturated and absent of oxygen at times for unknown lengths) and support vegetation of tall grasses. The soils in the Aridic-Mesic soil moisture-temperature regime are primarily Argids (arid warm Aridisols with thin horizons, dry for long periods, and have a clay layer) and Aridic Ustolls (arid warm Mollisols) and support vegetation of short grasses. The soils in the Ustic-Mesic soil moisture-temperature regime are primarily Ustipsamments (semi arid warm Entisols that are well sorted wind deposited sands) and Typic Ustolls (semi arid warm Mollisols) and support vegetation of mid and short grasses with lower topographic slopes supporting tall grasses. The soils in the Udic-Mesic soil moisture-temperature regime are primarily Udic Ustolls (sub humid warm Mollisols) and support vegetation of mid grasses and tall grasses. The soils in the Perudic-Mesic soil moisture-temperature regime are primarily Udolls (humid warm Mollisols that do not have a calcium carbonate layer) and support vegetation of tall grasses.

Development of plant communities and vegetation types is effected by the climatic characteristics of temperature, precipitation, and evapotranspiration demand; the soil characteristics of texture, structure, and chemical and mineral composition; and the landform topographic characteristics of slope, aspect, and elevation. Vegetation of the Northern Plains separates into 10 grassland vegetation types and 7 grassland with woodland or forest vegetation types. The vegetation of the Northern Plains map (figure 1) developed by Dr. W.C. Whitman (Barker and Whitman 1989) is a compilation of information from several sources supplementary to the basic map of potential natural vegetation by Kuchler (1964). Modifications to vegetation type designations, distributions, and boundaries were conflated into the base map from state vegetation maps for Montana (Ross and Hunter 1976, Hacker and Sparks 1977), Nebraska (Kaul 1975, Bose 1977), North Dakota (Shaver 1977), South Dakota (Baumberger 1977), and Wyoming (Shrader 1977). Vegetation type designations and distributions from scientific papers were added for Canada (Clarke, Campbell, and Campbell 1942; Moss and Campbell 1947; Coupland and Brayshaw 1953; Coupland 1950, 1961). A new concept of a plains rough fescue mixture along a portion of the northern border of North Dakota was introduced to the map details by Whitman and Barker (1989).

No living plant species are known to have originated in the Northern Plains. All plant species considered to be native to the Northern Plains originated and developed in other regions and sometime later migrated into the Northern Plains. The plant communities and vegetation types, however, are relatively young and began development in place about 5,000 years ago when the current climate with cycles of wet and dry periods began.

The Tall Grass Prairie, Bluestem-Switchgrass-Indiangrass Type, exists on the eastern margin of the Northern Plains Grasslands and extends from southern Manitoba through eastern North and South Dakota and western Minnesota southward into northwestern Iowa and northeastern Nebraska to the Platte River. The physiography of the region consists of the Manitoba Plain and the Red River Valley Plain of the Small Lakes Section and extends into the Dissected Till Plains Section of the Central Lowland Province. The climate is humid with evapotranspiration lower than precipitation. The soil moisture regime is Perudic and the soil temperature regime is Frigid in the north and Mesic in the south. The soils are primarily Aquolls in the north and Udolls in the south.

The Transition Mixed Grass Prairie, Wheatgrass-Bluestem-Needlegrass Type (figure 1), exists between the Tall Grass Prairie on the east and the Mixed Grass Prairie on the west and extends from east central Saskatchewan and southwestern Manitoba through east central North and South Dakota and east central Nebraska to the Platte River. The physiography of the region consists of the Saskatchewan Plain and the Glaciated Plains (Drift Prairie) of the Small Lakes Section of the Central Lowland Province and extends into the eastern portion of the High Plains Section of the Great Plains Province. The climate is sub humid with evapotranspiration greater than precipitation over most of the area except for subirrigated soils and topographic slope positions with water runin. The soil moisture regime is Udic and the soil temperature regime is Frigid in the north and Mesic in the south. The soils are primarily Udic Borolls in the north and Udic Ustolls in the south.

The Mixed Grass Prairie has a high mid grass component with some short grasses and some tall grasses present and is separated into three vegetation types based on differences resulting from soil texture and soil temperature regime.

The Mixed Grass Prairie, Wheatgrass-Needlegrass Type (figure 1), exists on semi arid cool soils between the Transition Mixed Grass Prairie on the east and the Short Grass Prairie on the west and extends from mid Saskatchewan through western North Dakota and eastern Montana to north central and northwestern South Dakota. The physiography of the region consists of the eastern portions of the Glaciated and Unglaciated sections of the Missouri Plateau Section, including the Alberta Plain, of the Great Plains Province. The climate is semi arid with evapotranspiration greater than precipitation. The soil moisture regime is Ustic and the soil temperature regime is Frigid. The soils are primarily Typic Borolls.

The Mixed Grass Prairie, Wheatgrass-Grama Type (figure 1), exists on semi arid warm clay soils south of the Wheatgrass-Needlegrass Type and is in southwestern South Dakota. The physiography of the region consists of the southeastern portion of the Unglaciated section of the Missouri Plateau Section of the Great Plains Province. The climate is semi arid with evapotranspiration greater than precipitation. The soil moisture regime is Ustic and the soil temperature regime is Mesic. The soils are primarily clay textured Typic Ustolls.

The Mixed Grass Prairie, Wheatgrass Type (figure 1), exists on semi arid warm dense clay soils south of the Wheatgrass-Needlegrass Type and is in northwestern South Dakota. The physiography of the region consists of the central portion of the Unglaciated section of the Missouri Plateau Section of the Great Plains Province. The climate is semi arid with evapotranspiration greater than precipitation. The soil moisture regime is Ustic and the soil temperature regime is Mesic. The soils are primarily dense clay textured Typic Ustolls.

The Northern Short Grass Prairie, Grama-Needlegrass-Wheatgrass Type (figure 1), exists on the western side of the Northern Plains Grasslands and extends from southeastern Alberta and southwestern Saskatchewan through central Montana and southward into northeastern Wyoming. The physiography of the region consists of the western portions of the Glaciated and Unglaciated sections of the Missouri Plateau Section of the Great Plains Province. The climate is arid with evapotranspiration greater than precipitation. The soil moisture regime is Aridic and the soil temperature regime is Frigid in the north and Mesic in the south. The soils are primarily Aridic Borolls and Torriorthents in the north and Argids and Aridic Ustolls in the south.

Dr. Whitman (Barker and Whitman 1989) continued the separation of this vegetation type from the Wheatgrass-Needlegrass Type because of the notable increase in the shortgrass component and the relative decrease of western wheatgrass and needle and thread. Cool-season grass species increase towards the northern portions and warm-season grass species increase towards the southern portions. The needlegrasses increase in the north. Blue grama and buffalograss increase in the south. Because of the presence of mid cool-season grasses, the Northern Shortgrass Prairie has sometimes been combined with the Northern Mixed Grass Prairie. However, these two vegetation types are distinct and should remain separated. The Grama-Needlegrass-Wheatgrass Type has the appearance of a shortgrass prairie and has an arid soil moisture regime, less soil horizon development, shallower soil depth to the accumulating soluble salts and developing argillic (clay) layer, shallower rooting depth, lower soil water holding capacity, greater evapotranspiration potential, and generally more xeric than the Wheatgrass-Needlegrass Type.

The Northern Short Grass Prairie, Saltgrass Type, exists on salt affected soils distributed in local areas across the Northern Short Grass Prairie region. Few plant species can tolerate the harsh environmental conditions of salt-affected areas. The tolerant species have mechanisms to exclude uptake of salts, or physiologically separate and discharge the undesired salts.

The Southern Short Grass Prairie, Blue grama-Buffalograss Type (figure 1), exists in northwestern Nebraska and extends into east central Wyoming north of the North Platte River. The physiography of the region consists of a small western portion of the High Plains Section of the Great Plains Province. The climate is arid with evapotranspiration greater than precipitation. The soil moisture regime is Aridic and the soil temperature regime is Mesic. The soils are primarily Argids and Aridic Ustolls.

The Sandhills Prairie, Bluestem-Sandreed-Grama-Needlegrass Type (figure 1), exists in the north central portion of Nebraska south of the Niobrara River and north of the Platte River. Other Sandhills Prairie areas exist scattered throughout the Northern Plains. Many areas are too small to map. A large area of Sandhills Prairie exists along the Sheyenne River in southeastern North Dakota and another large area exists near Swift Current, Saskatchewan. The physiography of the Nebraska Sandhills consists of the Sand Hills region of the High Plains Section of the Great Plains Province. The climate is semi arid with evapotranspiration greater than precipitation. The soil moisture regime is Ustic and the soil temperature regime is Mesic. The soils are primarily Ustipsamments.

The Foothills Prairie, Plains Rough Fescue Type (figure 1), exists as a fringe along the montane forest of the Rocky Mountain foothills from Alberta to south central Montana and along the aspen groveland and aspen parkland bordering the boreal forest zone in Alberta and Saskatchewan and the type mingles with the Wheatgrass-Bluestem-Needlegrass Type extending across Saskatchewan and southwestern Manitoba and into northern North Dakota. Plains Rough Fescue has continued to move south in the Transition Mixed Grass Prairie and the Mixed Grass Prairie of North Dakota. The physiography of the region consists of the northern portion of the Glaciated section of the Missouri Plateau Section of the Great Plains Province and the northern portion of the Small Lakes Section of the Central Lowland Province.

The Pacific Bunchgrass Prairie, Bluebunch-Fescue Type (figure 1), exists in the south central portion of Montana. Numerous other areas too small to map exist within the Great Plains. The physiography of the region consists of the Unglaciated section of the Missouri Plateau Section of the Great Plains Province.

The Badlands and River Breaks, Woody Draw and Savanna Types (figure 1), exist in central Montana along the Missouri and Musselshell Rivers, in western North Dakota along the Little Missouri River, and in southwestern South Dakota along the White River. The physiography of the region consists of the Unglaciated section of the Missouri Plateau Section of the Great Plains Province.

The Pine Savanna, Pine-Juniper-Bluebunch Type (figure 1), exists on rough uplands in south central and southeastern Montana, north central Wyoming, western South Dakota, and southwestern North Dakota. The physiography of the region is the Unglaciated section of the Missouri Plateau Section of the Great Plains Province.

The Black Hills Pine Forest, Pine-Spruce-Aspen Type (figure 1), exists in southwestern South Dakota and northeastern Wyoming. The physiography of the region consists of the Black Hills section of the Missouri Plateau Section of the Great Plains Province.

The Montane Forest, Pine-Fir-Spruce Type (figure 1), exists on the Sweetgrass Hills, and the Highwood, Bearpaw, Little Rocky, Moccasin, Judith, and Big Snowy mountains in Montana and the Cypress Hills in Saskatchewan. The physiography of the region consists of the laccolithic domed mountains in the Unglaciated section and the erosional upland remnant in the Glaciated section of the Missouri Plateau Section of the Great Plains Province.

The Upland Woodlands, Aspen-Ash-Oak-Juniper Types (figure 1), exist as scattered areas with various types of trees, shrubs, and grasses in North Dakota, Manitoba, and Saskatchewan. The physiography of the region consists of upland positions of the Small Lakes Section of the Central Lowland Province and of upland positions of the Unglaciated section of the Missouri Plateau Section of the Great Plains Province.

The Riparian Woodlands, Cottonwood-Ash-Elm Type (figure 1), exists along the floodplains of the larger rivers and streams and as small groves along minor drainage ways located throughout the Northern Plains.

The environmental and biological factors that affect development of plant communities and vegetation types are the same factors that affect soil development. The current climate with wet and dry periods, and the current soil moisture and soil temperature regimes have been operational for about 5,000 years. Soil moisture regimes affect distribution of plant species affiliations. The species affiliations that are the major vegetation types in the Northern Plains; Tall Grass Prairie, Transition Mixed Grass Prairie, Mixed Grass Prairie, and Short Grass Prairie; coincide with the four soil moisture regimes; Perudic, Udic, Ustic, and Aridic; respectively. The four soil moisture regimes are further separated into two soil temperature regimes; Frigid in the northern portions and Mesic in the southern portions. Soil temperature regimes affect composition and distribution of cool-season and warm-season grasses within the vegetation types. In the northern Frigid temperature regime, warm-season grass species decrease and cool-season grass species increase. In the southern Mesic temperature regime, cool-season grass species decrease and warm-season grass species increase.

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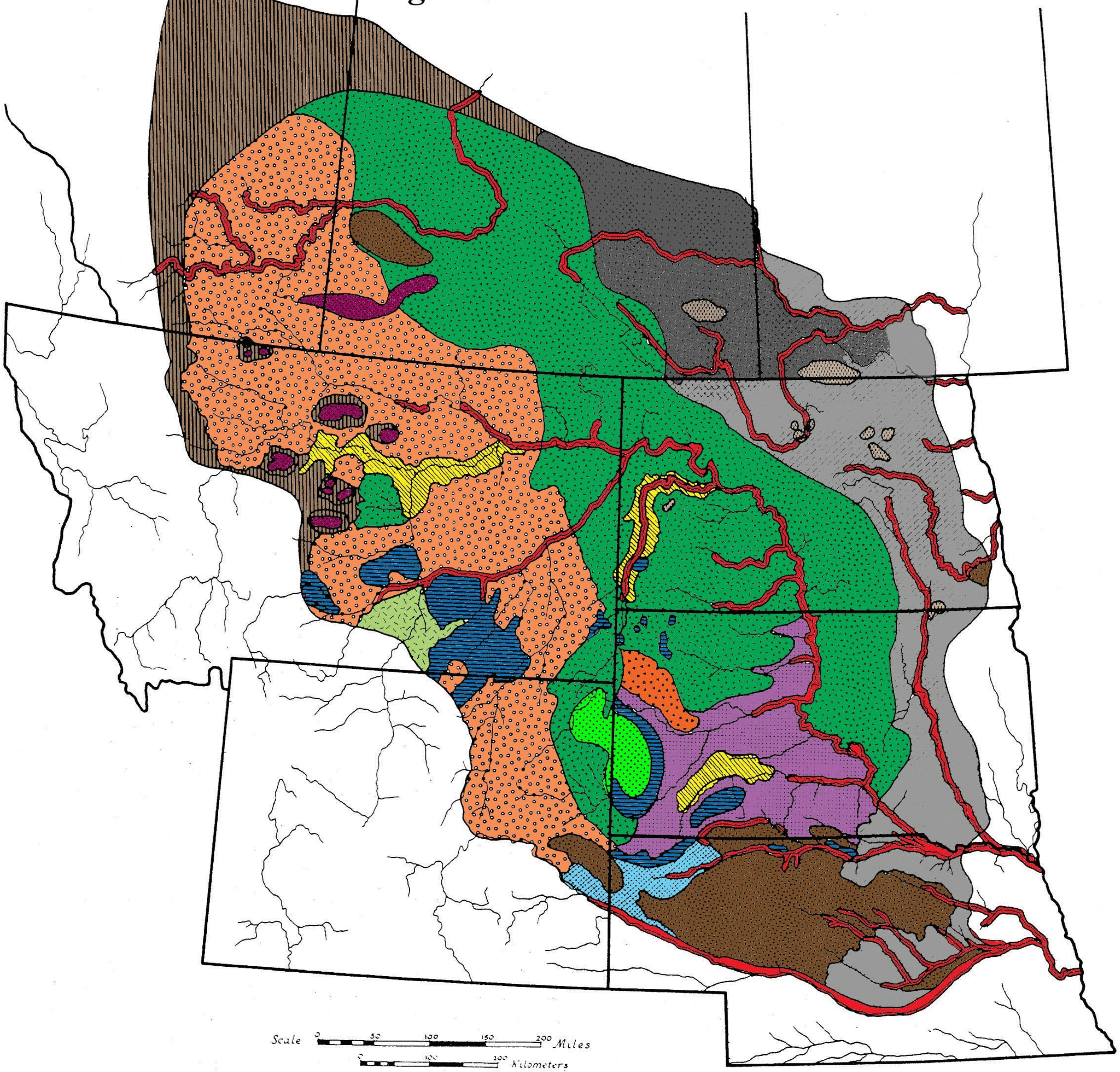
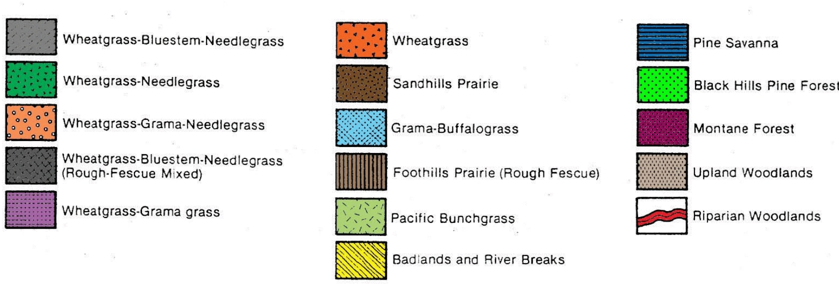
Vegetation of the Northern Plains



map from Barker and Whitman 1989



Ecosystem Mechanisms and Processes

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

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

Grass Tiller Growth

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

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

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

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

Grass tillers exhibit short shoot and long shoot strategies of stem elongation. Grasses with short shoots do not produce significant internode elongation during vegetative growth and the apical meristem remains below grazing or cutting height. Production of new leaf primordia continues until the apical meristem changes to reproductive status and developing leaves continue to expand until the flower stalk elongates (Dahl 1995). Grasses with long shoots elevate the apical meristem a short distance above ground level by internode elongation while still in the vegetative phase (Dahl 1995). After the apical meristem has changed from vegetative status, additional stem elongation occurs during the sexual reproductive phase. Grass species with long shoot tillers are nearly always decreased in pastures that are repeatedly grazed heavily (Branson 1953).

The flower bud primordia develop into the inflorescence, with the apical dome becoming the terminal spikelet. The first external evidence of flower stalk development is swelling of the enclosing sheath known as the "boot" stage. During the head emergence phenophase, 4 or 5 of the upper internodes, along with the attached leaf sheaths, elongate very rapidly by intercalary meristem cell development and the inflorescence reaches near maximum height. The flower (anthesis) phenophase occurs when the feathery stigmas (female parts) spread out and the anthers (male parts) are exposed (Langer 1972). Cool season grasses with the C_3 photosynthetic pathway are long day plants and reach the flower phenophase before 21 June during the period of increasing day length. Warm season grasses with the C_4 photosynthetic pathway are short day plants and reach the flower phenophase after 21 June during the period of decreasing day length and increasing night length (Weier et al. 1974, Leopold and Kriedemann 1975). The life cycle of a tiller with the apical meristem status changed to reproductive terminates during that growing season (Briske and Richards 1995).

Recruitment of new grass plants developed from seedlings is negligible in healthy grassland ecosystems. The frequency of true seedlings is extremely low in functioning grasslands, and establishment of seedlings occurs only during years with favorable moisture and temperature conditions (Wilson and Briske 1979, Briske and Richards 1995), in areas of reduced competition from vegetative tillers, and when resources are readily available to the growing seedling. Vegetative tiller growth is the dominant form of reproduction in semiarid and mesic grasslands (Belsky 1992, Chapman and Peat 1992, Briske and Richards 1995, Chapman 1996, Manske 1999a) not sexual reproduction and the development of seedlings.

Vegetative secondary tillers develop from lead tillers by the process of tillering. A vegetative tiller is a shoot derived from growth of an axillary bud (Dahl 1995) and is a complete unit with roots, stem, and leaves. All young tillers are dependent on the lead tiller for carbohydrates until they have developed their own root systems and mature leaves (Dahl 1995). After secondary tillers become independent, they remain in vascular connection with other tillers of the grass plant (Moser 1977, Dahl and Hyder 1977, Dahl 1995). There are two types of tillering: crown tillers and rhizome or stolon tillers. Crown tillers grow vertically close to the lead tiller and within the enveloping leaf sheath, and tend to have a tufted or bunch-type growth habit (Dahl and Hyder 1977, Dahl 1995). Rhizome tillers penetrate the enveloping leaf sheath and grow horizontally below the soil surface away from the lead tiller for a distance before beginning vertical growth. Rhizome growth may be either continuous, producing tillers at progressive intervals, or terminal, producing one tiller when the apex turns up and emerges from the soil (Dahl 1995). The rhizome type of tillering results in the spreading or creeping growth habit of sod-forming plants (Dahl and Hyder 1977, Dahl 1995). If the horizontal growth is aboveground, it is a stolon (Dahl 1995). Stolons have continuous growth and form tillers at progressive nodes (Dahl 1995). Grass plants can produce both crown tillers and rhizome tillers. Generally, one tiller growth type is produced by a grass species more than the other tiller type. However, the expressivity of tiller type can be influenced by several growth factors and environmental conditions, and can be manipulated by defoliation management (Manske 2011b).

Meristematic activity in axillary buds and the subsequent development of vegetative tillers is regulated by auxin, a growth-inhibiting hormone produced in the apical meristem and young developing leaves of lead tillers (Briske and Richards 1995). The physiological process by which the lead tiller exerts hormonal control over axillary bud growth is lead tiller (apical) dominance (Briske and Richards 1995). Tiller growth from axillary buds is inhibited indirectly by auxin, as the inhibiting hormone does not enter the axillary buds (Briske and Richards 1995). Auxin interferes with the metabolic function of cytokinin, a growth hormone (Briske and Richards 1995). Partial defoliation of young leaf material from grass tillers at phenological growth between the three and a half new leaf stage and the flower (anthesis) stage can stimulate vegetative growth of secondary tillers from axillary buds. Defoliation temporarily reduces the production of the blockage hormone, auxin (Briske and Richards 1994). This abrupt reduction of plant auxin in the lead tiller allows for cytokinin synthesis or utilization in multiple axillary buds, stimulating the development of vegetative tillers (Murphy and Briske 1992, Briske and Richards 1994). Several axillary buds develop into secondary tillers following partial defoliation of lead tillers at vegetative stages of phenological growth. Apparently, none of the developing secondary tillers have growth far enough advanced to take complete hormonal control over the other developing axillary buds (Manske 1996a).

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

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

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

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

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

Rhizosphere Organisms

The rhizosphere is the narrow zone of soil around active roots of perennial grassland plants and is comprised of bacteria, protozoa, nematodes, springtails, mites, endomycorrhizal fungi (Elliot 1978, Anderson et al. 1981, Harley and Smith 1983, Curl and Truelove 1986, Whipps 1990, Campbell and Greaves 1990) and ectomycorrhizal fungi (Caesar-TonThat et al. 2001b, Manske and Caesar-TonThat 2003, Manske 2007). The activity of rhizosphere organisms increases along the trophic hierarchy, starting with the bacteria. This microflora trophic level lacks chlorophyll and has low carbon (energy) content. Bacteria are microscopic single celled saprophitic organisms that consume large quantities of soil organic matter and are one of the primary producers of the rhizosphere. Increases in biomass and activity of the bacteria elevates the concentration of carbon dioxide (CO_2) resulting in stimulation of activity in the other rhizosphere organisms. Protozoa are single-celled microorganisms that are mainly small amoeba and feed primarily on bacteria. Nematodes are a diverse group of small nonsegmented worms. Most nematodes feed primarily on bacteria or fungi, some feed on protozoa, and some eat other nematodes. Springtails are the most abundant insect in grassland soils and they travel among rhizosphere structures. Minute springtails ingest considerable quantities of soil organic matter in order to eat fungi and bacteria. Mites are small eight-legged arachnids that travel among rhizosphere structures and feed on fungi, nematodes, small insects, and other mites. Mites help distribute fungus spores and bacteria through the soil by carrying them on their exoskeleton. Endomycorrhizal fungi are the other primary producers of the rhizosphere and are achlorophyllous saprophytes that live on dead organic matter and can not fix carbon because they lack chlorophyll. The bacteria and fungi are the microflora saprotrophic organisms at the bottom of the food chain and makeup the greatest biomass of the rhizosphere. Both bacteria and fungi contain high proportions of nitrogen in relation to their carbon content. The rhizosphere organisms of the microfauna trophic levels graze on bacteria or fungi and ingest greater quantities of nitrogen than they need for a balanced diet based on energy (carbon); the excess nitrogen is excreted as ammonium (NH_4). The primary symbiotic function of the endomycorrhizal fungi is to nitrify the ammonium (NH_4) excreted by rhizosphere organisms and convert it into nitrate (NO_3), which is a form of mineral nitrogen usable by grass plants. The elevated rhizosphere organism activity caused by the increase in available carbon compounds results in a greater quantity of organic nitrogen converted into mineral nitrogen (Coleman et al. 1983, Klein et al. 1988, Burrows and Pfleger 2002, Rillig et al. 2002, Bird et al. 2002, Driver et al. 2005).

Along with the improvement of ecosystem biogeochemical processes and the resulting increase in available mineral nitrogen, the increase of mycorrhizal fungi biomass and activity benefits other grassland ecosystem functions. Endomycorrhizal fungi develop arbuscules, vesicles, and hyphae within root tissue of the host plant (Harley and Smith 1983) and secrete adhesive polysaccharides that bond soil particles around grass roots forming the structural environment for rhizosphere organisms, and the adhesive polysaccharides bind soil into aggregates resulting in increased soil pore spaces, increased water holding capacity, and increased rooting depth. Endomycorrhizal fungi also move phosphorus, other mineral nutrients, and water to the plant roots for absorption (Moorman and Reeves 1979, Harley and Smith 1983, Allen and Allen 1990, Box and

Hammond 1990, Marschner 1992, Koide 1993, Marschner and Dell 1994, Smith and Read 1997).

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

Defoliation Resistance Mechanisms

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

Activation of the three primary defoliation resistance mechanisms requires proper timing of partial defoliation. The effects of defoliation are not simply the removal of herbage from grass plants (Langer 1963, 1972): foliage removal disrupts plant growth and photosynthesis, and defoliation also changes physiological processes in all parts of the plant; alters the plant community microclimate by changing light transmission, moisture relations, and temperature; and changes the soil environment, thereby affecting soil organism activity (Manske 2000a). Grass plants developed the defoliation resistance mechanisms in response to grazing during the period of coevoluation with graminivores (McNaughton 1979, 1983; Coleman et al. 1983; Briske 1991; Briske and Richards 1995; Manske 1999a, 2011b). The defoliation resistance mechanisms help grass tillers withstand and recover from partial defoliation by grazing. The three main resistance mechanisms are: compensatory internal physiological processes, internal vegetative production of secondary tillers from axillary buds, and external symbiotic rhizosphere organism activity (McNaughton 1979, 1983; Coleman et al. 1983; Ingham et al. 1985; Mueller and Richards 1986; Richards et al. 1988; Briske 1991; Murphy and Briske 1992; Briske and Richards 1994, 1995; Manske 1999a, 2011b).

Defoliation resistance mechanisms developed during the period of 30 to 20 mya as derivatives of the coevolution of grass plants, rhizosphere organisms, and large grazing mammalian graminivores following the cooling of the global climate in the Eocene that reduced forest ecosystems and increased grassland ecosystems. The defoliation resistance mechanisms are a complex assemblage of biogeochemical and physiological processes that involve intricate interactions among rhizosphere microorganisms, grass plants, and large grazing graminivores. Activation of these mechanisms provides important biological and physiological processes permitting native grasses to produce greater herbage biomass and to increase basal cover; these mechanisms also enable grass plants to replace lost leaf material, to restore disrupted physiological processes, and to vegetatively produce secondary tillers from axillary buds after partial defoliation by grazing. The defoliation resistance mechanisms function at variable levels of activation depending on the quantity of available mineral nitrogen in grassland ecosystem soil. When mineral nitrogen is available at 100 lbs/ac (112 kg/ha) or greater, the defoliation resistance mechanisms function at full activation (Manske 2011e). When mineral nitrogen is available at less than 100 lbs/ac (112 kg/ha), defoliation resistance mechanisms function at levels less than full activation (Manske 2009a, 2011d). In addition, the water (precipitation) use efficiency processes decrease in grass plants growing in ecosystems with less than 100 lbs/ac (112 kg/ha) available mineral nitrogen causing herbage biomass production to be reduced by 49.6% (Wight and Black 1972, 1979).

The quantity of available mineral nitrogen in grassland ecosystems is dependent on the rate of mineralization of soil organic nitrogen by rhizosphere organisms (Coleman et al. 1983). The larger the rhizosphere volume and microorganism biomass the greater the quantity of soil mineral nitrogen converted (Gorder, Manske, and Stroh 2004). Rhizosphere volume and microorganism biomass are limited by access to simple carbohydrate energy (Curl and Truelove 1986). Healthy grass plants capture and fix carbon during photosynthesis and produce carbohydrates in quantites greater than the amount needed for tiller growth and development (Coyne et al. 1995). Partial defoliation of grass tillers at vegetative phenological growth stages by large grazing graminivores causes greater quantities of exudates containing simple carbohydrates to be released from the grass tillers through the roots into the rhizosphere (Hamilton and Frank 2001). With the increase in availability of carbon compounds in the rhizosphere, the biomass and activity of the microorganisms increases (Anderson et al. 1981, Curl and Truelove 1986, Whipps 1990). The increase in rhizosphere organism biomass and activity results in greater rates of mineralization of soil organic nitrogen converting greater quantities of available mineral nitrogen (Coleman et al. 1983, Klein et al. 1988, Burrows and Pfleger 2002, Rillig et al. 2002, Bird et al. 2002, Driver et al. 2005). Mineral nitrogen available in quantities of 100 lbs/ac (112 kg/ha) or greater allow defoliated grass tillers full activation of the defoliation resistance mechanisms (Manske 2009a, 2011d, 2011e). Full activation of the compensatory internal physiological processes within grass plants accelerates growth rates of replacement leaves and shoots, increases photosynthetic capacity of remaining mature leaves, increases allocation of carbon and nitrogen, improves water (precipitation) use efficiency, and increases restoration of biological and physiological processes enabling rapid and complete recovery of partially defoliated grass tillers. Full activation of the asexual internal processes of vegetative production increases secondary tiller development from axillary buds and increases initiated tiller density during the grazing season. Full activation of the external symbiotic rhizosphere organism activity increases mineralization of mineral nitrogen, increases ecosystem biogeochemical cycling of essential elements, and improves belowground resource uptake competitiveness (Wight and Black 1972, 1979; McNaughton 1979, 1983; Coleman et al. 1983; Ingham et al. 1985; Mueller and Richards 1986; Richards et al. 1988; Briske 1991; Murphy and Briske 1992; Briske and Richards 1994, 1995; Manske 1999a, 2011b; Kochy and Wilson 2000).

Biogeochemical Processes

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

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

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

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

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

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

Atmospheric carbon dioxide (CO_2) is the ecosystem input source for carbon. Atmospheric carbon dioxide which composes about 0.03% of the gasses in the atmosphere, exists at concentrations of around 370 to 385 mg/kg and is not limiting on rangelands. The carbon dioxide is fixed with hydrogen from soil water during the plant process of photosynthesis which converts energy from sunlight into chemical energy and assimilates simple carbohydrates. Capturing energy by fixing carbon has a relatively low impact on the plant organisms that posses chlorophyll and has low biological costs to the ecosystem resources (Manske 2011b).

Soil water (H_2O) is infiltrated precipitation water and is the ecosystem input source for hydrogen. Soil water is absorbed through the roots and distributed throughout the plant within the xylem vascular tissue. When the rate of water absorption by the roots is less than the rate of water loss from transpiration through stomata openings, plant tissue develops water stress (Brown 1995). Plant water stress limits growth. In western North Dakota, the perennial plant growing season months have a long-term periodicity rate of water deficiency conditions at 32.7%, for a mean of 2.0 months with water deficiency per growing season (Manske et al. 2010).

Wet deposition of nitrogen oxides (NO, N_2O) following lightning discharges is the ecosystem input source for nitrogen (Manske 2009b). The source of nitrogen for plant growth is mineral nitrogen (NO_3, NH_4) converted from soil organic nitrogen by rhizosphere organisms. Low quantities of available soil mineral nitrogen below 100 lbs/ac (112 kg/ha) is the major limiting factor of herbage growth on rangelands (Wight and Black 1979) and limits productivity more often than low water on rangeland ecosystems (Tilman 1990). However, rangeland soils are not deficient of nitrogen. Most of the nitrogen is immobilized in the soil as organic nitrogen. Untilled rangeland soils contain about 3 to 8 tons of organic nitrogen per acre (Manske 2011a). Soil organic nitrogen must be mineralized by rhizosphere organisms to become plant usable mineral nitrogen. The quantity of rhizosphere organisms is the limiting factor in rangeland ecosystems low in mineral nitrogen. Biomass and activity of organisms in the rhizosphere are limited by access to energy from simple carbohydrates which can be exudated from grass lead tillers with partial defoliation by grazing graminivores when grass tillers are at vegetative growth stages. Transforming nitrogen from organic nitrogen to mineral nitrogen and back to organic nitrogen is complex and has a great impact on many organisms at multiple trophic levels and has high biological costs on the ecosystem resources (Manske 2011a, 2011b).

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

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

Failure of a rangeland ecosystem to replenish essential elements at quantities equal to or greater than the annual amount of essential elements lost or removed from the ecosystem inhibits ecosystem biogeochemical processes from functioning at potential levels causing incremental decreases in productivity and gradual degradation of the ecosystem.

Activation of Ecosystem Mechanisms and Processes

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

Proactive Management of Crested Wheatgrass

Crested wheatgrass is a long-lived perennial, cool season, drought tolerant, winter hardy grass with an extensive root system. It was introduced from Eurasia and has naturalized in the Northern Plains. Numerous accessions of plant material originating from Turkey, Iran, Kazakhstan, central Asia, western and southwestern Siberia, and the steppe region of European Russia have been brought to North America. A total of three recognized species were introduced: *Agropyron desertorum* (Fisch. ex Link) Schult. (Nordan type and MT Standard type), *Agropyron cristatum* (L.) Gaertn. (Fairway type), and *Agropyron fragile* (Roth) Candargy (Siberian type). Even though each species has distinct characteristics, specific identification of individual plants is difficult because the morphological variation has developed into a continuum as a result of the extensive intercrossing that has occurred since the 1930's.

Millions of acres of crested wheatgrass exist as mixtures or monocultures in the Northern Plains because it has been the principal grass selected for revegetation of previously plowed rangelands in the United States and Canada (Lorenz 1986). During the first 20 years of the 20th Century, millions of acres of rangeland were turned over with steel moldboard plows in order to fulfill the compliance requirements of the Homestead Acts of both countries and because of the high demand for wheat, flax, and a few other crops. The region was experiencing favorable climatic conditions during this period and cropland production was generally successful, which stimulated the plowing of additional acres of rangeland. Both Canada and the United States suffered economic depression during the late 1920's and many years with severe drought conditions during the 1930's. Much of the cropland areas were abandoned and exposed to wind and water erosion.

Crested wheatgrass was seeded into the abandoned cropland areas to reduce the erosion problems and stabilize the land. Crested wheatgrass successfully revegetated these exposed areas primarily because of its seedling vigor and its ability to survive unfavorable conditions of low precipitation and cold winters.

Some of the revegetated cropland were large enough to be used and managed separately as hay fields or spring pastures. However, much of the revegetated land were small parcels located within management units that consist mainly of some other type of plant cover. These small parcels of crested wheatgrass usually cannot be isolated and managed as separate units because the cost of fence material and separate livestock watering facilities cannot be economically justified. Proper management of these small parcels of crested wheatgrass is still a problem in the Northern Plains.

Crested wheatgrass is a very beneficial grass and has made significant contributions to the production of livestock in the Northern Plains (Lorenz 1986). However, crested wheatgrass hay fields and pastures have the potential to provide suitable habitat for pestiferous rangeland grasshopper population development. Crested wheatgrass stands persist after several years of heavy use as widely spaced large bunches or widely spaced single tillers and small bunches. These growth characteristics of open canopy provide favorable habitat for several pest grasshopper species (Onsager 1995, and pers. comm.). The majority of grasshopper “hot spots” in the Northern Plains are found on double used or poorly used crested wheatgrass hay fields and pastures. Management of crested wheatgrass favorable for pest grasshoppers needs to be terminated and management of crested wheatgrass favorable for livestock production and unfavorable for pest grasshopper production needs to be evaluated and implemented.

Study Areas

The objectives of this research project were to quantitatively describe the changes to vegetation structure during the growing season caused by mowing and grazing management practices on crested wheatgrass meadows and to document changes to grasshopper population abundance and composition that resulted from the management caused changes to grasshopper habitat. This collaborative project was conducted from the Range Research Laboratory at the NDSU Dickinson Research Extension Center (DREC), Dickinson, North Dakota, directed by Dr. Llewellyn L. Manske and was responsible for the vegetation data, and conducted from the Rangeland Insect Laboratory at the USDA Agricultural Research Service (ARS), Bozeman, Montana, that was moved mid study to Sidney, Montana, directed by Dr. Jerome A. Onsager and was responsible for the grasshopper data.

The initial study sites were located in the North Dakota Grasshopper IPM Demonstration Project Site within the McKenzie County Grazing District of the Little Missouri Grasslands, 21 miles (34 km) west of Watford City between 47° 35' and 47° 50' N. latitude and 104° 00' and 103° 45' W. longitude, North Dakota. The study sites were provided with the cooperation of the USDA Forest Service and the McKenzie County Grazing Association. The project was funded by the USDA Animal and Plant Health Inspection Service (APHIS), Plant Protection and Quarantine (PPQ), Cooperative Grasshopper Integrated Pest Management (GHIPM) Project during the 1993 and 1994 field seasons. The two research units agreed to continue research project data collection for the field seasons of 1995 to 1998 as separate but cooperative entities. The grasshopper data collection was continued from the USDA-ARS, Sidney, Montana, laboratory on the initial study sites. The vegetation data collection was continued on similar sites located a short distance east in Dunn County at the NDSU Dickinson Research Extension Center ranch, at 46° 48' N. latitude and 102° 48' W. longitude, near Manning, North Dakota.

Long-Term Regional Weather

The western North Dakota region has cold winters and hot summers typical of continental climates. Mean annual temperature is 40.9° F (4.9° C). January is the coldest month, with a mean temperature of 11.5° F (-11.4° C). July and August are the warmest months, with mean temperatures of 68.7° F (20.4° C) and 67.0° F (19.5° C), respectively. Long-term (1892-2010) mean annual precipitation is 16.03 inches (407.15 mm). The precipitation during the perennial plant growing season (April through October) is 13.54 inches (343.76 mm) and is 84.5% of the annual precipitation. June has the greatest monthly precipitation, at 3.55 inches (90.14 mm). The precipitation received in the three month period of May, June, and July is 8.13 inches (206.50 mm) and is 50.7% of the annual precipitation (Manske 2011f).

Water stress develops in perennial plants during water deficiency periods when the amount of rainfall is less than evapotranspiration demand. Water deficiency months were identified from historical temperature and precipitation data by the ombrothermic diagram technique (Emberger et al. 1963). The long-term (1892-2010) ombrothermic diagram shows near water deficiency conditions during August, September, and October, and favorable water relations during April, May, June, and July. Reoccurrence of water deficiency conditions during April, May, June, and July is 16.9%, 13.6%, 10.2%, and 38.1%, respectively, and during August, September, and October water deficiency reoccurs 52.5%, 50.0%, and 46.6% of the years, respectively. Long-term occurrence of water deficiency conditions is 32.7% of the growing season months, for a mean of 2.0 water deficient months per growing season (Manske et al. 2010).

Growing Season Precipitation

Growing season (April to September) precipitation for the McKenzie County study sites was taken from the Watford City ndawn weather station and reported by Onsager (2000) (table 13). Long-term (31 years) annual precipitation for the area was 14.41 inches (366.01 mm). Growing season precipitation for 1993 and 1995 was above normal. Growing season precipitation for 1994 and 1996 was below normal and for 1997 and 1998 conditions were dry with perennial plants under water stress some of the time. The growing season conditions progressively became warmer and dryer during the six years of data collection at the McKenzie County study sites.

Precipitation for the perennial plant growing season months (April through October) for the Dunn County study sites was taken from the DREC ranch weather station and reported by Manske (2013) (table 14). Long-term (31 years) annual precipitation for the area was 16.91 inches (429.51 mm). Growing season precipitation for 1993 to 1997 was normal each year and was above normal for 1998. Water deficiency conditions occurred during August, September, and October in 1993; July, August, and September in 1994; June and September in 1995; April and October in 1996; August in 1997; and April and September in 1998.

Management Treatments

Three crested wheatgrass management treatments were established at the McKenzie County location and each of the separate defoliation treatment areas were designed with two replicated vegetation sample sites. The crested wheatgrass mowing treatment was established on an existing crested wheatgrass hay field. The large area had been fenced separately and had not been grazed. Prior to 1989, the crested wheatgrass vegetation had been swathed for hay annually during early to mid July. The hay field consisted of large crested wheatgrass wolf plants widely spaced with greater than 50% bareground. After 1989, the cutting time was moved earlier to mid or late June, after the flower stage and before the seeds had matured. The mowing treatment plots were cut for hay during late June in 1993 and 1994. No grasshopper population data was collected on the crested wheatgrass mowing treatment study plots.

The crested wheatgrass seasonlong grazing treatment study plots were located on two large replicated areas that had been seeded with crested wheatgrass shortly after 1936. The crested wheatgrass plots were interspersed among native rangeland that had been managed as one extremely large pasture grazed seasonlong annually from 1 June to 31 October since the McKenzie County Grazing Association had been organized. The pasture was grazed during this same time period in 1993 and 1994, and from 1995 to 1998. One of the seeded crested wheatgrass areas was sampled for grasshopper population data during 1993 to 1998.

The crested wheatgrass spring grazing treatment study plots were in adjacent replicated pastures traditionally grazed during May after the calves had been branded. Prior to 1989, these two crested wheatgrass pastures had also been grazed during the fall after mid October for a month or so. After 1989, the fall grazing period was intended to have been terminated. The crested wheatgrass pastures were spring grazed at relatively high stocking rates during 1 to 31 May 1993 and from 28 April to 1 June 1994, and the pastures were fall grazed for a "short" period in 1993 after mid October. The spring grazing treatment was conducted during the May time period from 1995 to 1998 without any fall grazing periods. The spring grazing crested wheatgrass treatment pastures were sampled for grasshopper population data at two replicated study sites during 1993 to 1998.

Research activity on the grasshopper habitat study continued at two locations during 1995 to 1998. The grasshopper population data was collected at the initial study sites on the seasonlong grazing and spring grazing of crested wheatgrass treatments at the McKenzie County locations. The vegetation data was collected on similar study sites with two spring grazing crested wheatgrass during May management treatments at the Dunn County locations.

The spring grazing crested wheatgrass during May on a one pasture treatment was designed with two replicated pastures each with four vegetation sample sites. Each pasture was grazed for 30 or 31 days from early May stocked at 1.82 acres per cow-calf pair per month.

The spring grazing crested wheatgrass during May on a two pasture treatment was designed with two replicated pastures split in half creating two two pasture switchback systems with two grazing periods of 7 or 8 days each per half pasture. Each half pasture with two vegetation sample sites was grazed for a total of 15 or 16 days during May. The half pasture grazed first one year was grazed second the next year. Each two pasture twice-over switchback system was grazed for 30 or 31 days from early May stocked at 0.75 acres per cow-calf pair per month. After this study, the stocking rate was reduced to 1.0 acre per cow-calf pair per month and the management was simplified by grazing during 28 days in May with each half pasture grazed for two 7 day periods.

Procedures

Changes in residuum vegetation structure during the growing season caused by management practices on crested wheatgrass meadows were evaluated by aboveground herbage biomass, plant species basal cover, and bareground area collected at the McKenzie County sites during the growing seasons of 1993 and 1994 and by aboveground herbage biomass and plant species basal cover collected at the Dunn County sites during the growing seasons of 1995 to 1998.

Aboveground herbage biomass was collected by the standard clipping method (Cook and Stubbendieck 1986). All herbage biomass clipping sites were partially defoliated by the selected management treatment. The reported herbage biomass values represent the residuum vegetation and the regrowth vegetation resulting from the treatment. This study did not establish nondefoliated sample sites that show the vegetation response without the treatment. Clipped herbage material was collected monthly (May, June, July, and August) from five 0.25 m^2 quadrats (frames) during 1993 and from four 0.25 m^2 quadrats during 1994 at each replicated vegetation sample site on the mowing treatment, the seasonlong grazing treatment, and the spring grazing treatment at the McKenzie County research study sites. Clipped herbage material was collected monthly (May, June, July, August, and September) from five 0.25 m^2 quadrats (frames) during 1995 to 1998 at each replicated vegetation sample site on the spring grazing during May on the one pasture system and on the two pasture switchback system at the Dunn County research study sites. The herbage material in each frame was hand clipped to ground level and sorted in the field by biotype categories: domesticated grass, native grass, forbs, standing dead, and litter. The herbage of each biotype category from each frame was placed in labeled paper bags of known weight, oven dried at 140° F (60° C), and weighed. Herbage biomass in pounds per acre and relative composition for each biotype category was determined from the clipping data. Mean monthly herbage biomass for each biotype category was determined for each growing season.

Plant species basal cover was determined by the ten-pin point frame method (Cook and Stubbendieck 1986) with 2000 points collected along transect lines at each replicated vegetation sample site during peak growth between mid July and mid August each year. Basal cover plant species data were sorted into biotype categories: domesticated grass, native grass, sedges, forbs, litter, and bare soil. The bare soil category was the percent mineral soil not covered by live plants or litter. Basal cover and relative composition of biotype categories were determined from the ten-pin point frame data collected at the McKenzie County research study sites during 1993 and 1994, and at the Dunn County research study sites during 1995 to 1998.

Bareground area was determined with the line intercept method (Canfield 1941, Cook and Stubbendieck 1986) that was modified to measure linear length of intercepted open areas not covered by vegetation canopy. Ten 2000 cm (787.4 in) transect lines were established at each vegetation sample site at the McKenzie County research study sites. Bareground area percentage and combined bareground length of each transect were means of four readings per growing season conducted between June and August of 1993.

Vegetation structure during the growing season resulting from management treatments were evaluated with herbage biomass and basal cover data. The vegetation structure caused by the spring grazing treatment was compared to the vegetation structure caused by the seasonlong grazing treatment by percent difference data at the McKenzie County research study sites. The vegetation structure caused by the spring grazing during May on the two pasture switchback system was compared to the vegetation structure caused by the one pasture system by percent difference data at the Dunn County research study sites.

Grasshopper population density data was collected during 1993 to 1998 at the initial McKenzie County reseach study sites by a team of entomologists directed by Dr. Onsager using methods described by Onsager and Henry (1977). Each grasshopper study site was provided with a set of 40 aluminum wire rings, each 0.1 m^2, affixed to the ground in a 4 X 10 array with 8 meters between rings. Grasshopper populations were sampled at 7 to 10 day intervals during 1993, 1995, and 1998, and at 2 to 3 day intervals during 1994 and 1997. Sampling began as soon as the grasshopper study sites were accessible in the spring and terminated after killing frost in the fall. Total density was estimated by counting grasshoppers within each ring of the 40 wire ring array that had a total area of 4 m^2. The field data was converted into grasshopper days (GD) per m^2 which is an index of seasonal abundance for 3rd instar and older stages. The concept of grasshopper days (GD) is similar to that of animal unit months (AUM). A sweep net collection was taken along the perimeter of the 40 wire ring array each sampling period to establish composition of the population by species and by stage of development (Onsager 2000).

Results

The growing season residuum vegetation structure expected to negatively affect pestiferous rangeland grasshopper populations was greater plant herbage biomass, greater live plant basal cover, and reduced bareground areas with open vegetation canopy cover.

McKenzie County Study Sites

Effects from mowing treatments on crested wheatgrass meadows were evaluated. The growing season residuum vegetation structure resulting from the June mowing crested wheatgrass treatment at the McKenzie County study sites was described from monthly herbage biomass and mean monthly herbage biomass of the domesticated grass, total live, and standing biomass biotype categories, from basal cover of the domesticated grass and total live biotype categories, and from the bareground area percentage and combined bareground length per 2000 cm transect data.

The June mowing crested wheatgrass treatment was swathed during late June 1993; the hay yield was 414.77 lbs/ac leaving a residual biomass of 595.33 lbs/ac. The crested wheatgrass plants grew slowly during June and July reaching peak monthly biomass in August at 1142.83 lbs/ac (table 15). During the growing season of 1993, the aboveground vegetation biomass on the June mowing treatment consisted of 42.9% standing dead and litter and 57.1% live herbage. The live herbage biomass was 93.7% domesticated grass, 2.8% native grass, and 3.5% forbs including a small amount of alfalfa (table 16).

The 1993 growing season was the fifth year that the crested wheatgrass hay field had been swathed early in mid to late June and the area still consisted of large widely spaced crested wheatgrass wolf plants. The monthly herbage biomass of the domesticated grass, total live, and standing biomass biotype categories was moderate during June and July with peak biomass occurring in August. The mean monthly herbage biomass during the 1993 growing season for the domesticated grass, total live, and standing biomass biotype categories was 889.37 lbs/ac, 948.74 lbs/ac, and 1169.95 lbs/ac, respectively (table 15). The 1993 growing season basal cover of the domesticated grass and total live biotypes were extremely low at 12.3% and 19.6%, respectively, with 80.4% of the area without live plants (table 19).

The June mowing crested wheatgrass treatment was swathed during late June 1994; the hay yield was 618.22 lbs/ac leaving a residual biomass of 525.20 lbs/ac. The crested wheatgrass plants decreased in herbage weight during June, July, and August reaching a low monthly biomass of 427.80 lbs/ac (table 17). During the growing season of 1994, the aboveground vegetation biomass on the June mowing treatment consisted of 48.4% standing dead and litter and 51.6% live herbage. The live herbage biomass was 85.7% domesticated grass, 2.2% native grass, and 12.1% forbs (table 18).

The 1994 growing season was the sixth year that the crested wheatgrass hay field had been swathed early in mid to late June and showed little improvement. The monthly herbage biomass of the domesticated grass, total live, and standing biomass biotypes changed little during June, July, and August. The mean monthly herbage biomass during the 1994 growing season for the domesticated grass, total live, and standing biomass biotypes was 633.26 lbs/ac, 738.78 lbs/ac, and 1054.26 lbs/ac, respectively (table 17). The 1994 growing season basal cover of the domesticated grass and total live biotypes were remarkably low at 9.1% and 13.5%, respectively, with a 25.7% and 31.3% reduction in basal cover from the 1993 growing season, respectively (table 19).

Bare soil, or mineral soil not covered by live plants or litter, percentages measured with the ten-pin point frame method were extremely great at 53.8% and 68.0%, with a mean of 60.9%, on the June mowing treatment during the 1993 and 1994 growing seasons, respectively (table 19).

Bareground, or open canopy, area measured with the line intercept method was 74.5%, 1490 cm/2000 cm transect, on the June mowing treatment. The great reduction in plant cover was caused by a long history of mowing late during July. Six years of mowing earlier in late June had not yet turned the problem around (table 20).

Grasshopper population density data was not collected on the crested wheatgrass June mowing treatment plots. This hay field provided excellent pest grasshopper habitat consisting of widely spaced large bunches of crested wheatgrass having low herbage biomass, remarkably low live plant basal cover, and expansive bareground areas with abundant open vegetation canopy cover.

Effects from grazing treatments on crested wheatgrass meadows were evaluated. The residuum vegetation structure of crested wheatgrass meadows during the growing season on spring grazing treatments were compared with that on seasonlong grazing treatments at the McKenzie County study sites. Comparisons of the growing season residuum vegetation structure was evaluated using percent difference data for monthly herbage biomass and mean herbage biomass of the domesticated grass, total live, and standing biomass biotype categories and percent difference data for basal cover of the domesticated grass and total live biotype categories, and the bareground area percentage and combined bareground length per 2000 cm transects were evaluated from the grazing treatments at the McKenzie County study sites.

The seasonlong grazing crested wheatgrass treatment was lightly grazed during the period of 1 June to 31 October 1993 at moderate stocking rates leaving a mean residual standing biomass of 840.56 lbs/ac (table 21). Crested wheatgrass was at late phenological growth stages and decreasing in crude protein content during June. Cattle consumed little mature crested wheatgrass herbage after early June.

During the growing season of 1993, the aboveground vegetation biomass on the seasonlong grazing treatment consisted of 54.0% standing dead and litter and 46.0% live herbage. The live herbage biomass was 98.5% domesticated grass, 1.1% native grass, and 0.4% forbs (table 22).

The spring grazing crested wheatgrass treatment was heavily grazed for 31 days during May 1993 leaving a residual biomass of 331.11 lbs/ac. The crested wheatgrass plants grew slowly during June and July reaching peak monthly herbage biomass in August at 1807.55 lbs/ac (table 23). During the growing season of 1993, the aboveground vegetation biomass on the spring grazing treatment consisted of 35.0% standing dead and litter and 65.0% live herbage. The live herbage biomass was 97.5% domesticated grass, 2.4% native grass, and 0.2% forbs (table 24).

The monthly herbage biomass of the domesticated grass, total live, and standing biomass biotypes were lower on the spring grazing treatment during May, June, and July than those on the seasonlong grazing treatment during the 1993 growing season (tables 21 and 23). The domesticated grass herbage production greatly increased in August on the spring grazing treatment causing the monthly herbage biomass of the domesticated grass, total live, and standing biomass biotypes to increase with monthly biomass at 189.0%, 192.5%, and 128.5% greater than those on the seasonlong grazing treatment, respectively. As a result, the mean monthly herbage biomass for the domesticated grass, total live, and standing biomass biotypes were 28.0%, 29.5%, and 10.6% greater on the spring grazing treatment than those on the seasonlong grazing treatment, respectively (table 25). The 1993 growing season basal cover on the seasonlong grazing and spring grazing treatments of the domesticated grass biotype was 29.0% and 36.0% and of the total live biotype was 37.9% and 39.4%, respectively (tables 31 and 32). The basal cover of the domesticated grass biotype was 24.0% greater and of the total live biotype was 3.9% greater on the spring grazing treatment than those on the seasonlong grazing treatment, respectively (table 33).

The seasonlong grazing crested wheatgrass treatment areas were lightly grazed during the period of 1 June to 31 October 1994 at moderate stocking rates leaving a mean residual standing biomass of 968.94 lbs/ac (table 26). During the growing season of 1994, the aboveground vegetation biomass on the seasonlong grazing treatment consisted of 36.4% standing dead and litter and 63.6% live herbage. The live herbage biomass was 95.9% domesticated grass, 1.8% native grass, and 2.3% forbs (table 27). The light grazing during two growing seasons caused changes in herbage biomass production during the 1994 growing season compared to the 1993 growing season with a 27.2% increase in live herbage biomass and a 37.9% decrease in dead herbage (tables 21 and 26).

The spring grazing crested wheatgrass pastures were grazed for a month or so during the fall of 1993 after mid October and were heavily grazed for 35 days during late April to early June 1994 leaving a residual biomass of only 253.51 lbs/ac (table 28). The crested wheatgrass plants grew slowly during the growing season and never produced greater than 200 lbs/ac of new growth. During the growing season of 1994, the aboveground vegetation biomass on the spring grazing treatment consisted of 37.2% standing dead and litter and 62.8% live herbage. The live herbage biomass was 93.0% domesticated grass, 1.0% native grass, and 6.0% forbs (table 29). The late season fall grazing, heavy spring grazing, and less than normal growing season precipitation caused reductions in herbage biomass during the 1994 growing season compared to the 1993 growing season with a 49.5% decrease in live herbage biomass and a 44.5% decrease in dead herbage (tables 23 and 28).

The double use of fall grazing and heavy spring grazing on the spring grazing treatment was detrimental to the crested wheatgrass plants resulting in little herbage biomass production occurring during the 1994 growing season. The domesticated grass, total live, and standing biomass biotypes monthly herbage biomass were much lower on the spring grazing treatment during the 1994 growing season than those on the seasonlong grazing treatment. The mean monthly herbage biomass for the domesticated grass, total live, and standing biomass biotypes were 50.2%, 48.6%, and 48.1% lower on the spring grazing treatment than those on the seasonlong grazing treatment, respectively (table 30). The 1994 growing season basal cover of the domesticated grass biotype was 17.9% and 23.6% and of the total live biotype was 26.4% and 25.1% on the seasonlong grazing and spring grazing treatments, respectively (table 31 and 32). The basal cover of the domesticated grass biotype was 32.2% greater and the total live biotype was 4.7% lower on the spring grazing treatment than those on the seasonlong grazing treatment, respectively (table 33). The native grass decreased 42.8% and the total forbs decreased 62.8% during 1994 on the spring grazing treatment causing the decrease in total live basal cover (table 32).

Bare soil, or mineral soil not covered by live plants or litter, percentages measured with the ten-pin point point frame method was 6.6% and 7.3%, with a mean of 7.0%, on the seasonlong grazing treatment during the 1993 and 1994 growing seasons, respectively (table 31) and were 7.8% and 6.8%, with a mean of 7.3%, on the spring grazing treatment during the 1993 and 1994 growing seasons, respectively (table 32). Little difference in bare soil percentages were measured with the ten-pin point frame method on the seasonlong grazing and spring grazing treatments.

Bareground, or open canopy, area measured with the line intercept method was 30.9%, 618 cm/2000 cm transect, on the seasonlong grazing treatment (table 34) and was 19.3%, 386 cm/2000 cm transect, on the spring grazing treatment (table 35). The line intercept method measured 60.1% greater bareground area on the seasonlong grazing treatment than on the spring grazing treatment.

The lightly grazed seasonlong grazing crested wheatgrass treatment had greater dead herbage biomass during the 1993 and the 1994 growing seasons, had greater live herbage biomass in May, June, and July during the 1993 growing season, had greater live herbage biomass during the 1994 growing season, and had greater bareground area than that on the heavily grazed spring grazing treatment.

The heavily grazed spring grazing crested wheatgrass treatment had greater domesticated grass basal cover during the 1993 and 1994 growing seasons, had greater total live basal cover during the 1993 growing season, and had greater live herbage biomass in August and September during the 1993 growing season than that on the seasonlong grazing treatment.

In summary, the residuum vegetation structure resulting from the seasonlong grazing treatment and from the spring grazing treatment after two growing seasons was different.

The seasonlong grazing treatment had 71.8% greater standing dead biomass and 78.3% greater dead litter biomass than that on the spring grazing treatment. The seasonlong grazing treatment was lightly grazed with little herbage removal by cattle because the crested wheatgrass plants were at mature phenological growth stages and contained low nutrient quality during the summer grazing period causing most of the herbage that grew on the plots to die and remain on the plots.

The seasonlong grazing treatment had lower vegetation canopy cover with 21.3% lower domesticated grass basal cover and 60.1% greater bareground area than that on the spring grazing treatment. The seasonlong grazing treatment lacked grazing in May for stimulation of vegetative secondary tiller development between the 3.5 new leaf stage and the flower stage resulting in fewer new tillers produced each year.

The spring grazing treatment had 27.1% greater domesticated grass basal cover than that on the seasonlong grazing treatment. The increased tiller basal cover resulted from the grazing in May that stimulated vegetative secondary tiller development. Because of the greater domesticated grass basal cover on the spring grazing treatment, the domesticated grass herbage biomass should have also been greater. The herbage biomass of the domesticated grass biotype was not greater as a result of the heavy spring grazing that removed great quantities of plant biomass leaving insufficient leaf area to supply the needed photosynthetic products used for growth of additional leaf and stem biomass. The fall grazing removed great quantities of plant biomass from fall tillers and carryover tillers that later caused further reductions in the quantities of herbage biomass produced during the following growing season.

The plants on the seasonlong grazing treatment produced less herbage biomass than the plants on the spring grazing treatment, however, because of the heavy herbage biomass removal during the fall grazing and the spring grazing on the spring grazing treatment, the seasonlong grazing treatment had 18.0% greater domesticated grass herbage biomass, 16.6% greater total live herbage biomass, and 26.3% greater standing biomass than that on the spring grazing treatment.

The growing season vegetation structure on both the seasonlong grazing treatment and spring grazing treatment of crested wheatgrass meadows was highly desirable for grasshoppers. Mean annual grasshopper days (GD) per m^2 were great on both the seasonlong grazing treatment and the spring grazing treatment during each year of the study (Onsager 2000). The seasonlong grazing treatment had an annual mean of 1011 GD for the 9 pestiferous rangeland grasshoppers and had an annual mean of 1569 GD for the total of all grasshopper species. The spring grazing treatment had an annual mean of 978 GD for the 9 pestiferous rangeland grasshoppers and had an annual mean of 1645 GD for the total of all grasshopper species (table 36).

The same three grasshopper species, Mel sanguinipes, Mel infantilis, and Mel gladstoni, had great annual mean grasshopper days per m^2 on both grazing treatments with a combined total of 852 GD on the seasonlong grazing treatment and 706 GD on the spring grazing treatment (table 36). These three grasshopper species preferred crested wheatgrass meadows (Onsager 2000).

Population abundance of Pho nebrascensis increased to an annual mean of 126 GD on the seasonlong grazing treatment but remained at a low mean abundance of 16 GD on the spring grazing treatment (table 36). On the other hand, population abundance of three grasshopper species, Tra kiowa, Age deorum, and Mel femurrubrum, increased to annual means of 98 GD, 88 GD, and 35 GD, respectively, on the spring grazing treatment while remaining at low annual means of 14 GD, 4 GD, and 2 GD, respectively, on the seasonlong grazing treatment (table 36). One grasshopper species, Mel gladstoni, had similar mean annual grasshopper days per m^2 on both the seasonlong grazing treatment (52 GD) and the spring grazing treatment (53 GD) (table 36), however, the main increases in population abundance occurred during different years. The major increase in Mel gladstoni population abundance occurred in 1994 on the spring grazing treatment and occurred in 1995 on the seasonlong grazing treatment (Onsager 2000).

One of the abundant grasshopper species, Ope obscura, was considered to be primarily a pest on short grass prairie areas and preferred blue grama as its food plant (Pfadt 1994) was identified as a major pest on native rangeland managed with seasonlong grazing during this study (Onsager 2000), however, it was not abundant in the grasshopper populations on the two crested wheatgrass management treatments (table 36).

Grasshopper population infestations on both the seasonlong grazing treatment and spring grazing treatment had remarkable single season outbreak spikes during 1994 (figure 2). The same two grasshopper species, Mel sanguinipes and Mel infantilis, were the most prevalent grasshoppers involved in the 1994 outbreaks on both grazing treatments (Onsager 2000), however, the primary changes in vegetation structure on the two grazing treatments in 1994 compared to that in 1993 were different. In 1994, the basal cover of the domesticated grass biotype decreased 38.5% and the bareground area was 60.1% greater at 30.9% on the seasonlong grazing treatment, and, in 1994, the herbage biomass of the standing biomass biotype decreased 45.9% on the spring grazing treatment.

Grasshopper population assemblages again increased to outbreak levels in 1997 and 1998 on both the seasonlong grazing treatment and the spring grazing treatment (figure 2) (Onsager 2000), however, the main grasshopper species with the greatest increases in grasshopper days per m^2 were different on the two grazing treatments. Two grasshopper species, Mel sanguinipes and Age deorum, accounted for most of the outbreak increase in 1997 and 1998 on the spring grazing treatment with increases in abundance by Mel gladstoni contributing to the large outbreak population (Onsager 2000). One grasshopper species, Pho nebrascensis, accounted for most of the outbreak increase on the seasonlong grazing treatment with dramatic increases in abundance by Mel gladstoni and Enc costalis contributing to the large outbreak population (Onsager 2000).

Generally, the growing season residuum vegetation structure, thus the grasshopper habitat, on crested wheatgrass meadows resulting from the seasonlong grazing treatment and the spring grazing treatment were quite different. The standing herbage biomass was greater, except during August and September 1993; the basal cover was less; and the bareground area was much larger on the seasonlong grazing treatment than those on the spring grazing treatment. The standing herbage biomass was less, except during August and September 1993; the basal cover was greater; and the bareground area was much smaller on the spring grazing treatment than those on the seasonlong grazing treatment. It can reasonably be assumed that as long as the management of the grazing treatments continue without change, the differences in residuum vegetation structure resulting from the grazing treatments will also continue without change.

The primary changes in vegetation structure resulting from the seasonlong grazing treatment were reduced basal cover and larger bareground area; the grasshopper species that increased in abundance as a result of these habitat changes were: Mel sanguinipes with an annual mean of 547 GD increased during 1994; Mel infantilis with an annual mean of 253 GD increased during 1994; Pho nebrascensis with an annual mean of 126 GD increased during 1997 and 1998; Mel gladstoni with an annual mean of 52 GD increased during 1995 and 1998; and Enc costalis with an annual mean of 11 GD increased during 1997 and 1998 (table 36) (Onsager 2000).

The primary change in vegetation structure resulting from the spring grazing treatment was reduced standing herbage biomass; the grasshopper species that increased in abundance as a result of this habitat change were: Mel sanguinipes with an annual mean of 415 GD increased during 1994, 1997, and 1998; Mel infantilis with an annual mean of 238 GD increased during 1994; Tra kiowa with an annual mean of 98 GD increased during the study; Age deorum with an annual mean of 88 GD increased during 1997 and 1998; Mel gladstoni with an annual mean of 53 GD increased during 1994, 1997, and 1998; and Mel femurrubrum with an annual mean of 35 GD increased during the study (table 36) (Onsager 2000). Pestiferous rangeland grasshopper species increase in abundance when the vegetation structure of the habitat decreases in basal cover, increases in bareground area, and/or decreases in standing herbage biomass.

Dunn County Study Sites

Effects from grazing treatments on crested wheatgrass meadows were evaluated. The residuum vegetation structure during the growing season on spring grazing crested wheatgrass during May on a two pasture switchback system were compared with that on a one pasture system at the Dunn County study sites. Comparisons of the growing season residuum vegetation structure was evaluated using percent difference data for monthly herbage biomass and mean herbage biomass of the domesticated grass, total live, and standing biomass biotype categories and percent difference data for basal cover of the domesticated grass and total live biotype categories from the grazing treatments at the Dunn County study sites.

Spring grazing of crested wheatgrass during May is an ideal match between grass phenological growth stages and partial defoliation by large grazing graminivores to activate beneficial plant mechanisms and ecological processes. The majority of the crested wheatgrass lead tillers produce three and a half new leaves prior to 1 May and at that stage the tillers are physiologically ready for partial defoliation of less than 50% of the leaf biomass. A healthy dense stand of crested wheatgrass is capable of producing rapid rates of growth of herbage biomass during May. Some of the advanced lead tillers reach the flower stage by 28 May slowing the growth rate of those tillers. The remaining lead tillers would reach the flower stage before the second or third week in June if they were ungrazed. Partial defoliation after the 3.5 new leaf stage and before the flower stage activates mechanisms for vegetative production of secondary tillers. The secondary tillers grow rapidly reaching peak growth in early to mid July. After mid August the grass plants start the 2.5 month process to prepare for the winter low activity period. During that preparation period, cool season grasses, including crested wheatgrass, produce fall tillers that become next growing seasons vegetative tillers. The current seasons vegetative tillers that did not produce a seed head become carryover tillers; they will be able to survive the winter and grow during the following growing season as lead tillers that are destined to produce flowering seed heads.

The spring grazing crested wheatgrass during May on a one pasture system was grazed 30 or 31 days at a stocking rate of 1.82 ac per AUM during the 1995 to 1998 growing seasons leaving a mean domesticated grass lead tiller residual of 751.61 lbs/ac after the May grazing period, the mean secondary tiller regrowth in July was 337.52 lbs/ac (44.9% of the June residual lead tiller biomass), and the mean fall tiller growth in September was 144.58 lbs/ac (14.8% of the fully developed secondary tiller biomass in August) producing a mean monthly domesticated grass biomass of 912.09 lbs/ac (14.5% less than that on the two pasture system) (table 37). During the growing seasons of 1995 to 1998, the aboveground vegetation biomass of the spring grazing on a one pasture system consisted of 38.4% standing dead and litter and 61.6% live herbage. The live herbage biomass was 86.4% domesticated grass, 7.4% native grass, and 5.9% forbs (table 38).

The spring grazing crested wheatgrass during May on a two pasture switchback system was grazed 30 or 31 days at a stocking rate of 0.75 ac per AUM during the 1995 to 1998 growing seasons leaving a mean domesticated grass lead tiller residual of 721.04

lbs/ac after the May grazing period, the mean secondary tiller regrowth in July was 544.82 lbs/ac (75.6% of the June residual lead tiller biomass), and the mean fall tiller growth in September was 159.33 lbs/ac (14.5% of the fully developed secondary tiller biomass in August) producing a mean monthly domesticated grass biomass of 1066.16 lbs/ac (16.9% greater than that on the one pasture system) (table 39). During the growing seasons of 1995 to 1998, the aboveground vegetation biomass of the spring grazing on a two pasture switchback system consisted of 32.0% standing dead and litter and 68.0% live herbage. The live herbage biomass was 91.1% domesticated grass, 6.5% native grass, and 2.5% forbs (table 40).

The spring grazing on a two pasture twice-over switchback system activated greater vegetative tiller growth than the spring grazing on a one pasture system. The two pasture system produced 61.4% greater secondary tiller biomass and 10.2% greater fall tiller biomass than that produced on the one pasture system.

The mean monthly herbage biomass of the domesticated grass, total live, standing dead, and standing biomass biotypes on the spring grazing on a one pasture system was 912.09 lbs/ac, 1055.50 lbs/ac, 235.55 lbs/ac, and 1291.05 lbs/ac, respectively (table 37), and on the spring grazing on a two pasture system, the mean monthly herbage biomass of these biotypes was 1066.16 lbs/ac, 1170.75 lbs/ac, 106.73 lbs/ac, and 1277.48 lbs/ac, respectively (table 39). The two pasture system produced greater live residual herbage biomass than the one pasture system. The two pasture system produced 16.9% greater domesticated grass biomass and 10.9% greater total live biomass than that produced on the one pasture system (table 41). The one pasture system retained 120.7% greater standing dead biomass than that on the two pasture system as a result of the lighter stocking rate. The herbage biomass of the standing biomass biotype was nearly the same on both the one pasture system and the two pasture system (table 41). The standing biomass biotype on the one pasture system consisted of 70.7% domesticated grass, 10.9% native grass and forbs, and 18.2% standing dead herbage. On the two pasture system, the standing biomass biotype consisted of 83.5% domesticated grass, 8.2% native grass and forbs, and 8.4% standing dead herbage.

Basal cover during the 1995 to 1998 growing seasons of the domesticated grass biotype was 18.2% and 21.7% and of the total live biotype was 20.7% and 26.2% on the one pasture system and on the two pasture system, respectively (table 42). The basal cover of the domesticated grass biotype was 19.6% greater and of the total live biotype was 26.5% greater on the two pasture system than those on the one pasture system (table 43). The greater basal cover on the two pasture system indicated greater activation of the vegetative tiller producing mechanisms.

Bare soil, or mineral soil not covered by live plants or litter, percentages measured with the ten-pin point frame method was small at 3.0% and 2.4% on the one pasture system and on the two pasture system, respectively (table 42). The bare soil area on the one pasture system was 24.7% greater than that on the two pasture system.

The residuum vegetation structure resulting from spring grazing crested wheatgrass during May on a one pasture system and on a two pasture system were not desirable as habitat for pestiferous rangeland grasshoppers. Except during May and early June, the crested wheatgrass tillers were tall and dense through the entire growing season. The long shoot tillers had numerous senescent and live stem leaves that formed a dense canopy nearly covering the entire ground surface.

Grasshopper population density data were not collected on these Dunn County research study sites. However, during vegetation data collection, very few grasshoppers were observed. The small quantity of grasshoppers present were not a problem. The growing season residuum vegetation structure on the crested wheatgrass two pasture switchback spring grazing system had 16.9% greater domesticated grass biomass, 10.9% greater total live plant biomass, 19.6% greater domesticated grass basal cover, 26.5% greater total live plant basal cover, 61.4% greater secondary tiller biomass, and 10.2% greater fall tiller biomass than the residuum vegetation structure on the crested wheatgrass one pasture spring grazing system.

Greater activation of the plant defoliation resistance mechanisms and the ecosystem biogeochemical processes on the two pasture system resulted in greater livestock weight gain than on the one pasture system. During May, cows and calves gained 111 lbs/ac and 90 lbs/ac, respectively, on the two pasture system, and cows and calves gained 32 lbs/ac and 31 lbs/ac, respectively, on the one pasture system. Cow gains were 244.5% greater and calf gains were 186.2% greater per acre on the two pasture system than on the one pasture system. The great cow and calf weight performance on spring grazing of crested wheatgrass during May occurs only when the calves are one month old or older on 1 May.

Discussion

Crested wheatgrass starts early leaf greenup in mid April. The crested wheatgrass tillers have three and a half new leaves around 22 April that are highly nutritious forage for the very early and early hatching grasshoppers, which is four to five weeks earlier than native cool season grasses. Early boot stage occurs in mid May and the first stalks with flowers occurs around 28 May. Most of the lead tillers reach the flower stage during the following 10 to 14 days. The late flowering lead tillers should flower by 10 June. Seed development occurs after the flower stage and seeds reach maturity during the following 5 to 8 weeks (table 44) (Whitman et al. 1951, Manske 1999b).

The nutritional quality of ungrazed lead tillers of crested wheatgrass changes with the tillers' phenological development. Early season growth stages are high in crude protein and water. The early vegetative leaf stages contain levels of crude protein above 15% during early to mid May. As seed stalks begin to develop in mid May, crude protein levels begin to decrease. At the flower stage, lead tillers contain 13.5% crude protein. After the flower stage and during the seed development stage, crude protein levels remain above 9.6% until late June. As the ungrazed lead tillers mature, the fiber content increases and percent crude protein, water, and digestability decrease. By early July, crude protein levels drop below 7.8% and below 6.2% in early August (figure 3, table 44). Phosphorous levels drop below 0.18% in late July. The patterns of change in nutritional quality are similar from year to year because tiller phenological development is regulated primarily by photoperiod. Slight variations in nutritional quality result from annual variations in temperature, evaporation, and water stress. Nutritional quality can also be slightly altered by changes in rates of tiller growth and plant senescence. Growth rates are affected by the level of photosynthetic activity, which is affected by air and soil temperature, cloud cover, and availability of hydrogen for carbohydrate synthesis. Senescence rates increase with high temperatures, precipitaiton deficiency, and water stress (Whitman et al. 1951, Manske 1999b).

Crested wheatgrass meadows can be used one time per year without detrimental effects as hay fields, spring pastures, or summer pastures. Double heavy use of crested wheatgrass causes biological degradation. Even though this is a fact long-known, many crested wheatgrass pastures have two heavy uses per growing season with intense grazing occurring during the spring and fall. Some crested wheatgrass meadows are grazed in the spring and hayed during the summer, and others are hayed during the summer and grazed in the fall. Crested wheatgrass plants are hardy but they do not fully recover from two heavy uses during one growing season. Numerous biological problems develop in crested wheatgrass plants that are used heavy two times each year. Double heavy use decreases plant health with accompanying decreases in herbage production and plant density. Repeated double heavy use results in a depauperated stand that can have greater than 50% bare ground, while a properly managed stand with one use per year would be healthy and productive and would have no more than about 6% or 12% bare ground.

Double use of crested wheatgrass meadows that removes most of the standing dead vegetation has the potential to cause serious mineral deficiencies in the grazing cows blood. Mature lactating cows can develop milk fever or grass tetany while grazing lush spring crested wheatgrass vegetation. Milk fever is caused by a blood deficiency of calcium (Ca) and grass tetany is caused by a blood deficiency of magnesium (Mg). Crested wheatgrass herbage, however, is rarely deficient in calcium or magnesium during the growing season. Absorption of most minerals is by passive diffusion across the intestinal wall; some calcium is transported with a protein carrier. Only about half of the ingested minerals are absorbed through the intestinal wall into the cows blood system under normal conditions. During the early spring, the rate of forage passage through the cows digestive tract is accelerated when lush vegetation high in water and crude protein is consumed; greatly reducing the quantity of dietary minerals absorbed through the intestinal wall and potentially resulting in deficiencies of calcium or magnesium in the cows blood. Cattle grazing crested wheatgrass pastures containing sufficient amounts of dry carryover residual vegetation can maintain normal slow rates of forage passage through the digestive tract and normal rates of mineral absorption; which in effect, prevents the occurrence of mineral deficiencies in the blood and thus preventing the development of milk fever or grass tetany.

Hay Field

Cutting crested wheatgrass hay during mid to late July to maximize the dry matter yield also causes problems that decrease herbage production and plant density. Cutting the lead tillers after they have flowered and started to develop seeds prevents activation of the compensatory physiological processes and the vegetative reproduction by tillering processes. Removal of greater than 50% of the leaf material from mature lead tillers results in insufficient leaf area retained on the tiller for even partial foliage recovery using current photosynthetic assimilates. Tillers with 50% or more of the aboveground leaf material removed reduce root growth, root respiration, and root nutrient absorption (Crider 1955). Root mortality and decomposition begin within 2 days of haying mature tillers (Oswalt et al. 1959). Mature tillers must depend upon stored carbohydrates for replacement leaf growth (Briske and Richards 1995). There is a high biological cost to the tiller when the photosynthetic system needs to be replaced from stored carbohydrates. This implied reduction in efficiency results in reduced root growth, decreased tiller development, and low growth rates causing decreased tiller numbers, reduced total basal cover, and reduced quantities of herbage biomass produced (Coyne et al. 1995) and promotes the development of widely spaced wolf plants. Repeated late season haying of crested wheatgrass progressively reduces the quantities of stored carbohydrates.

Late cut mature crested wheatgrass hay has low crude protein content of around 6.4%. The nutrient content of late cut mature hay meets the dietary requirements of range cows only during the dry gestation prodution period. This is the only range cow production period that late cut mature hay has lower cost, by a few cents, than crested wheatgrass cut at the boot stage during mid May to early June (16 May to 10 June). Cutting crested wheatgrass hay at the boot stage reduces the dry matter yield by 300 lbs/ac (19%) and increases the crude protein yield by 87 lbs/ac (85%) (table 45). The forage feed costs per day from feeding late cut mature crested wheatgrass to range cows during the third trimester and early lactation production periods was 16% greater and 50% greater, respectively, compared the feed costs per day from feeding early cut at the boot stage hay. Feeding early cut boot stage hay has lower forage feed costs because the greater crude protein yield per acre reduces the crude protein cost per pound and thus reducing the feed cost per day (table 45) (Manske 2002).

Cutting crested wheatgrass hay during mid to late June did not improve herbage biomass production or tiller density after six years of treatment. Cutting crested wheatgrass hay early between the boot stage and the flower stage captures greater weight of crude protein per acre and activates the vegetative reproduction by tillering processes that increases tiller density and promotes development of rhizome tillers that fill in the space between bunches.

Spring Pasture

Crested wheatgrass meadows are excellent spring pastures during May. Crested wheatgrass is physiologically ready for grazing in early May. The three and a half new leaves are produced around 22 April, however, the leaf weight is not great enough to start grazing during late April. It is important to wait until 1 May when the herbage biomass quantity is sufficient for grazing. The ability to start grazing a month ahead of the proper grazing start date on native rangeland is the primary biological advantage of crested wheatgrass pastures and their priority use should be grazing during May as spring complementary pastures in conjunction with summer grazing native rangeland rotation systems.

The stocking rate for grazing crested wheatgrass during May can be relatively heavy because of the similar lead tiller rapid growth during the early portion of the growing season. Average stocking rates of crested wheatgrass May pastures in good to fair condition range from 0.60 to 1.00 acres/AUM in the drift prairie, from 1.00 to 1.50 acres/AUM in the Missouri coteau, and from 1.50 to 2.00 acres/AUM in the west river regions of the mixed grass prairie. The one spring pasture treatment in very good condition was stocked at 1.82 acres/AUM. The two spring pasture switchback system in excellent condition was stocked at 0.75 acres/AUM for four years then reduced to 1.00 acres/AUM during the following years. A high stocking rate can be repeated annually on spring complementary crested wheatgrass pastures when the grazing occurs during the period that the quantity of herbage biomass is increasing towards the peak level during late May. Vegetative tillers on a healthy dense stand of crested wheatgrass can produce 300 pounds of herbage biomass per acre per day until the lead tillers reach the flower stage starting around 28 May and lasting to about 10 June. This level of production can be maintained year after year if the stubble left after grazing at the end of May is three inches or taller and the pasture is not used again until next spring. Heavy use of crested wheatgrass plants one time during May require the remainder of the growing season to recover biologically.

The two pasture switchback spring grazing system activated greater compensatory physiological processes and greater vegetative tiller growth than the one pasture spring grazing system yielding greater domesticated grass and total live plant biomass production, greater domesticated grass and total live plant basal cover, and greater development of secondary tillers and fall tillers resulting in a residuum vegetation structure unfavorable for pestiferous rangeland grasshoppers.

Summer Pasture

Many beef production operations have greater land area planted with crested wheatgrass than can be used during May as spring complementary pastures for the main range cow herd. These beef operations are in need of additional summer grazingland for heifer development or for stocker steers. The crested wheatgrass acreage in excess of May complementary pastures can be used in a summer grazing system by implementation of twice-over grazing technology (Manske 1999a, 2011b).

There are two biological problems that need resolution in order for summer grazing of crested wheatgrass pastures to work and to be sustainable as a long-term practice. First, the high stocking rate used on the spring grazing treatment during May cannot be the stocking rate used during summer grazing of crested wheatgrass, and second, crested wheatgrass lead tiller forage drops below 9.6% crude protein during the third week in June and livestock lose weight shortly after.

The proper stocking rate used during summer grazing of crested wheatgrass should be the same stocking rate used to graze native rangeland on identical soil types. The total net primary production of crested wheatgrass herbage biomass during an entire growing season is about the same as that produced on native rangeland. Crested wheatgrass monocultures appear to produce greater herbage than native rangeland because ungrazed crested wheatgrass has one major growth period with most of the lead tillers growing together at a similar time and at a similar rate resulting in a high peak herbage biomass early in the growing season with little new growth occurring after mid to late June. Native rangeland, on the other hand, is a mixture of numerous cool season and warm season species with several growth periods not occurring together but spread throughout the early portion of the growing season resulting in a lower peak herbage biomass extended over a longer period of time, and producing about the same quantity of total new growth material as crested wheatgrass per acre in a year. Crested wheatgrass grazed only during May can support the higher spring stocking rate. The spring stocking rate used to graze summer crested wheatgrass pastures would be expected to produce negative effects on plant health similar to that of double heavy use. Stocking summer grazed crested wheatgrass pastures at the same rate used to graze native rangeland should be perpetually sustainable.

Maintaining nutritional quality of crested wheatgrass forage at or above livestock nutritional requirements for 120 days from early May to late August requires activation of the vegetative reproduction by tillering processes. Seasonlong grazing management of crested wheatgrass meadows provided adequate crude protein for lactating cows until the third week in June. At that time, cattle stop utilizing crested wheatgrass. The nutritional quality of crested wheatgrass lead tiller forage drops below 9.6% crude protein soon after the flower stage when the seeds are being filled (table 44, figure 3) (Whitman et al. 1951, Manske 1999b). Stimulation of vegetative secondary tillers, that have a crude protein content greater than 9.6%, would be able to extend the length of time for an additional two to two and a half months that the forage quality on crested wheatgrass summer pastures would meet the dietary requirements of lactating cows until late August.

The physiological processes for activation of vegetative reproduction of secondary tillers from axillary buds in crested wheatgrass is the same as in native range grasses. Secondary tiller development from axillary buds is regulated by lead tillers, through a process of lead tiller dominance. The lead tillers produce an inhibitory hormone that prevents the growth hormone from activating growth within axillary buds. Grazing that removes a small amount (25% to 33%) of leaf tissue from the aboveground portion of lead tillers after the three and a half new leaf stage and before the flower stage rapidly reduces the amount of inhibitory hormone in the tiller. With the inhibitory hormone reduced, the growth hormone stimulates vegetative reproduction and several secondary tillers develop from the axillary buds (Manske 2011b).

If no defoliation occurs before the flower stage, the lead tiller inhibits vegetative tiller development until the inhibitory hormone production naturally declines during the flower stage. This gradual hormone reduction permits one axillary bud to grow and develop into a secondary tiller, which in turn produces inhibitory hormones that prevent growth of the other axillary buds. Single tiller development after the flower stage on crested wheatgrass plants is, by default, primarily as crown tillers producing bunches, while multiple tiller development following biologically effective stimulation by grazing is mainly as rhizome tillers producing dense sod.

The period of activation of vegetative development of multiple secondary tillers in crested wheatgrass is between the three and a half new leaf stage and the flower stage. These phenological growth stages are the same in all grass species. However, the seasonal period when these phenological growth stages occur are different for the various grass species. For crested wheatgrass, these growth stages when activation of vegetative reproduction can occur develop between 1 May and 10 June each year. This 40 day stimulation period is then the duration of the first grazing period. The second grazing period is double the number of days of the first period and would be 80 days in duration. A summer twice-over rotation grazing system on crested wheatgrass pastures would be from 1 May until 29 August, with a duration of 120 days.

The most successful strategy for grazing crested wheatgrass during the summer has been with four equal sized pastures. Each pasture would be grazed for 10 days in succession during the first grazing period between 1 May and 10 June. Then during the second grazing period, each pasture would be grazed again for double the number of days it was grazed during the first grazing period. The second period would occur between 10 June and 29 August and each of the four equal sized pastures would be grazed for 20 days in the same sequence. The first pasture grazed in the sequence during one year was the last pasture grazed the previous year.

The number of days grazed are not counted by calendar dates; days grazed are counted by the number of 24 hour periods grazed from the date and time the cattle are turned into a pasture. If cattle are turned into pasture A at 9:00 am on 1 May, 10 days of grazing occurs at 9:00 am on 11 May, not on 10 May.

The summer grazed crested wheatgrass pastures must leave 50% of the leaf biomass at the end of the grazing season in order for biological recovery of the plants. That amount of leaf area is required to store enough carbohydrates for respiration during the winter dormancy and for healthy productive leaf growth the following growing season.

Management of Crested Wheatgrass Meadows

Crested wheatgrass plants are extremely hardy and persistent. However, crested wheatgrass plants can be degraded and productivity and plant density can be diminished in only a few years of unsuitable management.

Some of the management treatments evaluated in this study resulted in degradation of the crested wheatgrass plants. Crested wheatgrass cut annually for hay at the mature stage during early to mid July yielded a reduced quantity of dry matter with very low nutrient quality. This late cut treatment caused reductions in plant density and herbage biomass production. The resulting residuum habitat had widely spaced wolf plants with greater than 50% bareground and was highly desirable for pest grasshopper population increase. Crested wheatgrass cut annually for hay at the seed development stage during mid to late June yielded low quantities of dry matter weight and low to moderate nutrient quality. This haying treatment did not improve the thin plant density of medium sized bunches. The resulting residuum habitat consisted of 656.12 lbs/ac of crested wheatgrass at 10.7% basal cover with 74.5% bareground and was favorable for pest grasshopper population increase. Crested wheatgrass pastures grazed seasonlong at moderate stocking rates from early June to late October was at late phenological growth stages with low nutritional quality and had extremely low livestock utilization. The resulting residuum habitat consisted of 667.99 lbs/ac of crested wheatgrass at 23.4% basal cover with 30.9% bareground and was favorable for pest grasshopper population increase. Crested wheatgrass spring pastures grazed at excessively heavy stocking rates during May and frequently grazed a second time after mid October for a month or so had too much leaf area removed and replaced only a small portion of the leaf material grazed. The resulting residuum habitat consisted of 566.10 lbs/ac of crested wheatgrass at 29.8% basal cover with 19.3% bareground and was favorable for pest grasshopper population increase.

These four examples of crested wheatgrass meadows poorly managed with traditional concepts all developed the typical characteristics of open canopies with low herbage biomass, low plant basal cover, and large bare areas that are ideal habitats favorable for pestiferous rangeland grasshopper population development. Large quantities of pest grasshoppers are produced in the Northern Plains on similarly managed degraded crested wheatgrass meadows with characteristic open canopy and bare areas. Management of these degraded crested wheatgrass meadows should be changed.

Crested wheatgrass meadows can be managed to be favorable for livestock production and unfavorable for pest grasshopper production as early cut hay fields, as spring pastures grazed during May, and as summer pastures grazed from early May to late August.

Crested wheatgrass meadows in the Northern Plains can produce sufficient herbage biomass and nutritional quality to be used as hay fields. The timing of cutting is critical to activate the beneficial plant mechanisms, to capture the greatest quantity of nutrients per acre, and to develop the residuum vegetation structure to be unfavorable for pestiferous rangeland grasshoppers. Crested wheatgrass cut early between the boot stage and the flower stage during mid May to early June yielded 19% less dry matter and 85% greater nutrient quality than hay cut late at the mature stage. This early cut treatment caused increased plant density from rhizome tillers and increased herbage biomass production. The resulting residuum habitat was unfavorable for pest grasshopper population increase.

The priority use of crested wheatgrass meadows should be as spring complementary pastures grazed during May. Crested wheatgrass grazed in the spring between the three and a half new leaf stage and the peak flower stage during May increased plant density from rhizome tillers and increased herbage biomass production on a one pasture treatment or on the improved two pasture twice-over switchback system. Crested wheatgrass tillers develop through vegetative phenological growth stages from the three and a half new leaf stage to the flower stage during early to late May. The compensatory physiological processes and the vegetative reproduction by tillering processes can be activated during these phenological growth stages. Activation of the compensatory physiological processes within grass plants accelerate growth rates of replacement roots, leaves, and shoots, increases photosynthetic capacity of remaining mature leaves, increases allocation of carbon and nitrogen, improves water (precipitation) use effciency, and increases restoration of biological processes enabling rapid and complete recovery of partially defoliated grass tillers. Activation of the asexual processes of vegetative reproduction increases secondary tiller development from axillary buds and increases tiller density during the growing season. The spring grazing crested wheatgrass during May on the two pasture twice-over switchback system activates the compensatory physiological processes and the vegetative reproduction processes at greater levels than the activation of these processes by the one pasture treatment. As a result, the two pasture system produces greater domesticated grass biomass and basal cover, greater total live plant biomass and basal cover, and greater secondary tiller and fall tiller biomass resulting in greater cow and calf weight gain performance and greater growing season residuum vegetation structure that is unfavorable habitat for pestiferous rangeland grasshopper population development. The livestock are removed from the crested wheatgrass pastures at the end of May and moved to native rangeland rotation pastures. The quantity of leaf area remaining at the end of May must be sufficient to photosynthesize adequate quantities of carbohydrates to support the secondary tiller growth from nearly all of the activated axillary buds.

Summer grazing of crested wheatgrass meadows does not improve the plants to the highest biological status, does not return the greatest quantity of wealth per acre, and does not produce the most unfavorable habitat for pest grasshoppers as does spring grazing during May. However, summer grazing on four equal sized crested wheatgrass pastures for 120 days from early May to late August managed with the twice-over rotation technology based on a 40 day stimulation period is the most acceptable plan B use for crested wheatgrass meadows.

The poorly managed crested wheatgrass meadows in the Northern Plains that have the characteristic open canopy, low herbage biomass, low plant basal cover, and large bareground areas can produce grasshopper populations of 8 per square yard. Eight grasshoppers per square yard over an acre use 109.6 pounds of grass herbage per month.

During a 5.5 month growing season, 8 grasshoppers per square yard over an acre use 602.8 pounds of grass herbage. On one million acres of poorly managed crested wheatgrass in the Northern Plains, 8 grasshoppers per square yard use 602,800,000 pounds of grass herbage in one growing season. If the weight of herbage used by eight grasshoppers per square yard were converted to tons, it would be 301,400 tons of grass herbage. If one ton of crested wheatgrass hay cut early at the boot stage with 14.5% crude protein were worth $100.00, eight grasshoppers per square yard over an acre, during a 5.5 month growing season, on one million acres, would use $30,140,000.00 of hay.

The amount of this lost revenue that was contributed for pest grasshopper herbage use from your land can be determined by multiplying the acreage of poorly managed crested wheatgrass meadows with $30.14 per acre. The lost income resulting from grasshopper use of herbage on poorly managed crested wheatgrass meadows can be changed into increased net returns per acre by managing the crested wheatgrass meadows as hay fields cut early between the boot stage and the flower stage during mid May to early June, as spring pastures grazed between the three and a half new leaf stage and the peak flower stage during early to late May, or as four equal sized summer pastures grazed for 120 days from early May to late August managed with the twice-over rotation technology with the first grazing period of 40 days.

Table 13. Precipitation during growing season months (April-September), Watford City, ND.

	1993	1994	1995	1996	1997	1998
mm	456.56	266.67	322.22	233.33	194.44	227.78
inches	17.94	10.50	12.69	9.19	7.66	8.97

Data from Onsager 2000.

Table 14. Precipitation in inches and percent of long-term mean for perennial plant growing season months, western North Dakota, 1993-1998.

Years	Apr	May	Jun	Jul	Aug	Sep	Oct	Growing Season	Annual Total
Long-Term Mean 1982-2012	1.44	2.56	3.27	2.43	1.70	1.42	1.31	14.13	16.91
1993	1.41	1.71	4.57	5.10	1.24	0.18	0.05	14.26	17.36
% of LTM	97.92	66.80	139.76	209.88	72.94	12.68	3.82	100.92	102.66
1994	0.86	1.46	4.51	1.07	0.31	1.08	4.58	13.87	16.14
% of LTM	59.72	57.03	137.92	44.03	18.24	76.06	349.62	98.16	95.45
1995	1.01	4.32	0.68	4.62	3.16	0.00	0.67	14.46	16.24
% of LTM	70.14	168.75	20.80	190.12	185.88	0.00	51.15	102.34	96.04
1996	0.14	3.07	1.86	2.55	1.72	2.51	0.09	11.94	15.97
% of LTM	9.72	119.92	56.88	104.94	101.18	176.76	6.87	84.50	94.44
1997	2.89	0.95	5.02	5.41	0.76	1.75	0.78	17.56	18.61
% of LTM	200.69	37.11	153.52	222.63	44.71	123.24	59.54	124.27	110.05
1998	0.40	1.51	5.98	2.11	4.60	0.71	4.38	19.69	22.42
% of LTM	27.78	58.98	182.87	86.83	270.59	50.00	334.35	139.35	132.58
1993-1998	1.12	2.17	3.77	3.48	1.97	1.04	1.75	15.30	17.79
% of LTM	77.78	84.77	115.29	143.21	115.88	73.24	133.59	108.28	105.20

Table 15. Monthly herbage biomass (lbs/ac) for crested wheatgrass managed with June mowing, 1993.

Plant Biotype	May	Jun	Jul	Aug	Mean Monthly
Domesticated	1010.10	595.33	809.22	1142.83	889.37
Native Grass	0.00	101.16	0.00	3.93	26.27
Total Forbs	8.21	6.42	19.62	98.12	33.09
Total Live	1018.31	702.91	828.84	1244.88	948.74
Standing Dead	289.01	169.48	256.90	169.48	221.11
Standing Biomass	1307.32	872.39	1085.74	1414.36	1169.95
Litter	432.37	561.25	577.30	391.77	490.67
Total Dead	721.38	730.73	834.20	561.25	711.89
Total Biomass	1739.69	1433.64	1663.04	1806.13	1660.63

Table 16. Monthly composition (%) of herbage biomass for crested wheatgrass managed with June mowing, 1993.

Plant Biotype	May	Jun	Jul	Aug	Mean Monthly
Domesticated	99.19	84.70	97.63	91.81	93.74
Native Grass	0.00	14.39	0.00	0.32	2.77
Total Forbs	0.81	0.91	2.37	7.88	3.49
Total Live	58.53	49.03	49.84	68.93	57.13
Standing Dead	16.61	11.82	15.45	9.38	13.31
Standing Biomass	75.15	60.85	65.29	78.31	70.45
Litter	24.85	39.15	34.71	21.69	29.55
Total Dead	41.47	50.97	50.16	31.07	42.87
Total Biomass	1739.69	1433.64	1663.04	1806.13	1660.63

Table 17. Monthly herbage biomass (lbs/ac) for crested wheatgrass managed with June mowing, 1994.

Plant Biotype	May	Jun	Jul	Aug	Mean Monthly
Domesticated	1143.72	525.50	436.01	427.80	633.26
Native Grass	9.77	23.14	3.21	28.29	16.10
Total Forbs	285.62	26.16	30.33	15.56	89.42
Total Live	1439.11	574.80	469.55	471.65	738.78
Standing Dead	590.24	280.27	170.56	220.86	315.48
Standing Biomass	2029.35	855.07	640.11	692.51	1054.26
Litter	496.58	147.00	273.31	595.50	378.10
Total Dead	1086.82	427.27	443.87	816.36	693.58
Total Biomass	2525.93	1002.07	913.42	1288.01	1432.36

Table 18. Monthly composition (%) of herbage biomass for crested wheatgrass managed with June mowing, 1994.

Plant Biotype	May	Jun	Jul	Aug	Mean Monthly
Domesticated	79.47	91.42	92.86	90.70	85.72
Native Grass	0.68	4.03	0.68	6.00	2.18
Total Forbs	19.85	4.55	6.46	3.30	12.10
Total Live	56.97	57.36	51.41	36.62	51.58
Standing Dead	23.37	27.97	18.67	17.15	22.03
Standing Biomass	80.34	85.33	70.08	53.77	73.60
Litter	19.66	14.67	29.92	46.23	26.40
Total Dead	43.03	42.64	48.59	63.38	48.42
Total Biomass	2525.93	1002.07	913.42	1288.01	1432.36

Table 19. Basal cover (%) and composition (%) for crested wheatgrass managed with June mowing.

Plant Biotype	Basal Cover %		Composition %	
	1993	1994	1993	1994
Domesticated	12.25	9.10	62.50	67.56
Native Grass	3.75	0.78	19.13	5.79
Alfalfa	1.85	1.38	9.44	10.24
Total Forbs	1.75	2.21	8.93	16.41
Total Live	19.60	13.47		
Litter	26.60	18.55		
Bare Soil	53.80	67.98		

Table 20. Bareground area on crested wheatgrass managed with June mowing as mean of ten 2000 cm (787.4 in) transects.

Bareground Size		Percent Area	Bareground Combined Length	
cm	in	%	cm	in
0-5	0-2	25.5	510	200.9
6-10	2-4	23.4	467	184.0
11-20	4-8	23.0	460	180.9
21-30	8-12	14.9	298	117.2
31-40	12-16	7.9	157	61.8
41-50	16-20	3.7	74	29.2
51-90	20-35	1.7	34	13.3

Table 21. Monthly herbage biomass (lbs/ac) for crested wheatgrass managed with seasonlong grazing, 1993.

Plant Biotype	May	Jun	Jul	Aug	Mean Monthly
Domesticated		548.40	616.91	625.47	596.93
Native Grass		2.14	11.42	6.78	6.78
Total Forbs		1.78	4.28	0.71	2.26
Total Live		552.32	632.61	632.96	605.96
Standing Dead		200.88	311.84	191.07	234.60
Standing Biomass		753.20	944.45	824.03	840.56
Litter		411.03	458.85	560.89	476.92
Total Dead		611.91	770.69	751.96	711.52
Total Biomass		1164.23	1403.30	1384.92	1317.48

Table 22. Monthly composition (%) of herbage biomass for crested wheatgrass managed with seasonlong grazing, 1993.

Plant Biotype	May	Jun	Jul	Aug	Mean Monthly
Domesticated		99.29	97.52	98.82	98.51
Native Grass		0.39	1.81	1.07	1.12
Total Forbs		0.32	0.68	0.11	0.37
Total Live		47.44	45.08	45.70	45.99
Standing Dead		17.25	22.22	13.80	17.81
Standing Biomass		64.70	67.30	59.50	63.80
Litter		35.30	32.70	40.50	36.20
Total Dead		52.56	54.92	54.30	54.01
Total Biomass		1164.23	1403.30	1384.92	1317.48

Table 23. Monthly herbage biomass (lbs/ac) for crested wheatgrass managed with spring grazing, 1993.

Plant Biotype	May	Jun	Jul	Aug	Mean Monthly
Domesticated	331.11	400.69	517.36	1807.55	764.18
Native Grass	7.85	2.14	21.76	43.53	18.82
Total Forbs	2.85	1.07	2.14	0.00	1.52
Total Live	341.81	403.90	541.26	1851.08	784.51
Standing Dead	364.65	122.38	60.30	31.40	144.68
Standing Biomass	706.46	526.28	601.56	1882.48	929.20
Litter	408.54	208.73	257.61	234.77	277.41
Total Dead	773.19	331.11	317.91	266.17	422.10
Total Biomass	1115.00	735.01	859.17	2117.25	1206.61

Table 24. Monthly composition (%) of herbage biomass for crested wheatgrass managed with spring grazing, 1993.

Plant Biotype	May	Jun	Jul	Aug	Mean Monthly
Domesticated	96.87	99.21	95.58	97.65	97.47
Native Grass	2.30	0.53	4.02	2.35	2.40
Total Forbs	0.83	0.26	0.40	0.00	0.19
Total Live	30.66	54.95	63.00	87.43	65.02
Standing Dead	32.70	16.65	7.02	1.48	11.99
Standing Biomass	63.36	71.60	70.02	90.78	77.01
Litter	36.64	28.40	29.98	11.09	23.00
Total Dead	69.34	45.05	37.00	12.57	35.00
Total Biomass	1115.00	735.01	839.17	2117.25	1206.61

Table 25. Percent difference of monthly herbage biomass on the spring grazing compared to the seasonlong grazing of crested wheatgrass, 1993.

Plant Biotype	May	Jun	Jul	Aug	Mean Monthly
Domesticated		-26.93	-16.14	188.99	28.02
Native Grass		0.00	90.54	542.04	177.58
Total Forbs		-39.89	-50.00	-100.00	-32.74
Total Live		-26.87	-14.44	192.45	29.47
Standing Dead		-39.08	-80.66	-83.57	-38.33
Standing Biomass		-30.13	-36.31	128.45	10.55
Litter		-49.22	-43.86	-58.14	-41.83
Total Dead		-45.89	-58.75	-64.60	-40.68
Total Biomass		-36.87	-38.78	52.88	-8.42

Table 26. Monthly herbage biomass (lbs/ac) for crested wheatgrass managed with seasonlong grazing, 1994.

Plant Biotype	May	Jun	Jul	Aug	Mean Monthly
Domesticated	848.47	916.71	659.72	531.28	739.05
Native Grass	2.81	0.00	29.61	22.69	13.78
Total Forbs	20.87	29.70	18.91	2.00	17.87
Total Live	872.15	946.41	708.24	555.97	770.69
Standing Dead	336.02	175.46	131.30	150.21	198.25
Standing Biomass	1208.17	1121.87	839.54	706.18	968.94
Litter	220.95	284.73	219.79	249.05	243.63
Total Dead	556.97	460.19	351.09	399.26	441.88
Total Biomass	1429.12	1406.60	1059.33	955.23	1212.57

Table 27. Monthly composition (%) of herbage biomass for crested wheatgrass managed with seasonlong grazing, 1994.

Plant Biotype	May	Jun	Jul	Aug	Mean Monthly
Domesticated	97.28	96.86	93.15	95.56	95.89
Native Grass	0.32	0.00	4.18	4.08	1.79
Total Forbs	2.39	3.14	2.67	0.36	2.32
Total Live	61.03	67.28	66.86	58.20	63.56
Standing Dead	23.51	12.47	12.39	15.73	16.35
Standing Biomass	84.54	79.76	79.25	73.93	79.90
Litter	15.46	20.24	20.75	26.07	20.09
Total Dead	38.97	32.72	33.14	41.80	36.44
Total Biomass	1429.12	1406.60	1059.33	955.23	1212.57

Table 28. Monthly herbage biomass (lbs/ac) for crested wheatgrass managed with spring grazing, 1994.

Plant Biotype	May	Jun	Jul	Aug	Mean Monthly
Domesticated	253.51	438.60	389.27	390.70	368.02
Native Grass	15.70	0.00	0.00	0.00	3.93
Total Forbs	11.69	31.40	29.61	22.87	23.89
Total Live	280.90	470.00	418.88	413.57	395.84
Standing Dead	232.28	39.78	44.24	112.74	107.26
Standing Biomass	513.18	509.78	463.12	526.31	503.10
Litter	90.72	128.72	66.01	221.82	126.82
Total Dead	323.00	168.50	111.25	334.56	234.08
Total Biomass	603.90	638.50	529.13	748.13	629.92

Table 29. Monthly composition (%) of herbage biomass for crested wheatgrass managed with spring grazing, 1994.

Plant Biotype	May	Jun	Jul	Aug	Mean Monthly
Domesticated	90.25	93.32	92.93	94.47	92.97
Native Grass	5.59	0.00	0.00	0.00	0.99
Total Forbs	4.16	6.68	7.07	5.53	6.04
Total Live	46.51	73.61	79.16	55.28	62.84
Standing Dead	38.46	6.23	8.36	15.07	17.03
Standing Biomass	84.98	79.84	87.52	70.35	79.87
Litter	15.02	20.16	12.48	29.65	20.13
Total Dead	53.49	26.39	20.84	44.72	37.16
Total Biomass	603.90	638.50	529.13	748.13	629.92

Table 30. Percent difference of monthly herbage biomass on the spring grazing compared to the seasonlong grazing of crested wheatgrass, 1994.

Plant Biotype	May	Jun	Jul	Aug	Mean Monthly
Domesticated	-70.12	-52.15	-40.99	-26.46	-50.20
Native Grass	458.72	0.00	-100.00	-100.00	-71.48
Total Forbs	-43.99	5.72	56.58	1043.50	33.69
Total Live	-67.79	-50.34	-40.86	-25.61	-48.64
Standing Dead	-30.87	-77.33	-66.31	-24.95	-45.90
Standing Biomass	-57.52	-54.56	-44.84	-25.47	-48.08
Litter	-58.94	-54.79	-69.97	-10.93	-47.95
Total Dead	-42.01	-63.38	-68.31	-16.20	-47.03
Total Biomass	-57.74	-54.61	-50.05	-21.68	-48.05

Table 31. Basal cover (%) and composition (%) for crested wheatgrass managed with seasonlong grazing.

Plant Biotype	Basal Cover %		Composition %	
	1993	1994	1993	1994
Domesticated	29.04	17.85	76.62	67.72
Native Grass	5.88	6.00	15.51	22.76
Sedges	0.25	0.00	0.66	0.00
Total Forbs	2.73	2.51	7.20	9.52
Total Live	37.90	26.36		
Litter	55.47	66.34		
Bare Soil	6.63	7.30		

Table 32. Basal cover (%) and composition (%) for crested wheatgrass managed with spring grazing.

Plant Biotype	Basal Cover %		Composition %	
	1993	1994	1993	1994
Domesticated	36.00	23.60	91.42	93.99
Native Grass	1.45	0.83	3.68	3.31
Sedges	0.10	0.00	0.25	0.00
Total Forbs	1.83	0.68	4.65	2.71
Total Live	39.38	25.11		
Litter	52.83	68.09		
Bare Soil	7.79	6.80		

Table 33. Percent difference of basal cover on the spring grazing compared to the seasonlong grazing of crested wheatgrass, 1993-1994.

Plant Biotype	Difference %	
	1993	1994
Domesticated	23.97	32.21
Native Grass	-75.34	-86.17
Sedges	-60.00	0.00
Total Forbs	-32.97	-72.91
Total Live	3.91	-4.74
Litter	-4.76	2.64

Table 34. Bareground area on crested wheatgrass managed with seasonlong grazing as mean of ten 2000 cm (787.4 in) transects.

Bareground Size		Percent Area	Bareground Combined Length	
cm	in	%	cm	in
0-5	0-2	69.1	1382	544.1
6-10	2-4	18.7	374	147.2
11-20	4-8	7.5	150	59.1
21-30	8-12	1.6	32	12.6
31-40	12-16	3.1	62	24.4

Table 35. Bareground area on crested wheatgrass managed with spring grazing as mean of ten 2000 cm (787.4 in) transects.

Bareground Size		Percent Area	Bareground Combined Length	
cm	in	%	cm	in
0-5	0-2	80.7	1614	635.4
6-10	2-4	15.2	304	119.7
11-20	4-8	4.1	82	32.3
21-30	8-12	0.0	0	0
31-40	12-16	0.0	0	0

Table 36. Mean cumulative grasshopper days (GD) per m^2 and primary habitat use for pestiferous grasshoppers on crested wheatgrass managed with spring grazing and seasonlong grazing, 1993-1998.

					Mean Cumulative Grasshopper days per m^2	
Pestiferous Rangeland Grasshoppers	Hatch Group	Egg Pod Site	Basking Site	Daily Activity Site	Spring Grazing	Seasonlong Grazing
Mel san	Early	Bareground	Grd/Veg	Bareground	415	547
Mel inf	Early	Bareground	Bareground	Grd/Veg	238	253
Pho neb	Late	Bareground	Veg/Grd	Veg/Grd	16	126*
Tra kio	Intermediate	Bareground	Bareground	Bareground	98*	14
Age deo	Early	Bareground	Bareground	Bareground	88*	4
Mel gla	Late	Bareground	Bareground	Bareground	53	52
Mel fem	Intermediate	Bareground	Bareground	Grd/Veg	35*	2
Enc cos	Intermediate	Bareground	Bareground	Bareground	9	11
Ope obs	Late	Bareground	Veg/Grd	Veg/Grd	6	2
Total cumulative GD for the 9 pestiferous grasshoppers					978	1011
Total cumulative GD for the other 21 nonpestiferous grasshoppers					667	558
Total cumulative GD for all grasshoppers					1645	1569

Habitat use information from Cushing 1993, Pfadt 1994.
Grasshopper days per m^2 data from Onsager 2000.

Mean value is significantly greater than its complement*.

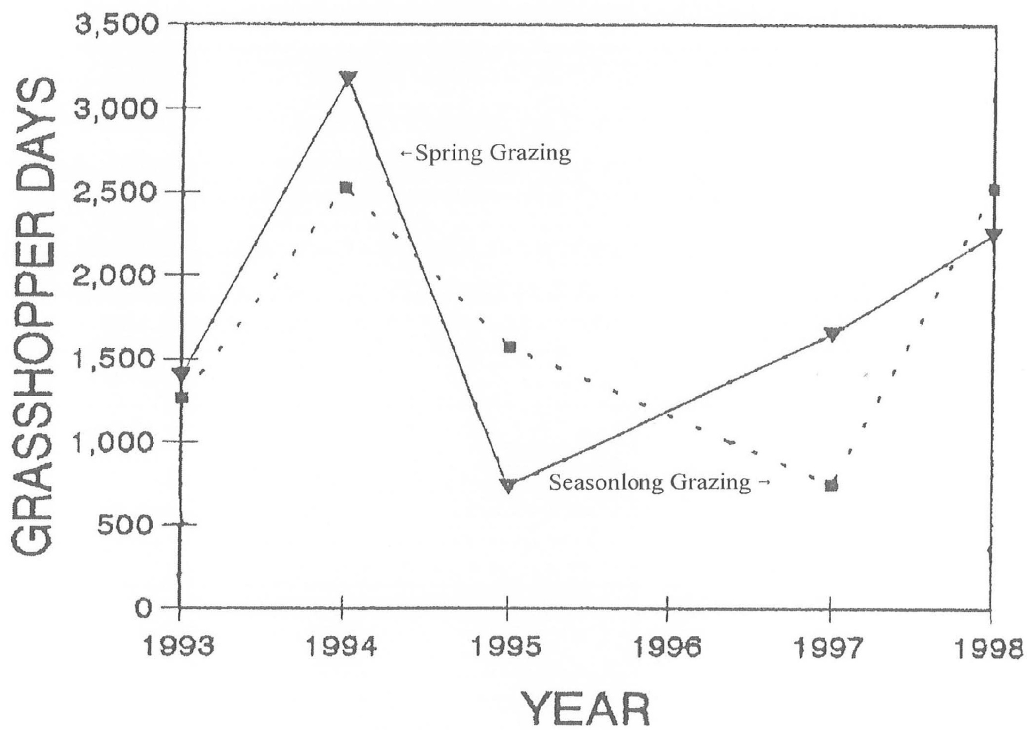


Figure 2. Grasshopper population abundance reported as grasshopper days per square meter on crested wheatgrass managed with spring grazing and seasonlong grazing. Data from Onsager 2000.

Table 37. Monthly herbage biomass (lbs/ac) for crested wheatgrass managed with spring grazing on one pasture system, 1995-1998.

Plant Biotype	May	Jun	Jul	Aug	Sep	Mean Monthly
Domesticated	625.13	751.61	1089.13	975.00	1119.58	912.09
Native Grass	69.28	58.72	79.19	76.37	107.86	78.28
Total Forbs	46.99	36.59	105.91	44.15	77.16	62.16
Total Live	741.40	861.74	1274.23	1095.52	1304.60	1055.50
Standing Dead	511.74	205.90	183.01	139.65	137.45	235.55
Standing Biomass	1253.14	1067.64	1457.24	1235.17	1442.05	1291.05
Litter	415.21	398.00	296.24	322.61	678.30	422.07
Total Dead	926.95	603.90	479.25	462.26	815.75	657.62
Total Biomass	1668.35	1465.64	1753.48	1557.78	2120.35	1713.12

Table 38. Monthly composition (%) of herbage biomass for crested wheatgrass managed with spring grazing on one pasture system, 1995-1998.

Plant Biotype	May	Jun	Jul	Aug	Sep	Mean Monthly
Domesticated	84.32	87.22	85.47	89.00	85.82	86.41
Native Grass	9.34	6.81	6.21	6.97	8.27	7.42
Total Forbs	6.34	4.25	8.31	4.03	5.91	5.89
Total Live	44.44	58.80	72.67	70.33	61.53	61.61
Standing Dead	30.67	14.05	10.44	8.96	6.48	13.75
Standing Biomass	75.11	72.84	83.11	79.29	68.00	75.36
Litter	24.89	27.16	16.89	20.71	31.99	24.64
Total Dead	55.56	41.20	27.33	29.67	38.47	38.38
Total Biomass	1668.35	1465.64	1753.48	1557.78	2120.35	1713.12

Table 39. Monthly herbage biomass (lbs/ac) for crested wheatgrass managed with spring grazing on two pasture twice-over switchback system, 1995-1998.

Plant Biotype	May	Jun	Jul	Aug	Sep	Mean Monthly
Domesticated	991.59	721.04	1265.86	1096.50	1255.83	1066.16
Native Grass	54.08	73.09	99.10	67.62	85.10	75.80
Total Forbs	8.36	21.20	45.51	33.61	35.28	28.79
Total Live	1054.03	815.33	1410.47	1197.73	1376.21	1170.75
Standing Dead	314.16	81.20	40.18	49.74	48.36	106.73
Standing Biomass	1368.19	896.53	1450.65	1247.47	1424.57	1277.48
Litter	524.53	433.34	297.89	339.92	628.32	444.80
Total Dead	838.69	514.54	338.07	389.66	676.68	551.53
Total Biomass	1892.72	1329.87	1748.54	1587.39	2052.89	1722.28

Table 40. Monthly composition (%) of herbage biomass for crested wheatgrass managed with spring grazing on two pasture twice-over switchback system, 1995-1998.

Plant Biotype	May	Jun	Jul	Aug	Sep	Mean Monthly
Domesticated	94.08	88.44	89.75	91.55	91.25	91.07
Native Grass	5.13	8.96	7.03	5.65	6.18	6.47
Total Forbs	0.79	2.60	3.23	2.81	2.56	2.46
Total Live	55.69	61.31	80.67	75.45	67.04	67.98
Standing Dead	16.60	6.11	2.30	3.13	2.36	6.20
Standing Biomass	72.29	67.41	82.96	78.59	69.39	74.17
Litter	27.71	32.59	17.04	21.41	30.61	25.83
Total Dead	44.31	38.69	19.33	24.55	32.96	32.02
Total Biomass	1892.72	1329.87	1748.54	1587.39	2052.89	1722.28

Table 41. Percentage difference of monthly herbage biomass on the two pasture system compared to the one pasture system of spring grazing crested wheatgrass, 1995-1998.

Plant Biotype	May	Jun	Jul	Aug	Sep	Mean Monthly
Domesticated	58.62	-4.07	16.23	12.46	12.17	16.89
Native Grass	-21.94	24.47	25.14	-11.46	-21.10	-3.17
Total Forbs	-82.21	-42.06	-57.03	-23.87	-54.28	-53.68
Total Live	42.17	-5.39	10.69	9.33	5.49	10.92
Standing Dead	-38.61	-60.56	-78.04	-64.38	-64.82	-54.69
Standing Biomass	9.18	-16.03	-0.45	1.00	-1.21	-1.05
Litter	26.33	8.88	0.56	5.37	-7.37	5.39
Total Dead	-9.52	-14.80	-29.46	-15.71	-17.05	-16.13
Total Biomass	13.45	-9.26	-0.28	1.90	-3.18	0.53

Table 42. Basal cover (%) and composition (%) for crested wheatgrass managed with spring grazing on two pastures and one pasture systems, 1995-1998.

Plant Biotype	Two Pasture System		One Pasture System	
	Basal Cover %	Composition %	Basal Cover %	Composition %
Domesticated	21.72	82.77	18.16	87.56
Native Grass	3.79	14.44	1.76	8.49
Sedges	0.24	0.91	0.20	0.96
Total Forbs	0.48	1.83	0.63	3.04
Total Live	26.24		20.74	
Litter	71.37		76.29	
Bare Soil	2.39		2.98	

Table 43. Percent difference of basal cover on the two pasture system compared to the one pasture system of spring grazing crested wheatgrass, 1995-1998.

Plant Biotype	Difference % 1995-1998
Domesticated	19.60
Native Grass	115.34
Sedges	20.00
Total Forbs	-23.81
Total Live	26.52
Litter	-6.45

Table 44. Crested wheatgrass weekly percent crude protein and phenological growth stages of ungrazed lead tillers.

Sample Date	Percent Crude Protein	Phenological Growth Stages
Apr 1		
13	15.5	Early leaf greenup
19	17.1	
25	16.2	Three and a half new leaves
May 4	19.0	Active leaf growth
10	21.0	
16	16.2	Flower stalk developing
23	14.5	
28	13.5	Flowering (anthesis)
Jun 6	12.1	
13	11.5	Seed developing
19	10.6	
26	9.7	
Jul 2	8.6	Seed maturing
8	7.5	
16	7.5	Seed mature
24	6.4	
30	6.4	Tiller drying
Aug 6	5.9	
13	5.8	
20	5.8	
26	5.8	
Sep 3	4.5	

Data from Whitman et al. 1951

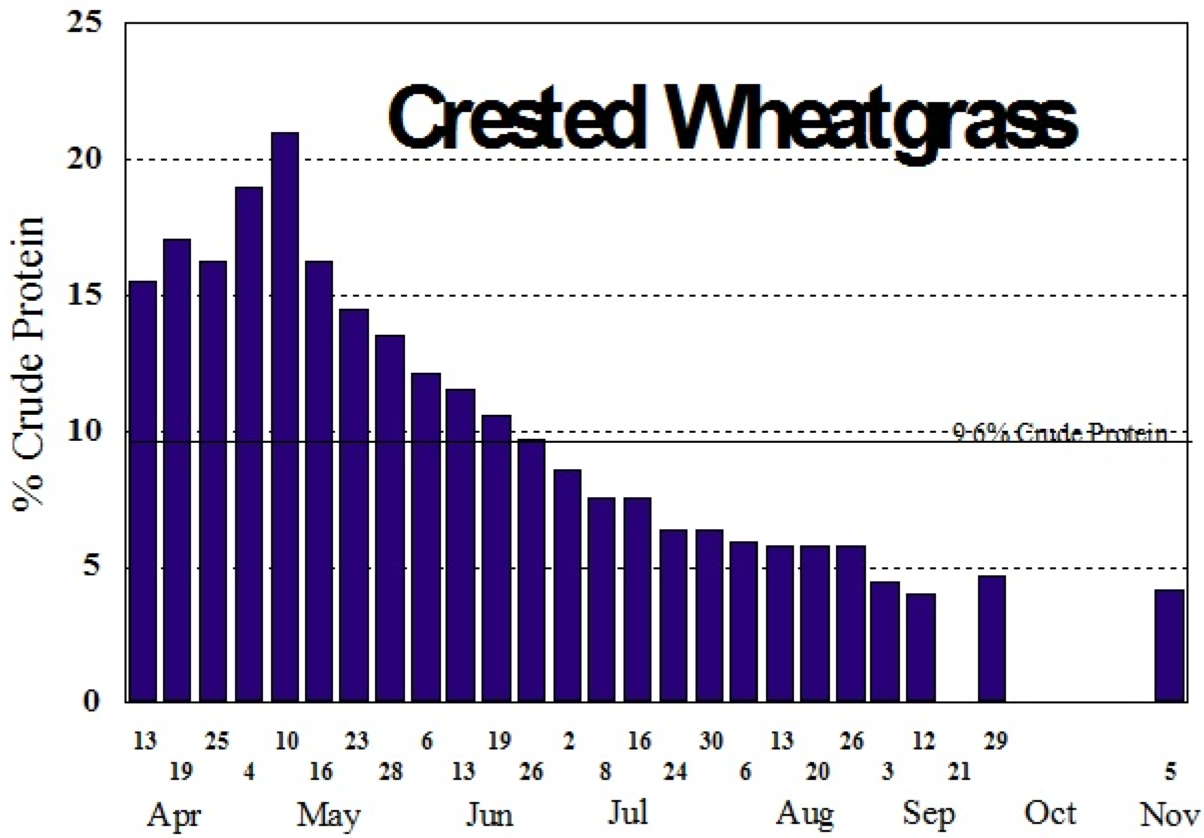


Fig 3. Mean percent crude protein of ungrazed crested wheatgrass in western North Dakota, data from Whitman et al. 1951.

Table 45. Forage dry matter biomass and crude protein yield and costs for crested wheatgrass hay cut at two growth stages.

	Costs/acre								
	Land Rent	Custom Work	Baling Costs	Production Costs $/ac	Forage Biomass Yield lb/ac	Forage Biomass Costs $/ton	Crude Protein %	Crude Protein Yield lb/ac	Crude Protein Costs $/lb
Crested Wheatgrass									
Mature	14.22	5.31	8.58	28.11	1600	34.80	6.4	102	0.28
Boot stage	14.22	5.31	6.97	26.50	1300	40.80	14.5	189	0.14

Data from Manske 2002.

Proactive Management of Native Rangeland

Management of native rangeland is in a prolonged period of transformation from using the old concepts of increaser and decreaser species and plant community succession for management of just the aboveground components to using the new concepts of defoliation resistance mechanisms and biogeochemical processes for management of all the aboveground and belowground components. The relatively recent inclusion of the biological and physiological mechanisms within plants, the biogeochemcial processes in soils, and the vital role of soil microorganisms in native rangeland ecosystem management is a major paradigm shift that may take longer than two generations of scientists and managers to accomplish.

Grass plants, rhizosphere soil microorganisms, defoliation resistance mechanisms, and grassland ecosystem biogeochemical processes all require activation through partial defoliation of grass leaves at vegetative phenological growth stages by grazing graminivores. Grass plants, soil organisms, and graminivores have coevolved complex symbiotic relationships. Large grazing graminivores depend on grass plants for nutritious forage. Grass plants depend on rhizosphere organisms for mineralization of essential elements, primarily nitrogen, from the soil organic matter. The main sources of soil organic matter are grazing animal waste and dead plant material. Rhizosphere organisms depend on grass plants for energy in the form of short carbon chains. Sufficient quantities of short carbon chain energy can be exudated from grass plants through the roots into the rhizosphere with removal of 25% to 33% of the aboveground leaf material by large graminivores while grass lead tillers are between the 3.5 new leaf stage and the flower stage. Grass plants produce double the leaf biomass than is needed for the plants existence to provide nutritious leaf forage to feed the large grazing graminivores.

Native rangelands are complex ecosystems consisting of numerous interactive biotic (living) and abiotic (nonliving) components. The biotic components are the plants, soil organisms, and large grazing graminivores that have biological and physiological requirements. The abiotic components include the major and minor essential elements that have transformable characteristics between organic and inorganic forms through biogeochemical processes. The major essential elements are carbon, hydrogen, nitrogen, and oxygen. The minor essential elements consist of seven macrominerals and ten microminerals that are required by most living organisms. The abiotic radiant energy from the sun is also an essential component.

Rangeland ecosystems are functioning units of coacting biotic organisms interacting with the abiotic components and the environment. The complex of mechanisms and processes connected with these extensive interactions have been collectively identified as defoliation resistance mechanisms and biogeochemical processes. If any of the numerous processes are not functioning at potential level, the ecosystem does not produce at potential levels. Management of rangeland ecosystems needs to meet the biological and physiological requirements of the biotic components and activate the biogeochemical processes that cycle the abiotic components. Mixed grass prairie communities require biologically effective partial defoliation by annually managed grazing graminivores in order to persist as healthy and productive ecosystems that maintain growing season residuum vegetation structure unfavorable for pestiferous rangeland grasshopper population development. Management of native rangeland favorable for pest grasshoppers should be terminated and management of native rangeland favorable for livestock production and unfavorable for pest grasshopper production needs to be evaluated and implemented.

Study Areas

The objectives of this research project were to quantitatively describe the changes to vegetation structure during the growing season caused by grazing management practices on native rangeland and to document changes to grasshopper population abundance and composition that resulted from the management caused changes to grasshopper habitat. This collaborative project was conducted from the Range Research Laboratory at the NDSU Dickinson Research Extension Center (DREC), Dickinson, North Dakota, directed by Dr. Llewellyn L. Manske and was responsible for the vegetation data, and conducted from the Rangeland Insect Laboratory at the USDA Agricultural Research Service (ARS), Bozeman, Montana, that was moved mid study to Sidney, Montana, directed by Dr. Jerome A. Onsager and was responsible for the grasshopper data.

The initial study sites were located in the North Dakota Grasshopper IPM Demonstration Project Site within the McKenzie County Grazing District of the Little Missouri Grasslands, 21 miles (34 km) west of Watford City between 47° 35' and 47° 50' N. latitude and 104° 00' and 103° 45' W. longitude, North Dakota. The study sites were provided with the cooperation of the USDA Forest Service and the McKenzie County Grazing Association. The project was funded by the USDA Animal and Plant Health Inspection Service (APHIS), Plant Protection and Quarantine (PPQ), Cooperative Grasshopper Integrated Pest Management (GHIPM) Project during the 1993 and 1994 field seasons. The two research units agreed to continue research project data collection for the field seasons of 1995 to 1998 as separate but cooperative entities. The grasshopper data collection was continued from the USDA-ARS, Sidney, Montana, laboratory on the initial study sites. The vegetation data collection was continued on similar sites located a short distance east in Dunn County at the NDSU Dickinson Research Extension Center ranch, at 46° 48' N. latitude and 102° 48' W. longitude, near Manning, North Dakota. The native rangeland vegetation at the McKenzie County and Dunn County locations is the Wheatgrass-Needlegrass Type (Barker and Whitman 1989) of the mixed grass prairie.

Long-Term Regional Weather

The western North Dakota region has cold winters and hot summers typical of continental climates. Mean annual temperature is 40.9º F (4.9º C). January is the coldest month, with a mean temperature of 11.5º F (-11.4º C). July and August are the warmest months, with mean temperatures of 68.7º F (20.4º C) and 67.0º F (19.5º C), respectively. Long-term (1892-2010) mean annual precipitation is 16.03 inches (407.15 mm). The precipitation during the perennial plant growing season (April through October) is 13.54 inches (343.76 mm) and is 84.5% of the annual precipitation. June has the greatest monthly precipitation, at 3.55 inches (90.14 mm). The precipitation received in the three month period of May, June, and July is 8.13 inches (206.50 mm) and is 50.7% of the annual precipitation (Manske 2011f).

Water stress develops in perennial plants during water deficiency periods when the amount of rainfall is less than evapotranspiration demand. Water deficiency months were identified from historical temperature and precipitation data by the ombrothermic diagram technique (Emberger et al. 1963). The long-term (1892-2010) ombrothermic diagram shows near water deficiency conditions during August, September, and October, and favorable water relations during April, May, June, and July. Reoccurrence of water deficiency conditions during April, May, June, and July is 16.9%, 13.6%, 10.2%, and 38.1%, respectively, and during August, September, and October water deficiency reoccurs 52.5%, 50.0%, and 46.6% of the years, respectively. Long-term occurrence of water deficiency conditions is 32.7% of the growing season months, for a mean of 2.0 water deficient months per growing season (Manske et al. 2010).

Growing Season Precipitation

Growing season (April to September) precipitation for the McKenzie County study sites was taken from the Watford City ndawn weather station and reported by Onsager 2000 (table 46). Long-term (31 years) annual precipitation for the area was 14.41 inches (366.01 mm). Growing season precipitation for 1993 and 1995 was above normal. Growing season precipitation for 1994 and 1996 was below normal and for 1997 and 1998 conditions were dry with perennial plants under water stress some of the time. The growing season conditions progressively became warmer and dryer during the six years of data collection at the McKenzie County study sites.

Precipitation for the perennial plant growing season months (April through October) for the Dunn County study sites was taken from the DREC ranch weather station and reported by Manske 2013 (table 47). Long-term (31 years) annual precipitation for the area was 16.91 inches (429.51 mm). Growing season precipitation for 1993 to 1997 was normal each year and was above normal for 1998. Water deficiency conditions occurred during August, September, and October in 1993; July, August, and September in 1994; June and September in 1995; April and October in 1996; August in 1997; and April and September in 1998.

Management Treatments

Two native rangeland grazing management treatments were established at the McKenzie County location on allotments with previously existing grazing practices. The management treatments were a seasonlong grazing system and a twice-over rotation grazing system.

The seasonlong grazing system study plots were established on two separate native rangeland areas within one large pasture. Each study plot had two replicated vegetation sample sites. The extremely large pasture had been grazed annually at moderate stocking rates from 1 June to 31 October since the McKenzie County Grazing Association had been organized. The pasture was grazed during the same time period in 1993 and 1994, and from 1995 and 1998. The seasonlong grazing of native rangeland treatment was sampled for grasshopper population data at two replicated study sites during 1993 to 1998.

The twice-over rotation grazing system was established on a four pasture allotment that had been managed with the twice-over system since 1989. Each pasture had two replicated vegetation sample sites. The four pastures were each grazed during two periods per growing season. The first period was during the 45 day interval from 1 June to 15 July. The second period was during mid July to mid or late October. Cow-calf pairs grazed the four pastures from 1 June to 31 October 1993 and from 1 June to 22 October 1994, and during similar time periods from 1995 to 1998. The twice-over grazing on native rangeland treatment was sampled for grasshopper population data at four replicated study sites with one in each pasture during 1993 to 1998.

Research activity on the grasshopper habitat study continued at two locations during 1994 to 1998. The grasshopper population data was collected at the initial study sites on the seasonlong grazing system and on the twice-over grazing system at the McKenzie County locations. The vegetation data was collected on similar study sites managed with a seasonlong grazing system and with a twice-over rotation grazing system at the Dunn County locations.

The seasonlong grazing system on native rangeland was designed with two replicated pastures. Each pasture had vegetation sample plots on a silty ecological site. Each pasture was grazed for 137 days from early June stocked at 2.86 acres per cow-calf pair per month.

The twice-over rotation grazing system on native rangeland was designed with two replicated systems each with three pastures. Each pasture had vegetation sample plots on a silty ecological site. Each pasture was grazed two times per growing season. Each system was grazed 137 days from early June stocked at 2.04 acres per cow-calf pair per month. After this study, the stocking rate was reduced to 2.2 acres per cow-calf pair per month.

Procedures

Changes in residuum vegetation structure during the growing season caused by management practices on native rangeland were evaluated by aboveground herbage biomass, plant species basal cover, and bareground area collected at the McKenzie County sites during the growing seasons of 1993 and 1994 and by aboveground herbage biomass and plant species basal cover collected at the Dunn County sites during the growing seasons of 1994 to 1998.

Aboveground herbage biomass was collected by the standard clipping method (Cook and Stubbendieck 1986). All herbage biomass clipping sites were partially defoliated by the selected management treatment. The reported herbage biomass values represent the residuum vegetation and the regrowth vegetation resulting from the treatment. This study did not establish nondefoliated sample sites that show the vegetation response without the treatment. Clipped herbage material was collected monthly (May, June, July, and August) from five 0.25 m^2 quadrats (frames) during 1993 and from four 0.25 m^2 quadrats during 1994 at each replicated vegetation sample site on the seasonlong grazing system, and on the twice-over rotation grazing system at the McKenzie County research study sites. Clipped herbage material was collected monthly (June, July, August, September, and October) from five 0.25 m^2 quadrats (frames) during 1994 to 1998 at each replicated vegetation sample site on the seasonlong grazing system and on the twice-over rotation grazing system at the Dunn County research study sites. The herbage material in each frame was hand clipped to ground level and sorted in the field by biotype categories: cool season grass, warm season grass, sedges, forbs, standing dead, and litter. The herbage of each biotype category from each frame was placed in labeled paper bags of known weight, oven dried at 140° F (60° C), and weighed. Herbage biomass in pounds per acre and relative composition for each biotype category was determined from the clipping data. Mean monthly herbage biomass for each biotype category was determined for the growing season.

Plant species basal cover was determined by the ten-pin point frame method (Cook and Stubbendieck 1986) with 2000 points collected along transect lines at each replicated vegetation sample site during peak growth between mid July and mid August each year. Basal cover plant species data were sorted into biotype categories: cool season grass, warm season grass, sedges, forbs, litter, and bare soil. The bare soil category was the percent mineral soil not covered by live plants or litter. Basal cover and relative composition of biotype categories were determined from the ten-pin point frame data collected at the McKenzie County research study sites during 1993 and 1994, and at the Dunn County research study sites during 1994 to 1998.

Bareground area was determined with the line intercept method (Canfield 1941, Cook and Stubbendieck 1986) that was modified to measure linear length of intercepted open areas not covered by vegetation canopy. Ten 2000 cm (787.4 in) transect lines were established at each vegetation sample site at the McKenzie County research study sites. Bareground area percentage and combined bareground length of each transect were means of four readings per growing season conducted between June and August of 1993 and 1994.

Vegetation structure during the growing season resulting from management treatments were evaluated with herbage biomass and basal cover data. The vegetation structure caused by the twice-over rotation grazing system was compared to the vegetation structure caused by the seasonlong grazing system by percent difference data at the McKenzie County research study sites and at the Dunn County research study sites.

Grasshopper population density data was collected during 1993 to 1998 at the initial McKenzie County reseach study sites by a team of entomologists directed by Dr. Onsager using methods described by Onsager and Henry (1977). Each grasshopper study site was provided with a set of 40 aluminum wire rings, each 0.1 m^2, affixed to the ground in a 4 X 10 array with 8 meters between rings. Grasshopper populations were sampled at 7 to 10 day intervals during 1993, 1995, and 1998, and at 2 to 3 day intervals during 1994 and 1997. Sampling began as soon as the grasshopper study sites were accessible in the spring and terminated after killing frost in the fall. Total density was estimated by counting grasshoppers within each ring of the 40 wire ring array that had a total area of 4 m^2. The field data was converted into grasshopper days (GD) per m^2 which is an index of seasonal abundance for 3rd instar and older stages. The concept of grasshopper days (GD) is similar to that of animal unit months (AUM). A sweep net collection was taken along the perimeter of the 40 wire ring array each sampling period to establish composition of the population by species and by stage of development (Onsager 2000).

Results

The growing season residuum vegetation structure expected to negatively affect pestiferous rangeland grasshopper populations was greater plant herbage biomass, greater live plant basal cover, and reduced bareground areas with open vegetation canopy cover.

This study compared the residuum vegetation structure of native rangeland during the growing season on a four pasture twice-over rotation grazing system with that on a seasonlong grazing system at the McKenzie County study sites and compared the residuum vegetation structure during the growing season on a three pasture twice-over rotation grazing system with that on a seasonlong grazing system at the Dunn County study sites. Comparisons of the growing season residuum vegetation structure was evaluated using percent difference data for monthly herbage biomass and mean herbage biomass of the native grass, total live, and standing biomass biotype categories and percent difference data for basal cover of the native grass and total live biotype categories from the seasonlong grazing system and the twice-over rotation grazing system at both the McKenzie County and Dunn County study sites. Bareground area percentage and combined bareground length per 2000 cm transects were evaluated from the native rangeland grazing treatments at the McKenzie County study sites.

McKenzie County Study Sites

The seasonlong grazing system on native rangeland was grazed from 1 June to 31 October at moderate stocking rates during the 1993 and 1994 growing seasons leaving a mean monthly residual standing biomass of 757.30 lbs/ac (table 48). During the growing seasons of 1993 and 1994, the aboveground vegetation biomass on the seasonlong grazing system consisted of 31.8% standing dead and litter and 68.2% live herbage. The live herbage biomass was 90.3% native grass (51.2% warm season grass and 39.0% cool season grass), 2.3% sedges, and 7.4% forbs (table 49).

The twice-over rotation grazing system on native rangeland was grazed from early June to mid or late October at moderate stocking rates during the 1993 and 1994 growing seasons leaving a mean monthly residual standing biomass of 1074.74 lbs/ac (table 50). During the growing seasons of 1993 and 1994, the aboveground vegetation biomass on the twice-over grazing system consisted of 40.8% standing dead and litter and 59.2% live herbage. The live herbage biomass was 91.1% native grass (78.8% cool season grass and 12.3% warm season grass), 1.0% sedges, and 7.9% forbs (table 51).

The mean monthly herbage biomass of the native grass, total live, and standing biomass biotypes on the seasonlong grazing system was 550.93 lbs/ac, 610.26 lbs/ac, and 757.30 lbs/ac, respectively (table 48), and on the twice-over grazing system was 755.38 lbs/ac, 828.99 lbs/ac, and 1074.74 lbs/ac, respectively (table 50). The twice-over grazing system produced greater live residual herbage biomass than the seasonlong grazing system. The twice-over grazing system produced 37.1% greater native grass biomass, 35.8% greater total live biomass, and 41.9% greater standing herbage biomass than that produced on the seasonlong grazing system (table 52). The standing herbage biomass biotype on the seasonlong grazing system consisted of 72.8% native grass, 31.5% cool season grass, 41.3% warm season grass, 1.9% sedges, 6.0% forbs, and 19.4% standing dead herbage. The standing herbage biomass biotype on the twice-over grazing system consisted of 70.3% native grass, 60.8% cool season grass, 9.5% warm season grass, 0.8% sedges, 6.1% forbs, and 22.9% standing dead herbage.

Basal cover during the 1993 and 1994 growing seasons on the seasonlong grazing system of the native grass and total live biotypes was 29.0% and 34.9%, respectively (table 53), and on the twice-over grazing system of the native grass and total live biotypes was 29.2% and 35.8%, respectively (table 54). The basal cover of the native grass biotype was 0.8% greater and of the total live biotype was 2.4% greater on the twice-over grazing system than those on the seasonlong grazing system (table 55). The differences of basal cover on the twice-over grazing system and the seasonlong grazing system were small.

Bare soil, or mineral soil not covered by live plants or litter, percentages measured with the ten-pin point frame method was 7.6% and 6.4% on the seasonlong grazing system and on the twice-over grazing system, respectively (tables 53 and 54). The bare soil on the seasonlong grazing system was 20.2% greater than that on the twice-over rotation grazing system.

Bareground, or open canopy, area measured with the line intercept method during the 1993 and 1994 growing seasons was 7.4%, 148 cm/2000 cm transect, on the seasonlong grazing system (table 56), and was 7.5%, 150 cm/2000 cm transect, on the twice-over grazing system (table 57). The bareground area on the seasonlong grazing system and on the twice-over grazing system were not different.

The residuum vegetation structure resulting from the two grazing management treatments were quite different, with the seasonlong grazing system composed primarily of short warm season grass and upland sedge and with the twice-over rotation grazing system composed primarily of mid height cool season grass.

The seasonlong grazing system had shorter height structure with relative cover of 46.3% short grass (table 58), had basal cover composition with 140.8% greater warm season grass and 53.7% greater upland sedge (table 53), and had herbage biomass composition with 315.9% greater warm season grass and 133.3% greater upland sedge (table 49) than those on the twice-over grazing system.

The twice-over rotation grazing system had taller height structure with relative cover of 53.8% mid height cool season grass (table 58), had basal cover composition with 47.4% greater cool season grass (table 54), and had herbage biomass composition with 101.8% greater cool season grass (table 51) than those on the seasonlong grazing system.

The residuum vegetation structure on the seasonlong grazing system was primarily short grass and sedges and was good pestiferous rangeland grasshopper habitat. The residuum vegetation structure on the twice-over rotation grazing system was primarily mid height cool season grasses and was poor pestiferous rangeland grasshopper habitat.

Mean cumulative grasshopper days (GD) per m^2 were significantly greater on the seasonlong grazing system than on the twice-over rotation grazing system (Onsager 2000) (table 59). The seasonlong grazing system had an annual mean of 358 GD for the 9 pestiferous rangeland grasshoppers and had an annual mean of 748 GD for the total of all grasshopper species. The twice-over grazing system had an annual mean of 122 GD for the 9 pestiferous rangeland grasshoppers and had an annual mean of 229 GD for the total of all grasshopper species (table 59).

One grasshopper species, Mel sanguinipes, had elevated annual mean grasshopper days per m^2 on both grazing systems with 87 GD on the seasonlong grazing system and 78 GD on the twice-over grazing system (table 59). Population abundance of four grasshopper species, Mel gladstoni, Ope obscura, Enc costalis, and Mel infantilis, increased significantly to annual means of 88 GD, 71 GD, 57 GD, and 26 GD, respectively, on the seasonlong grazing system while remaining at low annual means of 3 GD, 6 GD, 10 GD, and 5 GD, respectively, on the twice-over grazing system (table 59). No grasshopper species had population abundance at significantly greater grasshopper days on the twice-over grazing system than on the seasonlong grazing system (Onsager 2000) (table 59). Four grasshopper species, Pho nebrascensis, Mel femurrubrum, Tra kiowa, and Age deorum, had low population abundance on both the seasonlong grazing system and the twice-over grazing system (table 59).

Grasshopper populations on the seasonlong grazing system had moderate densities between 3.8/yd^2 and 6.9/yd^2 with monthly forage use between 38.6 lbs/ac and 80.8 lbs/ac during 1993 to 1995 (table 60). Grasshopper populations on the twice-over grazing system had low densities between 1.2/yd^2 and 2.8/yd^2 with monthly forage use between 14.2 lbs/ac and 36.2 lbs/ac during 1993 to 1995 (table 60).

Grasshopper population assemblage increased to outbreak levels in 1997 and 1998 on the seasonlong grazing system (figure 4) (Onsager 2000). Grasshopper densities on the seasonlong grazing system increased greatly to 15.4/yd^2 in 1997 with monthly forage use of 186.5 lbs/ac and densities increased further to 22.4/yd^2 in 1998 with monthly forage use of 307.7 lbs/ac (table 60).

This huge grasshopper population outbreak did not occur on the twice-over rotation grazing system (figure 4) (Onsager 2000). Grasshopper densities on the twice-over grazing system remained low at 1.8/yd^2 in 1997 with monthly forage use of 21.2 lbs/ac and densities increased slightly to 4.7/yd^2 in 1998 with monthly forage use of 47.7 lbs/ac (table 60).

The residuum vegetation structure on the seasonlong grazing system was comprised primarily of short stature warm season grass and upland sedge which was the major factor that permitted the grasshopper population assemblages to greatly increase above outbreak levels. The outbreak assemblage consisted of three major species, Enc costalis, Mel gladstoni, and Ope obscura. All three species hatch with intermediate or late groups after early June reducing the development time to hard frost by greater than a month compared to the hatch time of the very early or early groups.

In order for grasshopper species that hatch after early June to survive in northern habitats, nymphal development, adult growth and maturation, mating, egg development, and egg deposition needs to progress at near physiological capabilities. Sustentation of these high rates of growth and development depend on the body temperature to be at optimum during most of the daylight hours. Maintaining body temperature at optimum requires readily accessible direct sunlight. In order for late hatching grasshopper populations to increase above outbreak quantities, a huge proportion of the nymphal population must develop to the adult stage at near potential rates and successfully deposit large numbers of eggs during a minimum of two consecutive years.

The taller residuum vegetation structure on the twice-over rotation grazing system was comprised primarily of mid height cool season grass that restricted grasshopper access to direct sunlight decreasing the length of time that body temperature could be maintained at optimum levels causing reduction in the rates of growth and development that delayed adult maturation and egg development impeding egg deposition and thus preventing the population assemblage from increasing to outbreak numbers.

The vegetation structure on the twice-over grazing system successfully prevented population increases of all the grasshopper species that hatched after early June with the late and intermediate groups and also prevented population increases of the grasshopper species hatching before June with the early group that preferred to bask on bareground (table 59). The vegetation structure on the twice-over grazing system was not fully successful at preventing population increases of the grasshopper species hatching with the early group that were capable of basking both on bareground and on vegetation (table 59).

Onsager (2000) determined that nymphal development of the 3rd instar to the 5th instar of Mel sanguinipes was significantly slower and required 2.6 days longer for development per instar on the twice-over grazing system with a mean of 11.5 days per instar than that on the seasonlong grazing system with a mean of 8.9 days per instar resulting in a delay of 7.8 days for the appearance of adults on the twice-over grazing system. This delay in nymphal development had a major impact on the proportion of the nymphal population that became adults. The population density counts conducted by Onsager (2000) revealed that the twice-over grazing system with a mean density of 0.60 adults/m^2 (0.5/yd^2) produced fewer adult grasshoppers than that produced on the seasonlong grazing system with a mean density of 2.05 adults/m^2 (1.71/yd^2). Onsager (2000) gave two explanations that would cause the measured delay in instar development. The vegetation structure on the twice-over grazing system interfered with the amount of direct sunlight reaching the grasshopper microhabitat causing the ambient air temperature to become cooler and/or preventing efficient thermoregulation of nymphal body temperature. In addition, Onsager (2000) showed that, although the statistical average daily survival rates for nymphs on the twice-over grazing system and on the seasonlong grazing system were not significantly different, the slightly lower biological survival rate for nymphs on the twice-over grazing system over the longer delayed development time for three instar stages could result in the great difference in the measured densities of adult grasshoppers with 70.7% fewer adult grasshoppers per square meter on the twice-over grazing system than on the seasonlong grazing system. Greatly reduced densities of adult grasshopper would deposit lower quantities of viable eggs that season and produce fewer hatchlings the next growing season.

Dunn County Study Sites

The seasonlong grazing system on native rangeland was grazed from early June to mid October at a stocking rate of 2.86 ac/AUM during the 1994 to 1998 growing seasons leaving a mean monthly residual standing herbage biomass of 689.29 lbs/ac (table 61). During the growing seasons of 1994 to 1998, the aboveground vegetation biomass on the seasonlong grazing system consisted of 27.5% standing dead and litter and 72.5% live herbage. The live herbage biomass was 66.3% native grass (38.4% cool season grass and 27.6% warm season grass), 24.2% sedges, and 9.6% forbs (table 62).

The twice-over rotation grazing system on native rangeland was grazed from early June to mid October at a stocking rate of 2.04 ac/AUM during the 1994 to 1998 growing seasons leaving a mean monthly residual standing herbage biomass of 823.72 lbs/ac (table 63). During the growing seasons of 1994 to 1998, the aboveground vegetation biomass on the twice-over grazing system consisted of 26.2% standing dead and litter and 73.8% live herbage. The live herbage biomass was 70.7% native grass (29.4% cool season grass and 41.3% warm season grass), 18.3% sedges, and 11.0% forbs (table 64).

The peak monthly herbage biomass during July of the native grass, total live, and standing biomass biotypes on the seasonlong grazing system was 407.47 lbs/ac, 663.74 lbs/ac, and 688.74 lbs/ac, respectively (table 61), and on the twice-over grazing system was 623.51 lbs/ac, 898.49 lbs/ac, and 948.87 lbs/ac, respectively (table 63). The twice-over grazing system produced greater peak live residual herbage biomass than the seasonlong grazing system. The twice-over grazing system produced 53.0% greater native grass biomass, 35.4% greater total live biomass, and 37.8% greater standing herbage biomass than that produced on the seasonlong grazing system during peak production in July (table 65). The composition of the native grass biotype on the seasonlong grazing system consisted of 58.6% cool season grass and 41.4% warm season grass in July. The composition of the native grass biotype on the twice-over grazing system consisted of 48.2% cool season grass and 51.8% warm season grass in July.

The mean monthly herbage biomass of the native grass, total live, and standing biomass biotypes on the seasonlong grazing system was 418.70 lbs/ac, 631.77 lbs/ac, and 689.29 lbs/ac, respectively (table 61), and on the twice-over grazing system was 534.53 lbs/ac, 755.70 lbs/ac, and 823.72 lbs/ac, respectively (table 63). The twice-over grazing system produced greater live residual herbage biomass during the growing season than the seasonlong grazing system. The twice-over grazing system produced 27.7% greater native grass biomass, 19.6% greater total live biomass, and 19.5% greater standing herbage biomass than that produced on the seasonlong grazing system (table 65). The standing herbage biomass biotype on the seasonlong grazing system consisted of 60.7% native grass, 35.5% cool season grass, 25.3% warm season grass, 22.1% sedges, 8.8% forbs, and 8.3% standing dead herbage. The standing herbage biomass biotype on the twice-over grazing system consisted of 64.9% native grass, 27.0% cool season grass, 37.9%

warm season grass, 16.8% sedges, 10.1% forbs, and 8.3% standing dead herbage.

Basal cover during the 1994 to 1998 growing seasons on the seasonlong grazing system of the native grass, sedges, and total live biotypes was 14.8%, 8.8%, and 26.2%, respectively (table 66), and on the twice-over grazing system of the native grass, sedges, and total live biotypes was 20.7%, 3.6%, and 26.4%, respectively (table 66). The basal cover of the native grass biotype was 39.4% greater and of the total live biotype was 0.8% greater on the twice-over grazing system than on the seasonlong grazing system (table 67). The basal cover of the sedge biotype was 146.1% greater on the seasonlong grazing system than on the twice-over grazing system. The sedge biotype on the seasonlong grazing system composed 24.2% of the live herbage biomass (table 62), and 33.5% of the live basal cover (table 66). The sedge biotype on the twice-over grazing system composed 18.3% of the live herbage biomass (table 64), and 13.5% of the live basal cover (table 66).

Bare soil, or mineral soil not covered by live plants or litter, percentages measured with the ten-pin point frame method were low at 1.3% and 1.1% on the seasonlong grazing system and on the twice-over grazing system, respectively (table 66). The bare soil on the seasonlong grazing system was 18.2% greater than that on the twice-over rotation grazing system.

Grasshopper population density data were not collected on these Dunn County native rangeland research study sites. However, during vegetation data collection, very few grasshoppers were observed on the seasonlong grazing system and on the twice-over grazing system. The small quantity of grasshoppers present were not a problem. Furthermore, the growing season residuum vegetation structure on native rangeland managed with the twice-over rotation grazing strategy produced 27.7% greater native grass herbage biomass, 19.6% greater total live herbage biomass, 19.5% greater standing herbage biomass, and 39.4% greater native grass basal cover than that produced on native rangeland managed with the seasonlong grazing system.

Greater activation of the plant defoliation resistance mechanisms and the ecosystem biogeochemical processes on the twice-over grazing system resulted in greater livestock weight gain than on the seasonlong grazing system. During the growing season from early June to mid October, cows and calves gained 9.4 lbs/ac and 33.6 lbs/ac, respectively, on the twice-over grazing system, and cows and calves gained 3.7 lbs/ac and 22.6 lbs/ac, respectively, on the seasonlong grazing system. Cow gains were 157.2% greater and calf gains were 49.2% greater per acre on the twice-over grazing system than on the seasonlong grazing system.

Discussion

Native rangeland cool season grasses start early leaf greenup in mid April and grow slowly until early May, reaching 59% of the leaf growth in height by mid May. Most cool season grasses reach the three and a half new leaf stage around early June, reach 94% of the leaf growth in height by late June, and 100% of the leaf growth in height by late July. A few early developing cool season grasses start flower stalk development during mid May to early June. The other cool season grasses develop flower stalks during June. The needlegrasses start the flower stage during early June, with most cool season grasses starting to flower before 21 June. Flower stalks reach 94% of the growth in height by late June and 100% of the growth in height by late July when seeds are mature and being shed (Whitman et al. 1951, Goetz 1963, Manske 2000c).

The nutritional quality of ungrazed lead tillers of native rangeland cool season grasses changes with the tillers' phenological development. Early season growth stages during May have high crude protein levels above 16%. The early vegetative leaf stages contain levels of crude protein above 15% during early to mid June. As seed stalks begin to develop in early June, crude protein levels begin to decrease. At the flower stage, lead tillers contain 15% crude protein. After the flower stage and during the seed development stage, crude protein levels remain above 9.6% until mid July. As the ungrazed lead tillers mature, the fiber content increases and percent crude protein, water, and digestibility decrease. During late July, crude protein levels drop below 8.0% and below 6.5% in late August (figure 5) (Whitman et al. 1951, Manske 2008a). Crude protein levels of grazing activated cool season secondary tillers increase above 9.6% during July and August to 13.2% in early September, decrease during September, and drop below 9.6% in early to mid October (Sedivec 1999, Manske 2008a). Phosphorus levels of lead tillers drop below 0.18% in late July, when plants reach the mature seed stage (Whitman et al. 1951, Manske 2008b).

Native rangeland warm season grasses start early leaf greenup in mid May, reaching 44% of the leaf growth in height by early June, and most warm season grasses reach the three and a half new leaf stage around mid June. Warm season grasses reach 85% of the leaf growth in height by late June and reach 100% of the growth in height by late July. Flower stalk development starts during mid June, with the flower stage starting after 21 June. Most warm season grasses reach the flower stage by 15 July. The warm season flower stalks reach 91% of the growth in height by late July and reach 100% growth in height by late August when the seeds are mature and being shed (Whitman et al. 1951, Goetz 1963, Manske 2000c).

The nutritional quality of ungrazed lead tillers of native rangeland warm season grasses changes with the tillers' phenological development. Early season growth stages during May have high crude protein levels above 15%. The early vegetative leaf stages contain levels of crude above 13% during early to mid June. As seed stalks begin to develop in mid June, crude protein levels begin to decrease. At the flower stage, lead tillers contain 12.2% crude protein. After the flower stage and during the seed development stage, crude protein levels remain above 9.6% until late July. As the ungrazed lead tillers mature, the fiber content increases and percent crude protein, water, and digestibility decrease. During mid August, crude protein levels drop below 7.0% and below 6.0% in early September (figure 6) (Whitman et al. 1951, Manske 2008a). Crude protein levels of grazing activated warm season secondary tillers increase above 9.0% during August to 10.0% in early September, decrease during September, and drop below 9.6% in late September (Sedivec 1999, Manske 2008a). Phosphorus levels of lead tillers drop below 0.18% in late August, when plants reach the mature seed stage (Whitman et al. 1951, Manske 2008b).

Native rangelands are optimally grazed by large graminivores as summer pastures from 1 June to mid October. Prior to early June, the cool season and warm season grasses are not physiologically capable of full recovery from grazing defoliation. After mid October, the nutritional quality of the herbage from the combination of lead tillers, vegetative tillers, and activated secondary tillers drops below the requirements of lactating beef cows.

Biologically effective management of native rangelands places first priority on meeting the biological and physiological requirements of the grass plants, soil organisms, and grazing animals, and to cycle the essential elements. The second priority is the diminishment of the factors that reduce ecosystem productivity and the enhancement of the factors that benefit ecosystem productivity. Perennial grass growth in the Northern Plains is restricted to a 6 month growing season, from mid April to mid October. Native rangeland grasses require 1.5 months of growth in the spring to reach grazing readyness resulting in a 4.5 month grazing season, from early June to mid October.

The early greenup of rangeland grass in the spring is not from new seedlings but from vegetative carryover tillers that did not produce a seedhead during the previous growing season. Spring growth of carryover tillers depends both on carbohydrate reserves and on photosynthetic products from the portions of previous years leaves that overwintered without cell wall rupture and regreened with chlorophyll. Grass tiller growth and development depend, in part, on some carbohydrate reserves in early spring because the amount of photosynthetic product synthesized by the green carryover leaves and the first couple of early growing new leaves is insufficient to meet the total requirements for leaf growth (Coyne et al. 1995). Grass growth also requires that the tiller maintains adequate leaf area with a combination of carryover leaves and new leaves to provide photosynthetic product for growth of sequential new leaves. The total nonstructural carbohydrates of a grass tiller are at low levels following the huge reduction of reserves during the winter respiration period, and the carbohydrate reserves remaining in the roots and crowns are needed for both root growth and initial leaf growth during early spring. The low quantity of reserve carbohydrates are not adequate to supply the entire amount required to support root growth and also support leaf growth causing a reduction in active growth until sufficient leaf area is produced to provide the photosynthetic assimilates required for plant growth and other processes (Coyne et al. 1995). Removal of aboveground leaf material from grass tillers not yet at the three and a half new leaf stage deprives tillers of foliage needed for photosynthesis and increases the demand upon already low levels of carbohydrate reserves. Premature grazing results in greatly reduced growth rates of herbage production (Coyne et al. 1995) causing decreased peak herbage biomass later in the growing season (Manske 2000b). Grazing that starts in mid to late May on native rangeland before the tillers reach the 3.5 new leaf stage results in a reduction of 45% to 60% from the potential herbage biomass that growing season (Campbell 1952, Rogler et al. 1962, Manske 2000b).

During the growing season, grass growth can be reduced by the environmental factors of inhibiting cool temperatures during the spring and fall and hot temperatures during the summer and by unevenly distributed precipitation. The precipitation received during the three month period, May, June, and July, is 50.7% of the annual precipitation, which is usually accompanied with generally low water deficiency conditions that reoccur with an average monthly rate during each of these three months at 20.6% of the growing seasons, and promotes rapid grass growth and development. Grass growth is limited during the three month period, August, September, and October, when the precipitation received is 25% of the annual amount and water deficiency conditions are usually high and reoccur with an average monthly rate during each of these three months at 49.7% of the growing seasons (Manske et al. 2010, Manske 2011f).

Low water infiltration on native rangelands and shallow soil water storage depths aggravate problems of grass plant growth between rain events. Restricted water infiltration increases the proportion of runoff precipitation, decreasing the quantity of water available for plant growth, and reducing the quantity of the effective precipitation. Low water infiltration rates and shallow water storage depths indicate inadequate soil aggregation and low soil fungi biomass. Aggregation of soil develops when an adequate biomass of soil fungi secrete large amounts of insoluable extracellular polysaccharids that have adhesive qualities (Caesar-TonThat and Cochran 2000; Caesar-TonThat et al. 2001a, 2001b; Caesar-TonThat 2002; Manske and Caesar-TonThat 2003). Aggregation of soil enlarges soil pore size, improves soil pore distribution, and stabilizes soil particles, resulting in improved water infiltration and increased soil water storage capacity (Caesar-TonThat et al. 2001b, Manske and Caesar-TonThat 2003). Greater soil aggregation increases the effectiveness of the precipitation received, increases the quantity of soil water available for plant growth, and reduces plant growth problems between rain events.

Water from precipitation is important for grass growth. However, herbage production in temperate rangelands is more often limited by deficiencies in mineral nitrogen than by water (Tilman 1990). Rangelands deficient in available soil mineral nitrogen produce less than potential quantities of herbage biomass (Wight and Black 1972). Native rangelands with a mineral nitrogen deficiency produce herbage weight per inch of precipitation received at 49.6% below the weight of herbage produced per inch of precipitation on rangeland without a mineral nitrogen deficiency (Wight and Black 1979).

Rangeland soils are not deficient of nitrogen. Most of the nitrogen is immobilized in the soil as organic nitrogen. Rangeland soils in the Northern Plains contain about 5 to 6 tons, with a range of 3 to 8 tons, of organic nitrogen per acre. The organic nitrogen is not available for plant use. Soil organic nitrogen must be converted into mineral nitrogen through mineralization by soil microorganisms. The quantity of soil organism biomass is the limiting factor in rangeland ecosystems low in mineral nitrogen. The rhizosphere soil organism biomass and activity are limited by access to short carbon chain energy. The primary producer trophic level in the rhizosphere are achlorophyllous saprophytes and can not fix carbon for energy. Greater quantities of carbon compound energy exudated into the rhizosphere increases the biomass and activity of the soil organisms resulting in increased mineralization of nitrogen, increased biogeochemical cycling of essential elements, and improvements of belowground resource competitiveness (Manske 1999a, 2011b). Mineral nitrogen available at 100 lbs/ac or greater is needed for herbage biomass weight to be produced at ecosystem potential levels (Wight and Black 1972).

The three month period, May, June, and July, is the period that receives the greatest amount of rainfall and is the short period of the growing season when grass lead tillers grow the most in height and weight. Cool season grasses develop to the 3.5 new leaf stage by early June and start the flower stage before 21 June. Warm season grasses develop to the 3.5 new leaf stage by mid June and reach the flower stage by mid July. Cool season grass lead tillers drop below 9.6% crude protein during the third week of July and warm season grass lead tillers drop below 9.6% crude protein during the fourth week of July (Manske 2000b, 2000c, 2008a). After mid to late July, native rangeland pastures managed with traditional concepts typically consists of herbage below the nutritional requirements of lactating beef cows. These cows lose body weight and decrease in daily milk production. The calves' average daily gain drops below 2.0 pounds per day (Manske 2002).

The herbage quality greatly declines on traditionally managed rangeland after July because little replacement leaf and shoot growth takes place and almost no new tiller growth occurs. Beef producers recognize the resulting decrease in cow and calf performance and usually try to compensate for the resulting reduced animal growth rates with nutrient supplementation. However, improvement of the nutritional quality of the herbage to meet the nutritional requirements of lactating beef cows during the latter portion of the grazing season until mid October can be accomplished by activation of the compensatory physiological processes within grazed grass plants that accelerate growth rates of replacement roots, leaves, and shoots, increases photosynthetic capacity of remaining mature leaves, increases allocation of carbon and nitrogen, improves water (precipitation) use efficiency, and increases restoration of biological processes enabling rapid and complete recovery of partially defoliated grass tillers, and by activation of the asexual processes of vegetative reproduction that increases secondary tiller development from axillary buds and increases tiller density during the growing season (Manske 1999a, 2011b). The resulting growth of replacement leaves and shoots and new secondary tillers from activation of the compensatory physiological processes and of the asexual processes of vegetative reproduction improves the nutritional quality of the available herbage during the latter portion of the grazing season above the nutrient requirements of lactating beef cows and supports animal weight performance at near genetic potentials (Manske 2002).

Almost every rangeland grass tiller grows during two growing seasons. The lead tillers that produced seed heads terminate at the end of the second growing season. Vegetative tillers that did not produce seed heads, activated secondary tillers, and fall initiated tillers that have grown during one growing season survive over the winter on stored carbohydrate reserves and grow again during the next growing season. The quantity of carbohydrates stored during the winter hardening process, that occurs from mid August to hard frost, is closely related to the amount of active leaf material on each tiller during that period. Tillers with abundant leaf area during late summer and early fall can store adequate quantities of carbohydrates to survive the winter and produce robust leaves the following spring. Traditionally managed grazing of grass tillers during mid August to mid October that removes excessive leaf material from carryover tillers causes inadequate quantities of carbohydrates to be stored. Plants that have low carbohydrate reserves and survive the winter dormancy period produce tillers with reduced height and weight. Some of the tillers with low carbohydrate reserves deplete their stores through winter respiration before spring, causing winter kill of those tillers. Grazing native rangeland after mid October exacerbates these problems causing ecosystem degradation. The factors that reduce ecosystem productivity need not to occur.

Management of Native Rangelands

There are numerous factors that can negatively effect rangeland ecosystems and could cause reductions in productivity. Most of these negative factors have countermeasures that nullify or supersede the detrimental effects. During the period of 30 to 20 mya following global climate cooling, complex rangeland ecosystems developed as a result of the coevolution among modern native grasses, rhizosphere soil organisms, and large grazing mammalian graminivores. Numerous intricate interactive biological, physiological, and biogeochemical processes developed coincidentally with the coevolutionary creations. The primary processes are: internal compensatory physiological processes, internal asexual processes of vegetative reproduction, external symbiotic rhizosphere organism processes, and ecological biogeochemical processes. These critical processes permit rangeland ecosystems to function at potential levels. Unfortunately, these processes do not automatically function at full potential capacity. These processes require activation and they require adequate availability of carbon, hydrogen, nitrogen, and oxygen.

The twice-over rotation grazing management strategy is the biologically effective management practice that activates the beneficial defoliation resistance mechanisms and the biogeochemical processes. Partial defoliation controlled with the twice-over rotation grazing management strategy removes 25% to 33% of the leaf material from grass lead tillers at phenological growth between the three and a half new leaf stage and the flower (anthesis) stage during early June to mid July activates the beneficial processes. Full functionality of the defoliation resistance mechanisms requires mineral nitrogen to be available at 100 lbs/ac or greater and requires the quantity of available carbon fixed through photosynthesis from 75% to 67% of the leaf area of grass lead tillers prior to peak herbage biomass and from 50% of the leaf area post peak biomass (Manske 2010a, 2010b).

The twice-over rotation grazing management strategy uses three to six native rangeland pastures. Each of the pastures in the rotation is partially defoliated by grazing for 7 to 17 days during the first period, the 45 day interval from 1 June to 15 July when partial defoliation of grass lead tillers can activate the beneficial defoliation resistance mechanisms and biogeochemical processes. The length in 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 grazable forage each pasture contributes to the complete system. The forage is measured as animal unit months (AUM's) of forage. The number of days grazed are not counted by calendar dates; days grazed are counted by the number of 24 hour periods grazed from the date and time the cattle are turned into a pasture. During the second grazing period, when lead tillers are maturing and defoliation by grazing is only moderately beneficial, the 90 day interval after mid July and before mid October, each pasture is grazed for double the number of days it was grazed during the first period. The pasture grazed first in the rotation sequence during one year is the last pasture grazed during the previous year (Manske 1999a, 2011b).

Management of native rangelands requires annual partial defoliation by large grazing graminivores managed by the biologically effective twice-over rotation strategy that coordinates defoliation events with grass phenological growth stages. The twice-over strategy activates the defoliation resistance mechanisms and the biogeochemical processes, and then maintains their functionality at potential levels. The twice-over strategy also meets the biological requirements of the grass plants and the rhizosphere organisms, and meets the nutritional requirements of the grazing animals during the entire grazing season. Biologically effective management of native rangeland ecosystems sustains healthy renewable natural resources that simultaneously provide greater forage for livestock, better habitat for prairie wildlife, more aesthetic prairie landscapes for recreation and sightseeing, increased food and fiber for people, and provides greater growing season residuum vegetation structure that is unfavorable habitat for pestiferous rangeland grasshopper population development.

Table 46. Precipitation during growing season months (April-September), Watford City, ND.

	1993	1994	1995	1996	1997	1998
mm	456.56	266.67	322.22	233.33	194.44	227.78
inches	17.94	10.50	12.69	9.19	7.66	8.97

Data from Onsager 2000.

Table 47. Precipitation in inches and percent of long-term mean for perennial plant growing season months, western North Dakota, 1993-1998.

Years	Apr	May	Jun	Jul	Aug	Sep	Oct	Growing Season	Annual Total
Long-Term Mean 1982-2012	1.44	2.56	3.27	2.43	1.70	1.42	1.31	14.13	16.91
1993	1.41	1.71	4.57	5.10	1.24	0.18	0.05	14.26	17.36
% of LTM	97.92	66.80	139.76	209.88	72.94	12.68	3.82	100.92	102.66
1994	0.86	1.46	4.51	1.07	0.31	1.08	4.58	13.87	16.14
% of LTM	59.72	57.03	137.92	44.03	18.24	76.06	349.62	98.16	95.45
1995	1.01	4.32	0.68	4.62	3.16	0.00	0.67	14.46	16.24
% of LTM	70.14	168.75	20.80	190.12	185.88	0.00	51.15	102.34	96.04
1996	0.14	3.07	1.86	2.55	1.72	2.51	0.09	11.94	15.97
% of LTM	9.72	119.92	56.88	104.94	101.18	176.76	6.87	84.50	94.44
1997	2.89	0.95	5.02	5.41	0.76	1.75	0.78	17.56	18.61
% of LTM	200.69	37.11	153.52	222.63	44.71	123.24	59.54	124.27	110.05
1998	0.40	1.51	5.98	2.11	4.60	0.71	4.38	19.69	22.42
% of LTM	27.78	58.98	182.87	86.83	270.59	50.00	334.35	139.35	132.58
1993-1998	1.12	2.17	3.77	3.48	1.97	1.04	1.75	15.30	17.79
% of LTM	77.78	84.77	115.29	143.21	115.88	73.24	133.59	108.28	105.20

Table 48. Monthly herbage biomass (lbs/ac) for native rangeland managed with the seasonlong system, 1993-1994.

Plant Biotype	May	Jun	Jul	Aug	Mean Monthly
Native Grass	489.62	554.99	632.53	465.27	550.93
Cool Season	292.53	258.42	284.37	171.98	238.26
Warm Season	197.09	296.57	348.16	293.29	312.67
Sedges	4.87	34.79	6.35	1.18	14.11
Total Forbs	108.05	47.08	54.91	33.69	45.23
Total Live	602.54	636.85	693.79	500.14	610.26
Standing Dead	207.12	131.60	152.88	156.66	147.05
Standing Biomass	809.66	768.45	846.66	656.80	757.30
Litter	70.96	141.67	160.81	111.69	138.06
Total Dead	278.08	273.27	313.69	268.35	285.10
Total Biomass	880.62	910.12	1007.47	768.49	895.36

Table 49. Monthly composition (%) of herbage biomass for native rangeland managed with the seasonlong system, 1993-1994.

Plant Biotype	May	Jun	Jul	Aug	Mean Monthly
Native Grass	81.26	87.15	91.17	93.03	90.28
Cool Season	48.55	40.58	40.99	34.39	39.04
Warm Season	32.71	46.57	50.18	58.64	51.24
Sedges	0.81	5.46	0.92	0.24	2.31
Total Forbs	17.93	7.39	7.91	6.74	7.41
Total Live	68.42	69.97	68.86	65.08	68.16
Standing Dead	23.52	14.46	15.17	20.39	16.42
Standing Biomass	91.94	84.93	84.04	85.47	84.58
Litter	8.06	15.57	15.96	14.53	15.42
Total Dead	31.58	30.03	31.14	34.92	31.84
Total Biomass	880.62	910.12	1007.47	768.49	895.36

Table 50. Monthly herbage biomass (lbs/ac) for native rangeland managed with the twice-over rotation system, 1993-1994.

Plant Biotype	May	Jun	Jul	Aug	Mean Monthly
Native Grass	403.84	721.19	751.47	793.48	755.38
Cool Season	380.08	656.34	642.65	660.80	653.26
Warm Season	23.76	64.85	108.83	132.68	102.12
Sedges	6.84	7.52	10.84	6.27	8.21
Total Forbs	84.98	74.35	66.73	55.14	65.41
Total Live	495.65	803.05	829.04	854.88	828.99
Standing Dead	222.09	206.79	195.98	334.48	245.75
Standing Biomass	717.74	1009.84	1025.01	1189.36	1074.74
Litter	250.27	245.84	251.68	476.87	324.80
Total Dead	472.36	452.63	447.66	811.35	570.55
Total Biomass	968.01	1255.68	1276.69	1666.23	1399.53

Table 51. Monthly composition (%) of herbage biomass for native rangeland managed with the twice-over rotation system, 1993-1994.

Plant Biotype	May	Jun	Jul	Aug	Mean Monthly
Native Grass	81.48	89.81	90.64	92.82	91.12
Cool Season	76.68	81.73	77.52	77.30	78.80
Warm Season	4.79	8.08	13.13	15.52	12.32
Sedges	1.38	0.94	1.31	0.73	0.99
Total Forbs	17.15	9.26	8.05	6.45	7.89
Total Live	51.20	63.95	64.94	51.31	59.23
Standing Dead	22.94	16.47	15.35	20.07	17.56
Standing Biomass	74.15	80.42	80.29	71.38	76.79
Litter	25.85	19.58	19.71	28.62	23.21
Total Dead	48.80	36.05	35.06	48.69	40.77
Total Biomass	968.01	1255.68	1276.69	1666.23	1399.53

Table 52. Percent difference of monthly herbage biomass on the twice-over rotation system compared to the seasonlong system on native rangeland management, 1993-1994.

Plant Biotype	May	Jun	Jul	Aug	Mean Monthly
Native Grass	-17.52	29.95	18.80	70.54	37.11
Cool Season	29.93	153.98	125.99	284.23	174.18
Warm Season	-87.94	-78.13	-68.74	-54.76	-67.34
Sedges	40.45	-78.38	70.71	431.36	-41.81
Total Forbs	-21.35	57.92	21.53	63.67	44.62
Total Live	-17.74	26.10	19.49	70.93	35.84
Standing Dead	7.23	57.14	28.19	113.51	67.12
Standing Biomass	-11.35	31.41	21.07	81.08	41.92
Litter	252.69	73.53	56.51	326.96	135.26
Total Dead	69.86	65.63	42.71	202.35	100.12
Total Biomass	9.92	37.97	26.72	116.82	56.31

Table 53. Basal cover (%) and composition (%) for native rangeland managed with the seasonlong system, 1993-1994.

Plant Biotype	Basal Cover %	Composition %
Native Grass	28.96	82.88
Cool Season	15.99	45.76
Warm Season	12.97	37.12
Sedges	2.34	6.70
Total Forbs	3.65	10.45
Total Live	34.94	
Litter	57.44	
Bare Soil	7.63	

Table 54. Basal cover (%) and composition (%) for native rangeland managed with the twice-over rotation system, 1993-1994.

Plant Biotype	Basal Cover %	Composition %
Native Grass	29.20	81.63
Cool Season	24.13	67.46
Warm Season	5.07	14.17
Sedges	1.56	4.36
Total Forbs	5.01	14.01
Total Live	35.77	
Litter	57.89	
Bare Soil	6.35	

Table 55. Percent difference of basal cover on the twice-over rotation system compared to the seasonlong system of native rangeland management, 1993-1994.

Plant Biotype	Difference % 1995-1998
Native Grass	0.83
Cool Season	50.91
Warm Season	-60.91
Sedges	-33.33
Total Forbs	37.26
Total Live	2.38
Litter	0.78

Table 56. Bareground area on native rangeland managed with the seasonlong system as mean of twenty 2000 cm (787.4 in) transects.

Bareground Size		Percent Area	Bareground Combined Length	
cm	in	%	cm	in
0-5	0-2	92.6	1852	729.1
6-10	2-4	5.5	110	43.3
11-20	4-8	1.9	38	15.0
21-30	8-12	0.0	0	0

Table 57. Bareground area on native rangeland managed with the twice-over rotation system as mean of twenty 2000 cm (787.4 in) transects.

Bareground Size		Percent Area	Bareground Combined Length	
cm	in	%	cm	in
0-5	0-2	92.5	1850	728.4
6-10	2-4	6.3	126	49.6
11-20	4-8	1.2	24	9.4
21-30	8-12	0.0	0	0

Table 58. Plant community height structure based on mean % relative cover of mid grasses and short grasses, 1993-1994.

	Twice-over Rotation Relative Cover %	Seasonlong System Relative Cover %
Mid Grasses	53.76	42.90
western wheatgrass	19.41	28.40
needle and thread	3.68	1.29
green needlegrass	30.67	13.21
Short Grasses	28.20	46.31
prairie junegrass	1.21	2.26
blue grama	21.93	36.91
upland sedges	5.07	7.15

Table 59. Mean cumulative grasshopper days (GD) per m^2 and primary habitat use for pestiferous grasshoppers on native rangeland managed with the twice-over rotation system and the seasonlong system, 1993-1998.

					Mean Cumulative Grasshopper days per m^2	
Pestiferous Rangeland Grasshoppers	Hatch Group	Egg Pod Site	Basking Site	Daily Activity Site	Twice-over Grazing	Seasonlong Grazing
Mel gla	Late	Bareground	Bareground	Bareground	3	88*
Mel san	Early	Bareground	Grd/Veg	Bareground	78	87
Ope obs	Late	Bareground	Veg/Grd	Veg/Grd	6	71*
Enc cos	Intermediate	Bareground	Bareground	Bareground	10	57*
Mel inf	Early	Bareground	Bareground	Grd/Veg	5	26*
Pho neb	Late	Bareground	Veg/Grd	Veg/Grd	6	16
Mel fem	Intermediate	Bareground	Bareground	Grd/Veg	9	5
Tra kio	Intermediate	Bareground	Bareground	Bareground	3	6
Age deo	Early	Bareground	Bareground	Bareground	2	2
Total cumulative GD for the 9 pestiferous grasshoppers					122	358
Total cumulative GD for the other 21 nonpestiferous grasshoppers					107	390
Total cumulative GD for all grasshoppers					229	748*

Habitat use information from Cushing 1993, Pfadt 1994.
Grasshopper days per m^2 data from Onsager 2000.

Mean value is significantly greater than its complement*.

Table 60. Grasshopper density (per m^2 and per yd^2) and forage use per month (kg/ha and lbs/ac) on native rangeland managed with the twice-over rotation system and the seasonlong system, 1993-1998.

Grazing Management System	1993	1994	1995	1996	1997	1998
Twice-over						
Density						
$\#/m^2$	2.6	1.4	3.3		2.1	5.6
$\#/yd^2$	2.2	1.2	2.8		1.8	4.7
Forage use/month						
kg/ha	26.9	15.9	40.5		23.7	53.4
lbs/ac	24.0	14.2	36.2		21.2	47.7
Seasonlong						
Density						
$\#/m^2$	8.3	4.6	6.2		18.4	26.8
$\#/yd^2$	6.9	3.8	5.2		15.4	22.4
Forage use/month						
kg/ha	90.5	43.2	70.4		208.8	344.6
lbs/ac	80.8	38.6	62.9		186.5	307.7

Data from Onsager 2000.

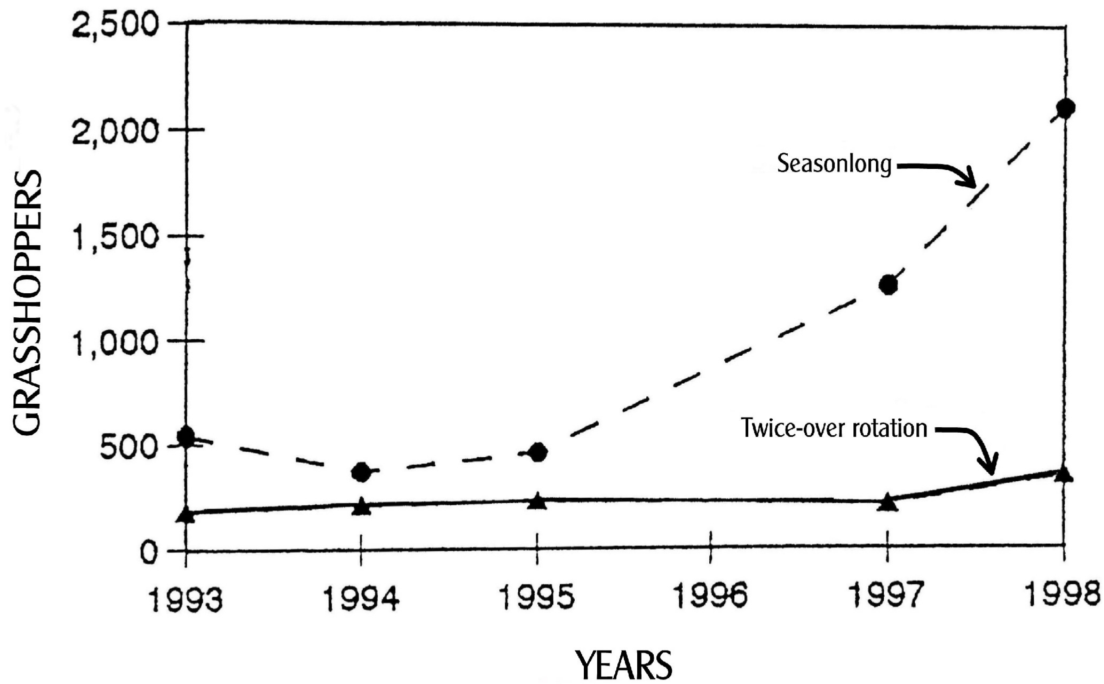


Figure 4. Grasshopper population abundance reported as grasshopper days per square meter on native rangeland managed with the twice-over rotation and the seasonlong systems. Data from Onsager 2000.

Table 61. Monthly herbage biomass (lbs/ac) for native rangeland managed with the seasonlong system, 1994-1998.

Plant Biotype	Jun	Jul	Aug	Sep	Oct	Mean Monthly
Native Grass	405.20	407.47	397.80	527.59	355.43	418.70
Cool Season	269.23	238.60	220.69	299.75	193.77	244.41
Warm Season	135.97	168.87	177.11	227.84	161.66	174.29
Sedges	175.48	197.98	218.58	113.58	57.74	152.67
Total Forbs	78.77	58.29	46.05	49.64	69.25	60.40
Total Live	659.45	663.74	662.43	690.81	482.42	631.77
Standing Dead	62.17	25.00	16.00	84.01	100.43	57.52
Standing Biomass	721.62	688.74	678.43	774.82	582.85	689.29
Litter	173.78	93.17	142.64	207.93	292.13	181.93
Total Dead	235.95	118.17	158.64	291.94	392.56	239.45
Total Biomass	895.40	781.91	821.07	982.75	874.98	871.22

Table 62. Monthly composition (%) of herbage biomass for native rangeland managed with the seasonlong system, 1994-1998.

Plant Biotype	Jun	Jul	Aug	Sep	Oct	Mean Monthly
Native Grass	61.45	61.39	60.05	76.37	73.68	66.27
Cool Season	40.83	35.95	33.32	43.39	40.17	38.69
Warm Season	20.62	25.44	26.74	32.98	33.51	27.59
Sedges	26.61	29.83	33.00	16.44	11.97	24.17
Total Forbs	11.94	8.78	6.95	7.19	14.35	9.56
Total Live	73.65	84.89	80.68	70.29	55.13	72.52
Standing Dead	6.94	3.20	1.95	8.55	11.48	6.60
Standing Biomass	80.59	88.08	82.63	78.84	66.61	79.12
Litter	19.41	11.92	17.37	21.16	33.39	20.88
Total Dead	26.35	15.11	19.32	29.71	44.87	27.48
Total Biomass	895.40	781.91	821.07	982.75	874.98	871.22

Table 63. Monthly herbage biomass (lbs/ac) for native rangeland managed with the twice-over rotation system, 1994-1998.

Plant Biotype	Jun	Jul	Aug	Sep	Oct	Mean Monthly
Native Grass	481.47	623.51	534.88	561.34	471.44	534.53
Cool Season	245.38	300.47	184.70	223.38	157.57	222.30
Warm Season	236.09	323.04	350.18	337.96	313.87	312.23
Sedges	168.89	204.38	137.31	80.84	99.65	138.21
Total Forbs	113.25	70.60	70.31	116.52	44.10	82.96
Total Live	763.61	898.49	742.50	758.70	615.19	755.70
Standing Dead	49.18	50.38	40.09	138.79	61.65	68.02
Standing Biomass	812.79	948.87	782.59	897.49	676.84	823.72
Litter	163.86	127.13	99.94	301.40	311.19	200.70
Total Dead	213.04	177.51	140.03	440.19	372.84	268.72
Total Biomass	976.65	1076.00	882.53	1198.89	988.03	1024.42

Table 64. Monthly composition (%) of herbage biomass for native rangeland managed with the twice-over rotation system, 1994-1998.

Plant Biotype	Jun	Jul	Aug	Sep	Oct	Mean Monthly
Native Grass	63.05	69.40	72.04	73.99	76.63	70.73
Cool Season	32.13	33.44	24.88	29.44	25.61	29.42
Warm Season	30.92	35.95	47.16	44.54	51.02	41.32
Sedges	22.12	22.75	18.49	10.66	16.20	18.29
Total Forbs	14.83	7.86	9.47	15.36	7.17	10.98
Total Live	78.19	83.50	84.13	63.28	62.26	73.77
Standing Dead	5.04	4.68	4.54	11.58	6.24	6.64
Standing Biomass	83.22	88.18	88.68	74.86	68.50	80.41
Litter	16.78	11.82	11.32	25.14	31.50	19.59
Total Dead	21.81	16.50	15.87	36.72	37.74	26.23
Total Biomass	976.65	1076.00	882.53	1198.89	988.03	1024.42

Table 65. Percent difference of monthly herbage biomass on the twice-over rotation system compared to the seasonlong system of native rangeland management, 1994-1998.

Plant Biotype	Jun	Jul	Aug	Sep	Oct	Mean Monthly
Native Grass	18.82	53.02	34.46	6.40	32.64	27.66
Cool Season	-8.86	25.93	-16.31	-25.48	-18.68	-9.05
Warm Season	73.63	91.30	97.72	48.33	94.15	79.14
Sedges	-3.76	3.23	-37.18	-28.83	-23.62	-9.47
Total Forbs	43.77	21.12	52.68	134.73	-36.32	37.35
Total Live	15.79	35.37	12.09	9.83	27.52	19.62
Standing Dead	-20.89	101.52	150.56	65.21	-38.61	18.25
Standing Biomass	12.63	37.77	15.35	15.83	16.13	19.50
Litter	-5.71	36.45	-29.94	44.95	6.52	10.32
Total Dead	-9.71	50.22	-11.73	50.78	-5.02	12.22
Total Biomass	9.07	37.61	7.49	21.99	12.92	17.58

Table 66. Basal cover (%) and composition (%) for native rangeland managed with the twice-over rotation and the seasonlong systems, 1994-1998.

	Twice-over rotation		Seasonlong	
Plant Biotype	Basal Cover %	Composition %	Basal Cover %	Composition %
Native Grass	20.68	78.33	14.84	56.68
Cool Season	5.30	20.08	5.14	19.63
Warm Season	15.38	58.26	9.70	37.05
Sedges	3.56	13.48	8.76	33.46
Total Forbs	2.16	8.18	2.58	9.85
Total Live	26.40		26.18	
Litter	72.50		72.52	
Bare Soil	1.10		1.30	

Table 67. Percent difference of basal cover on the twice-over rotation system compared to the seasonlong system of native rangeland management, 1994-1998.

Plant Biotype	Difference % 1994-1998
Native Grass	39.35
Cool Season	3.11
Warm Season	58.56
Sedges	-59.36
Total Forbs	-16.28
Total Live	0.84
Litter	-0.03

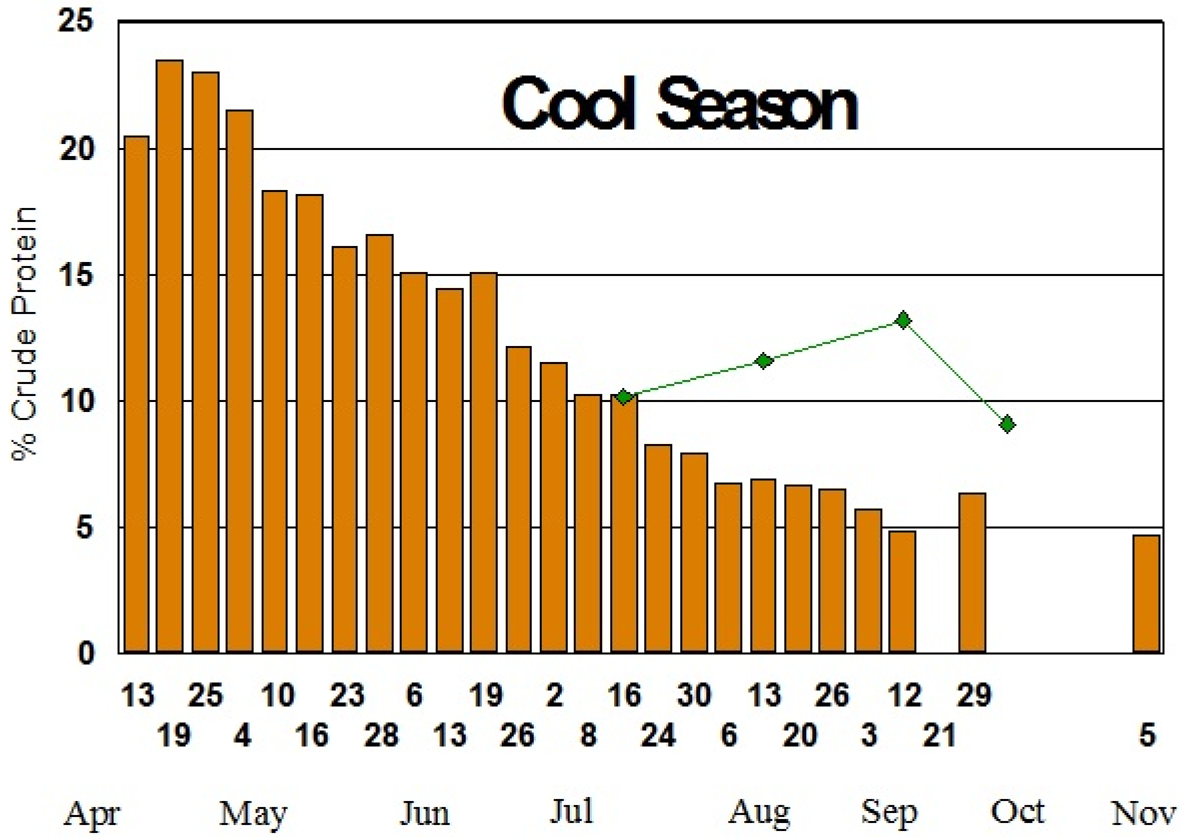


Fig 5. Mean percent crude protein of ungrazed native range cool season grasses in western North Dakota, data from Whitman et al. 1951 and secondary tiller data from Sedivec 1999.

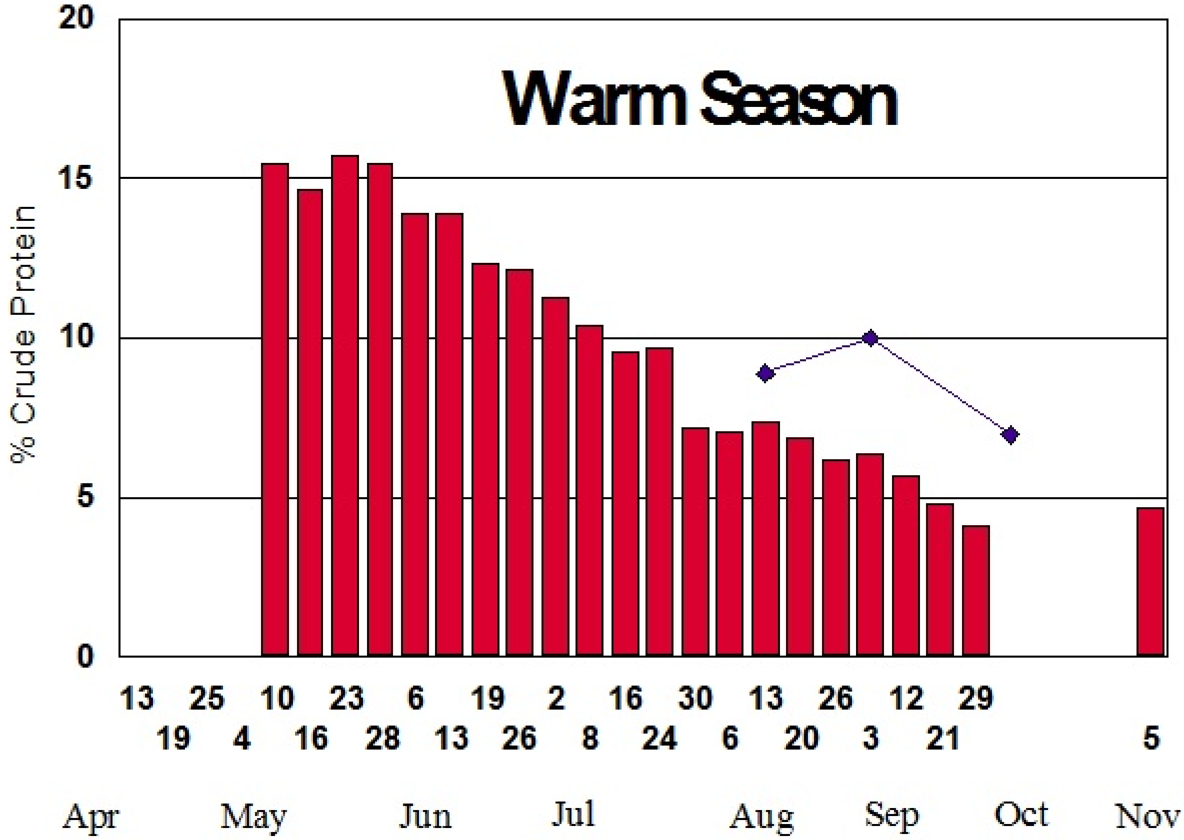


Fig 6. Mean percent crude protein of ungrazed native range warm season grasses in western North Dakota, data from Whitman et al. 1951 and secondary tiller data from Sedivec 1999.

Compendium:

Proactive Management of Grasshopper Habitat

Most agricultural families of the Northern Plains have heroic stories of family members battling grasshoppers. Almost every ranch and farm in the Northern Plains has suffered from grasshopper infestations at sometime in the past. Large scale grasshopper outbreaks extending throughout the western portion of North America occurred during the 1930's and 1980's and smaller scale regional outbreaks have occurred almost every year someplace in the Northern Plains. It is realistic to predict that grasshopper outbreaks will occur in the near future someplace in the Northern Plains.

Grasshoppers exist at low population densities and do not cause problems during growing seasons between outbreaks. All of the pestiferous rangeland grasshopper species of the Northern Plains remain year after year on the land where they hatch. During growing seasons that the population numbers greatly increase, the grasshoppers will move to new areas with green food plants after they have consumed and destroyed all the available food plants at the hatch sites. The large increase in population numbers is the problem. A few grasshoppers do not eat much, but huge quantities of grasshoppers consume and destroy large quantities of food plants. Land management practices that permit resident populations of grasshoppers to increase to outbreak numbers need to be changed. Land managers create their own grasshopper problems with poor land management practices. Biologically effective management of the residuum vegetation structure of grasshopper habitat can maintain grasshopper populations at tolerable low densities. Proactive management of grasshopper habitat must reduce the grasshoppers strengths and exploit the grasshoppers weaknesses.

Grasshoppers have a major survival strength that relegates proactive management of grasshopper habitat to a neverending annual challenge. Grasshoppers have high fecundity potential, each adult female can produce 100 to 200 viable eggs. Because of this remarkable inherent ability, grasshoppers can increase the population density multifold from one growing season to the next. A one year lapse in land management diligence can lead to a major grasshopper outbreak.

Fortunately, grasshoppers have two major weaknesses that render grasshopper population numbers vulnerable to proactive management of the residuum vegetation structure of their habitat. The first weakness is that grasshoppers are cold blooded and are unable to regulate their body temperature metabolically. Grasshoppers need to bask on open bareground areas to collect direct incident solar radiation to raise their body temperatures to the preferred optimal high levels above 95° F (35° C). When grasshoppers can not achieve the optimal body temperature during most of the day, their growth and development rates slow, the length of time nymphs are at each instar stage increases, nymph mortality increases, the number of nymphs reaching the adult stage decreases, maturation time after adults fledge increases, the quantity of viable eggs produced by each adult female greatly decreases, and the resident grasshopper population remains low.

The second vulnerable weakness is that grasshopper eggs require a total of 500 to 600 DD day-degrees of heat from direct incident solar radiation for complete development of the embryo; this includes about 400 DD of heat during the first summer and an additional 150 DD of heat during the following spring to complete embryonic development and hatching. All except one of the pestiferous rangeland grasshoppers deposit their egg pods below the soil surface in bareground patches. Bareground egg pod sites accumulate heat units rapidly and increase the rates of embryonic development. Shading of the soil surface at the egg laying sites from grass canopy cover reduces the quantity of incident solar radiation that decreases the accumulation of heat units, reduces the rate of embryo development delaying egg hatch, and reduces the number of hatchlings produced.

The pestiferous rangeland grasshoppers that coexist on your grazinglands can be diminished to tolerable densities with the typical reactive short-term chemical insecticide spray treatments or the grasshoppers can be sustained at low population numbers by proactive long-term management of their habitat.

Grass plants, soil microorganisms, and large grazing graminivores coevolved and develop extensive interactions that permit grassland ecosystems to function effectively. The defoliation resistance mechanisms that developed within grass plants provide important biological and physiological processes so grass plants can produce greater herbage biomass that replaces lost leaf material, restore disrupted vital processes, and vegetatively reproduce secondary tillers from axillary buds that increase grass tiller density and reduce bareground areas. The soil microorganisms in the rhizosphere and the biogeochemical processes cycle large quantities of plant available essential elements between the organic and inorganic forms. Activation of the defoliation resistance mechanisms and the biogeochemical processes requires partial defoliation by grazing that removes about 25% to 33% of the aboveground leaf material of grass lead tillers between the 3.5 new leaf stage and the flower stage and results in greatly increased ecosystem productivity that is favorable for livestock production. Proactive management of the residuum vegetation structure of grasshopper habitat uses the ecosystem mechanisms and processes to increase aboveground herbage biomass, increase grass plant basal cover, and decrease bareground area creating habitat conditions unfavorable for pest grasshopper production.

Pestiferous rangeland grasshopper population numbers in the Northern Plains can be held at tolerable low densities by proactive management of the grasshopper habitat by using the recently discovered grasshopper biology and population dynamics and the technologies for activation of the defoliation resistance mechanisms and the biogeochemical processes.

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