EXTENT OF DEFOLIATION AND LEAF DEVELOPMENTAL STAGE EFFECTS ON PRODUCTIVITY OF COOL SEASON PASTURE GRASSES UNDER MANAGED GRAZING IN SOUTHERN WISCONSIN

by

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GENERAL INTRODUCTION

Pastures Native to North America

> "I have always had a real affection for grass. It seems to stand for quietness and strength, [which] must be permanently a part of our agriculture if this nation is to have the strength it will need in the future. One of the greatest mistakes [European settlers] made when they spread over this country was to do a poor job with grass. Now we are beginning to see the weaknesses of an agriculture stripped of grass. A countryside shorn and stripped of thick, green grass, it seems to me, loses a primary source of strength. The more we fail to realize this, the more difficult it will be to maintain and build up our great agricultural and soil resources – yes, and our human resources too" – *U.S. Secretary of Agriculture Henry A. Wallace*, excerpt from "The Strength and Quietness of Grass" (1940), (Kirschenmann, 2009).

The first Europeans to arrive in North America found anything but a primeval landscape. Instead, they encountered a land that had been significantly altered by humans through use of fire, sophisticated agricultural techniques, mining, and road and mound building (Mann, 2006). The indigenous peoples used fire not only to create and maintain prairies, but also to manage forests. The climate which had ultimately been responsible for the eastward expansion of tall grass prairies disappeared a thousand years before European settlers arrived. Manmade fires, however, had preserved grasslands in areas such as southern Wisconsin, Illinois, Indiana, and parts of Ohio by halting the process of ecological succession which would have ultimately allowed these areas to become dominated by trees as the natural climax vegetation (Williams,

1989). In fact, when Lewis and Clark headed west on their expeditions they were exploring not a wilderness, but a vast pasture managed by and for Native Americans (Lott, 2002).

The abundance of bison in North America actually increased with the arrival of Columbus, largely due to Eurasian diseases that decreased the amount of Native American hunting. These huge bison herds were a symptom of the destruction of the human-animal-environment system that the Native Americans had operated for centuries before European contact, rather than an example of the "natural" undisturbed grassland-wildlife system (Geist, 1998; Mann, 2006). European settlers also suffered from their own flawed mindsets. They referred to the Great Plains as "the Great American Desert" because of its lack of trees. This reflected the European farming mentality typical of the 18th and 19th Centuries (Manning, 1997). The value of grassland and its true potential, as well as its unique requirements, went largely unrecognized. Governmental policies, along with farming practices of early settlers, were ill-suited to the Great Plains. In the end, large tracts of natural grassland, the result of an interaction between climate, topology, soil, plant, grazing animals, and manmade fire, were plowed under for crop production.

As European settlers moved into the state of Wisconsin, much of the landscape was converted to crop fields, but a proportion was left as pasture. The best land was always used for cultivated crops, however, while pasture and hay were relegated to more marginal soils. The harsh climates of both Northeastern and North Central U.S. preclude year-round grazing, contrary to practices in maritime Britain for example, and thus colonists focused on winter feed, or crop farming, rather than pastoral agriculture (Kendall, 1944).

Industrial agriculture, ushered in by Henry Ford's introduction of the mass-produced Fordson tractor in the 1920s, effectively changed the "culture" of agriculture to one of big machinery. Industrial farming required a different type of relationship with the land which further reduced the importance of pasture for grazing livestock (Bell, 2004; Fitzgerald, 2003). Expensive equipment encouraged hay versus pasture-based systems due to the need to justify capital investment. Specialization meant that labor patterns on the farm changed and more emphasis was placed on the cow, rather than its forage. Increasing use of the Holstein dairy cow shifted farmers further away from pasture. The potential for high milk production with this breed caused farmers to focus primarily on specific feed rations and supplements, rather than pasture management. As demand increased for fresh milk, the federal government instituted milk price supports, encouraging the maximization of year-round production (Bateman, 1968).

The Great Depression and World Wars I and II brought with them economic uncertainty and labor shortages, further increasing the need for stable crop production in the form of hay and silage. After the wars, however, farmers found they had a tremendous capability to produce. They were being supported primarily by unlimited inexpensive energy and advances in mechanization and technology, such as tractors, fertilizers, and pesticides (Hallberg, 1988). In 1920, Wisconsin surpassed New England and New York as the main center of dairy manufacturing and by 1950, the state was well on its way to earning the title of "America's Dairyland" (Cross, 2001).

Setting the Stage: A Change in Dairy Farm Economics and Structure

> "It is likely that without some support and encouragement, many farmers who could and should adopt a grazing system to survive will fail to do so and consequently may go out of business." – (Fales, 1992)

Agriculture is continuously evolving as farmers adapt to various changes and pressures around them. Beginning in the early 1970s, the cost of petroleum and petroleum based products (such as fertilizer) skyrocketed, sending ripples through the US economy. In the late 1980s, milk and dairy product prices became much more volatile than the previous two decades. With the relative costs of inputs still high and a decline in federal subsidies for agricultural commodities, dairy producers suffered from a severe cost-price squeeze which continues to this day. Supply factors that contributed to the decline in real milk prices included improvements in technology and management, increased milk per cow, slow growth in labor costs, and lower feed prices. Even though the demand for fluid milk remains strong, milk prices have not kept up with costs (Blayney, 2004; Wise, 2011).

Subsequent reductions in profits jeopardize the viability of small family farms (less than 100-200 cows). The trend towards fewer, but larger farms regionally and nationally, might lead one to predict that these farmers will have no other choice but to increase the size of their operation to capture economies of scale or go out of business. There are environmental, social, and economic concerns, however, that have modified this trend. Increased public awareness of the impact of animal manure, pesticides, and fertilizers, as well as more stringent legislation designed to protect the environment, have caused many dairy farmers to move away from increasing cow and crop production and towards decreasing input costs. The cost of land has

also gone up due to increased urbanization, relegating dairy to less productive land classes more suitable for pasture than row cropping (Fales, 1992).

The effects of a rapidly changing agricultural structure on the economy and culture, community and environment, and home and family of small U.S. farmers are central to understanding why some farms have switched to alternative agricultural methods and why most have not, despite these challenges of uncertainty (Bell, 2004). Twenty years ago, the structure of dairy farming in Wisconsin was as homogenous as it had been in the 1950s. Almost all farms utilized semi-confinement methods, where most feed provided to cows was harvested mechanically and then delivered to them in the barn. Pastures were used non-intensively, if at all. Although the US dairy industry had shifted towards large confinement operations from a system previously dominated by mid-sized confinement dairies, a second structural trend has been the emergence of moderate-sized dairies using alternative management strategies (Brock and Barham, 2009).

The largest sector (in farm numbers) of these new dairy management systems is broadly identified as Management Intensive Rotational Grazing (MIRG). Spontaneous growth of the "intensive grazing" movement in the Northeast and North Central U.S. is an example of farmers adapting to economic pressures and has proven to be a viable means for small farmers to remain profitable by dramatically cutting costs. Even though milk production per cow is lower with grazing, the reduction in overall farm operating costs makes MIRG economically competitive with confinement operations (Kriegl, 2005).

The Rise of MIRG as an Agricultural and Social Movement

> "For years, I fought and borrowed to bring feed to the cow. Then I finally figured out that I could bring the cow to the grass." – *Anonymous grass farmer* (Hassanein and Kloppenburg, 1995)

Management Intensive Rotational Grazing (MIRG) entails livestock grazing in relatively small paddocks at high densities for short durations of time. The underlying principle is to intensively manage livestock in a manner that controls the timing and extent of grazing of forage plants so that a pasture can provide reliable forage of appropriate quality and quantity throughout the growing season. MIRG is an agricultural, as well as social, movement that has become increasingly accepted and adopted by a number of dairy and beef farmers in Wisconsin. Some farmers have adopted MIRG out of a desire to become a better land steward and improve their quality of life, by reducing environmental and health problems associated with industrial farming (Ostrom, 2000). Others may have found grazing to be in line with their personal and professional goals or philosophy regarding livestock and resource management.

Generally, grass farmers are strong advocates for the exchange of technology and information that benefits the grazing producer. This farmer-to-farmer information exchange was critical for the emergence of MIRG as a new livestock management strategy in the early 1990s (Hassanein and Kloppenburg, 1995). Grazing networks, or groups of people farming in the same county or region, play an important role in the adoption of grass-based farming in Wisconsin. These networks provide social spaces where farmers and their families can exchange information, build community, provide support to one another, and foster new ideas.

Grazier networks are at the heart of the MIRG movement mainly because MIRG is a production method that requires knowledge not easily transferred by traditional dairy management information sources. Grazier meetings and pasture walks facilitate open dialogue and recommendations from experienced grass farmers rather than “cookbook” solutions (CIAS, 2000). Personal stories from veteran farmers serve as valuable reference points from which to evaluate prospective farm and lifestyle changes and make sensible long-term choices (Fitzgerald, 2003).

Grazier networks can be seen as local expressions of a wider alternative agriculture movement as well as conduits of general grazing knowledge. Hassanein writes, however, that local knowledge is “so tightly bound to an individual (or cultural group) that it is difficult to communicate it to others who have not directly experienced it” (Hassanein, 1999). One might try to make the argument then, that knowledge produced by a specific farmer on a specific piece of land in a particular year is not replicable. The growth of grazier networks in the last 20 years suggest, however, that personal, local knowledge is indeed valuable on a larger scale. That is, across slight differences in terrain, soil type, environment, and management variables there are fundamental plant responses to specific grazing regimes. The question is whether or not agricultural professionals can support this fundamentally replicable, yet localized, type of inquiry throughout the scientific community (Hassanein, 1999).

Institutional Support Comes Slowly

"It takes a long time to turn the supertanker around" – *Anonymous grass farmer* (McNair, 1992)

Localized information on how to manage pastures efficiently was especially needed in the U.S. given that land-grant university pasture research and support declined significantly after 1950. As noted earlier, when Wisconsin became known as "America's Dairyland", increased milk production became the only goal. Agricultural research tends to mirror on-farm trends and there was no exception to this rule at land-grant university experimental research stations, where pasture was held in relatively low esteem compared to arable crops. Early pasture research, when it was conducted, focused on components of the pasture ecosystem (i.e. – forage species evaluation and fertilizer trials). "Attempts to show how given [grazing] treatments translated into economic benefit for the farmer" generally were not made. At first the 'intensive grazing' movement received very little institutional support (nationally or regionally). It was criticized as "hopelessly revisionist" and "unprogressive" because it failed to fit into the current paradigm for U.S. agriculture (Fales, 1992).

Grazing communities were guilty of turning away from land-grant universities as well, however. They did so not necessarily because they thought institutionalized agricultural science could not help them, but because it had not helped them previously. Graziers were generally not optimistic about the prospects for redirecting researchers towards projects supportive of grass farming (Hassanein and Kloppenburg, 1995). In the late 1980s, however, agricultural scientists, academics, and rural advocates started to change their perspective of pasture-based

livestock production. They saw an opportunity to participate in the adaptive process and began to slowly change the course of the "supertanker". The direction of agricultural research in Wisconsin shifted when a group of rotational graziers, the Southern Wisconsin Farmers' Research Network (SWFRN) – now GrassWorks Inc. – began conducting low-input cropping on-farm experiments. These farmers found the agricultural research related to on-farm chemical use reduction and Management Intensive Rotational Grazing (MIRG) to be lacking and decided to disseminate their own research results through field days.

A nonprofit advocacy organization, the Wisconsin Rural Development Center, supported activities of the SWFRN and was able to obtain legislative funding for a Sustainable Agriculture Program housed in the Wisconsin Department of Agriculture, Trade, and Consumer Protection (DATCAP). Established in 1986, this small grants program funded numerous grazing network projects (Krome, 1988). Throughout the 1990s, grant money was issued to farmers who were willing to adopt more sustainable practices such as reducing use of commercial fertilizers, chemical pesticides, and fossil fuels, and preventing soil erosion by planting pasture (DATCAP, 1995).

Interactive Relationships and Growing Support for MIRG

> "Our analysis showed that knowing graziers and using them as an information source was most influential in determining whether [or not] agriculture professionals would make MIRG recommendations to other farmers" – *S. Steele* (CIAS, 1998)

In a survey done by the Center for Integrated Agriculture Systems (CIAS) in 1998, it was noted that most agriculture professionals actually reported being familiar with MIRG or 'intensive grazing' and more than three-quarters of those interviewed accepted it to be a viable alternative. When asked to rank the sources having the greatest influence on their MIRG recommendations, however, 43% of agricultural professionals placed farmers first while only 20% ranked professional colleagues as their top source of information. The fact that agricultural professionals are even looking to farmers for MIRG information, implies a much more interactive relationship than was witnessed only a decade previous (CIAS, 1998).

Knowledge exchange within grazier networks is not just horizontal anymore – what some might consider to be "reversals" in learning are occurring. Rotational graziers have been teaching academics who are willing to learn from them. In turn, grass farmers are not only looking to each other for answers, but are willing to learn what they can from agricultural scientists (i.e. – inviting them to participate in conferences) (Hassanein and Kloppenburg, 1995). Research positions have come about at institutions like the University of Wisconsin-Madison and the USDA Dairy Forage Research Center because of the grazing community's interest in having ecologists and agronomists address grazing related problems. Grazing is still a relatively small component of UW-Madison and USDA research, but it is significant, especially since there

are very few grazing related grant opportunities in general and even fewer federally funded projects.

The research goals of our grazing project came into being in 2007 during a meeting of Wisconsin grazing network coordinators and farmers. USDA Dairy Forage Research Agronomist Geoffrey Brink asked those attending the meeting to identify primary management factors influencing pasture productivity under their control, as well as what specific research questions related to those factors they would like to see addressed. Two questions that were repeatedly asked were (1) How does grazing using the "take half-leave half" rule effect pasture productivity, and (2) How does productivity change when mature grasses are "mob-grazed", a management alternative to grazing at a vegetative stage.

These questions led to the implementation of two treatments on four cool-season pasture grasses in South Central Wisconsin. Above and belowground productivity of these grasses was assessed under Management Intensive Rotational Grazing (MIRG) treatments of different extents of defoliation (50 or 100% biomass removal) at two different leaf developmental stages (either vegetative or mature stage at grazing).

ABSTRACT

Considerable differences exist among cool-season grass species in their production potential and general response to management intensive rotational grazing (MIRG) techniques. At the U.S. Dairy Forage Research Center in Prairie du Sac, Wisconsin a rotational grazing experiment was conducted in order to examine the interactive effects of management and environmental factors on above and belowground productivity of four temperate perennial pasture grasses: meadow fescue [*Schedonorus pratensis* (Huds.) P. Beauv.], orchardgrass (*Dactylis glomerata* L.), common quackgrass (*Elymus repens* L.), and reed canarygrass (*Phalaris arundinacea* L.). The management factors of interest were extent of defoliation (50 or 100% biomass removal) and leaf stage of grasses (vegetative or mature) at grazing. The environmental factors measured across each managed grazing scenario were available light, soil moisture and temperature, and soil nitrogen availability. Since environmental factors can have an effect on above and belowground productivity, statistical tests for possible correlations between environmental mechanisms and management factors on annual forage production were performed. While changes in extent of defoliation had no significant effect on the ANPP of orchardgrass and reed canarygrass, leaf stage did with the grazing of mature grasses producing significantly more forage annually ($p<0.01$) than vegetative grasses. Leaf stage at grazing by extent of defoliation interactions on ANPP were found for both meadow fescue ($p=0.001$) and quackgrass ($p=0.005$). Root production also varied across species, with no effect of treatment on BNPP of orchardgrass and quackgrass. Leaf stage did have an effect on BNPP of meadow fescue, however, with the grazing of mature grasses producing significantly more root biomass annually ($p=0.11$) than vegetative grasses. Both leaf stage and extent of defoliation affected the BNPP of reed canarygrass ($p<0.03$). Only some environmental factors were significantly affected by each grazing management strategy and they varied across species. Soil moisture was significant for meadow fescue ($p=0.01$) and reed canarygrass ($p<0.10$), pre-graze leaf area index (LAI) for orchardgrass ($p=0.005$) and reed canarygrass ($p=0.002$), and net ammonification for meadow fescue plots ($p=0.01$). Soil moisture could help explain the significant changes in ANPP and BNPP for reed canarygrass, but not for meadow fescue. In conclusion, ANPP and BNPP vary significantly across temperate perennial grass species, management strategies, and select environmental factors. Therefore, producers should be informed as to the growth mechanisms underlying the responses observed for individual forage species. An understanding of species specific responses to certain defoliation regimes and environmental conditions would help to identify appropriate grazing practices for particular pasture management situations.

1.1 INTRODUCTION

Plant-herbivore interactions cannot be considered in isolation from the agroecosystem in which they occur. They affect primary and secondary production, energy flow, and nutrient cycling. In general, all possible ecological consequences of herbivores can be explained by four broad mechanisms: plant factors contributing to grazer preference (plant nutritive quality and defense mechanisms), tolerance to grazing (plant capacity to re-grow), disturbance caused by grazers in the environment and alteration of nutrient cycling, and interactions between these three mechanisms (Augustine and McNaughton, 1998; Crawley, 1983; de Mazancourt et al., 1999). Complex ecological models used to describe the direct and indirect effects of these interactions are based on a series of feedback loops in which disturbances brought on by grazers produce shifts in resource availability (Jeffries, 1988). Several field experiments have been undertaken to determine how herbivory alters such response variables as net primary productivity and nutrient cycling. The first of which, specifically above and belowground net primary productivity (ANPP and BNPP), was the focus of this grazing experiment.

There is sufficient evidence in support of opposing claims that net primary productivity of graminoid plants can both decrease and increase with grazing. McNaughton and Jeffries concluded that a direct effect of herbivory is increased production of forage beyond that of ungrazed plants (the “grazing optimization hypothesis”) (Jeffries, 1988; McNaughton, 1979). Each forage species, however, conceivably has a unique response to grazing. For example, some are termed “increasers”, or those in which grazing enhances primary production, while others are “decreasers”, or those negatively affected by herbivory (Del-Val and Crawley, 2005). This

411 differential response, or normal fitness reaction of a species under a gradient of defoliation, is
412 defined as tolerance to grazing and reflects a plant's capacity to re-grow after herbivory
413 (Strauss and Agrawal, 1999).

414 From an agronomic standpoint, tolerance to grazing depends not only on the specific
415 pasture species in question and its response to herbivory, but also the type of grazing being
416 implemented, which together determine realized dry matter yields. There are many benefits,
417 both agronomic and environmental, from rotationally grazing livestock, yet most pastures in
418 the U.S. are continuously grazed. For rotational grazing to be successful, however, the timing of
419 rotations must be adjusted to the growth (or leaf) stage of the forage. Unfortunately rotational
420 grazing is often reduced to standardized animal shifts (from paddock to paddock) based on rigid
421 time schedules rather than in response to forage leaf stage or growth rate (Undersander, 2002).

422 Thus, tolerance to grazing and subsequent changes in net primary productivity should
423 conceivably vary across (1) species specific developmental characteristics, (2) pasture
424 management strategies, and (3) their interactions with environmental factors. Developmental
425 characteristics – those involving processes at the individual plant level – that influence
426 tolerance to herbivory include, but are not limited to, relative growth rate, leaf developmental
427 stage, flowering time, reallocation of resources from roots to shoots, plant architecture, and
428 associations with mycorrhizae. Environmental factors – those involving processes at the
429 ecosystem level rather than at the individual plant level – that may lead to increased
430 production with defoliation include the recycling of nutrients from feces and urine, increased
431 light intensities upon potentially more active underlying foliage, and enhanced soil moisture

due to reduction of the transpiration surface (McNaughton, 1979; McNaughton, 1992; Strauss and Agrawal, 1999).

Producers can manage for some developmental factors at grazing time such as leaf stage of grasses and amount of biomass removed, which combine to determine frequency of grazing events per season. Specific species are more or less tolerant to different degrees of grazing frequency and thus livestock management practices determine whether a significant effect or little effect at all is had on seasonal productivity. By controlling when and how much forage is removed, producers can more accurately manage grazing lands to meet specific goals for production, nutritive value, and persistence. More information is needed, however, on how specific grazing management practices affect both annual productivity (ANPP and BNPP) of perennial pasture and resource availability throughout the growing season.

When grazing strategies increase growth rates or overall production levels, the response is termed overcompensation (Belsky, 1986). This increase in aboveground production occurs under certain management conditions more than others and has been found to be more likely when intervals between grazing events are lengthened (Ferraro and Oesterheld, 2002; Oesterheld and McNaughton, 1988). It has not only been demonstrated that total aboveground production is stimulated by defoliation, but also maximized for most pasture species at moderate grazing intensities where periods of time between defoliation events were approximately 24 days (Georgiadis et al., 1989). Increased productivity under moderate to heavy grazing may be explained by the higher photosynthetic rate at the base of the canopy where more light becomes available, as compared with a dense canopy under conditions of light or no grazing (McNaughton, 1979).

Increased nutrient deposition from urine and feces of herbivores has been shown to have mixed results, increasing primary productivity in some cases and negatively affecting aboveground production in others (Ferraro and Oesterheld, 2002; Georgiadis et al., 1989; Skinner and Comas, 2010). A final mechanism of interest that could increase production in response to defoliation is higher soil moisture levels. Defoliation reduces total leaf-area, or transpiration surface, which can lead to better rain-use efficiency and increased soil moisture (Skinner and Comas, 2010; Varnamkhasti et al., 1995).

It has also been demonstrated that moderately grazed grasslands have better developed root systems (BNPP), which enables higher uptake of water and nutrients, given they are available, for increased long-term productivity and pasture resilience (Vandermaarel and Titlyanova, 1989). Although some studies have shown that intense defoliation reduces root growth (Briske, 1991; Thornton and Millard, 1996), others have demonstrated that more severe foliage clipping results in a greater stimulation of subsequent root growth after a lengthened defoliation interval of 3 to 4 weeks (Dunn and Engel, 1971). Furthermore, certain rhizomatous species have been found to suffer from intraspecific competition for root development and thus actually produce less root biomass under light as compared to moderate grazing intensities (Harker and Osullivan, 1993; Mapfumo et al., 2002). More information is needed, however, on species specific belowground production responses to defoliation in order to make sound management recommendations.

This grazing experiment was designed to examine the interactive effects of pasture management and environmental factors on above and belowground net primary productivity of four temperate pasture grasses: meadow fescue [*Schedonorus pratensis* (Huds.) P. Beauv.],

orchardgrass (*Dactylis glomerata* L.), common quackgrass (*Elymus repens* L.), and reed canarygrass (*Phalaris arundinacea* L.). The management factors, or experimental treatments, of interest were extent of defoliation and leaf developmental stage of grasses at grazing. The environmental factors measured across each managed grazing scenario were available light, soil moisture and temperature, and soil nitrogen availability. Since environmental factors can have an effect on aboveground productivity, we wanted to test for possible correlations between environmental mechanisms and pasture management strategies on total annual forage and root production.

While previous studies have documented general effects of residue height and leaf stage at grazing on overall productivity of several temperate perennial grasses, few have attempted to describe environmental and developmental mechanisms underlying the response observed. Knowledge of these mechanisms would not only provide a better understanding of species specific responses to defoliation, but also help indentify appropriate grazing management practices.

1.2 MATERIALS AND METHODS

1.2.1 Study Site

The grazing experiment was conducted in the spring, summer, and fall of 2010 at the U.S. Dairy Forage Research Center near Prairie du Sac, Wisconsin (43°20’24”N-89°43’12”W) on an 8.0-ha pasture (Fig. 1) comprised of a McHenry silt loam (fine-loamy, mixed, superactive,

mesic Typic Hapludalf), a Richwood silt loam (fine-silty, mixed, superactive, mesic Typic Argiudoll), and a St. Charles silt loam (fine-silty, mixed, superactive, mesic Typic Hapludalf). Composite samples of soil in the upper 15 cm averaged 25% clay, 53% silt, and 22% sand. Soil pH using distilled water averaged 6.5. Total annual precipitation in 2010 was 40.3 inches. The long-term annual precipitation (30-year average) for Prairie du Sac, WI is 33 inches. Mean maximum and minimum air temperatures for 2010 were 14.41°C and 2.62°C respectively. Long-term annual max and min air temperatures (30-year average) for Prairie du Sac, WI are 13.62°C and 2.38°C respectively.

In May, 2006, seed of 'Bartura' meadow fescue [*Schedonorus pratensis* (Huds.) P. Beauv.], 'Bronc' orchardgrass (*Dactylis glomerata* L.), common quackgrass (*Elymus repens* L.), and 'Palaton' reed canarygrass (*Phalaris arundinacea* L.) was sown at 11.2, 11.2, 22.4, and 6.7 kg ha^{-1}, respectively, in a prepared seedbed with a Brillion® seeder in 0.4-ha pastures. The site was fertilized with 50 kg N ha^{-1} as NH_4NO_3 in late April and early September of 2010.

1.2.2 Experimental Design

A portion of each 0.4-ha pasture was divided into experimental plots in a split-split-plot arrangement of a randomized complete block with grass species as the whole plot, leaf stage of grass when grazed as the subplot, and extent of defoliation as the sub-subplot in four replicates (Fig.1). Each plot was 4.6- by 7.6-m and was grazed throughout the growing season by Holstein heifers (average body weight of 460 kg) whenever the grass reached a vegetative (2-4 leaves) or mature (elongated/reproductive) stage to remove 50 or 100% of biomass on a height basis.

The experimental design included treatment plots in which 75% of aboveground biomass was removed (Fig. 1), but that data is not included in this thesis. All of the plots were grazed from April to October (Table 1) by 4 to 6 heifers for 24 to 72 hrs. Water was constantly available so as not to disrupt grazing habits.

Average sward height and leaf stage, either vegetative or mature (Moore et al., 1991), of the grasses in each experimental plot was used to determine time of grazing. Cattle began grazing plots when each grass reached a maximum target height (vegetative = 30 cm; mature = 45 – 50 cm) and ceased when a minimum target height was reached (vegetative and mature = 15 and 25 cm, respectively, for 50% removal; vegetative and mature = 2 and 5 cm, respectively, for 100% removal). Forage height was measured at 50-cm intervals along duplicate 6-m diagonal transects in each plot by extending plant material against a meter stick. Extreme differences in height, due to manure or urine spots, were avoided during the process. The 12 forage heights collected along each transect were averaged to produce an average pre and post graze sward height for each plot.

1.2.3 Vegetation Sampling

Aboveground net primary productivity (ANPP) for the 2010 season was estimated using a 25- by 100-cm (0.25 m^2) rising plate meter (Sanderson et al., 2001). Dimensions of the plate meter reflected those of the quadrat used to assess forage nutritive value. Five stratified random plate meter measurements were collected within each plot, before and after each grazing event, and their average was calculated. Forage beneath the third plate meter

measurement within either the vegetative 100% or mature 100% treatment was clipped to a 5-cm target stubble height, dried at 55°C for 48 hours, ground in a 1mm Wiley mill, and weighed.

Dry weights of herbage were regressed against the respective plate meter measurements to develop equations that permitted prediction of herbage mass produced by grasses subject to all maturity and utilization treatments. A plate meter calibration was developed for the 2010 growing season: $y = 5.28x - 26.25$; $r^2 = 0.68$.

Belowground net primary productivity (BNPP) was estimated in 2010 from root in-growth cores (Fahey, 1999). Two mesh cores 5-cm in diameter and 15-cm in length, containing original soil sieved free of all visible existing root material, were installed within each treatment on April 13th 2010. The cores were removed at the end of the season on November 10th 2010. Roots were washed free of soil over a 1-mm sieve, dried at 65°C for 48 h, and weighed.

1.2.4 Soil Nitrogen Availability

Baseline soil carbon and nitrogen levels were determined (Sollins, 1999) in summer 2009 (Table 2). To determine soil nitrogen availability during the 2010 grazing season, five soil cores, 15-cm in depth, were extracted from each experimental plot (using a 1.9-cm diameter stainless steel soil probe) and composited in a single bag. Samples were processed within 48 hours, with one part of each sample immediately extracted with 2M KCL and another incubated for 7 days before extraction (Robertson, 1999). Analysis of the first sample (T0) for immediate inorganic nitrogen availability and the second (T7-T0) for mineralization rates was completed using the microplate procedure adapted from Rhine et al. (Rhine et al., 1998).

1.2.5 Soil Temperature, Soil Moisture, and Leaf Area Index (LAI)

During the 2010 grazing season, soil temperature measurements were collected every other week with a 10-cm soil temperature probe. Soil moisture measurements were collected every other week with a TH20 soil moisture probe by Dynamax Inc. and a Field Scout TDR 300 soil moisture meter by Spectrum Technologies.

Defined as the amount of leaf area in a canopy per unit ground area, Leaf Area Index (LAI) measurements were collected weekly using an AccuPAR LP-80 Ceptometer [Decagon Devices, Inc., Pullman, WA (Campbell, 1989)]. LAI was calculated as a function of intercepted photosynthetically active radiation (PAR). Intercepted PAR was determined by measuring incoming PAR above and below the leaf canopy.

Soil temperature, soil moisture, and LAI measurements were collected at 5 randomly chosen points in each experimental plot (either biweekly or weekly as noted above).

1.2.6 Statistical Analysis

Averages calculated from subsamples collected within each experimental unit were used in ANOVA linear mixed-effects (LME) modeling using the maximum likelihood algorithm. All modeling was done using S-Plus 7.2 (Insightful Corp., Seattle WA; 2005). Saturated models were constructed to analyze response variables as a function of management treatments, once we accounted for the random-effects of block (plot) and sub-block (strip).

586 To test the significance of the two fixed-effects or grazing treatments (Extent and Leaf;
587 Table 4) we dropped one of the treatment terms and compared it to a model with both
588 treatment terms. Then we dropped the second treatment term and compared this model
589 (containing only the intercept term) to the previous model which included only one treatment
590 term using a likelihood ratio test (Crawley, 2002). If models were significantly different
591 ($p<0.05$), the model with the lower Akaike's information criterion (AIC) was retained. If not, we
592 selected the simpler model.
593 Separate model selection procedures were run for each grass species (QGR, RCG, OGR,
594 and MDF; Table 4) to test for treatment effects on ANPP, BNPP, root-shoot ratio, soil
595 temperature, soil moisture, pre-graze leaf area index (LAI), and inorganic nitrogen.
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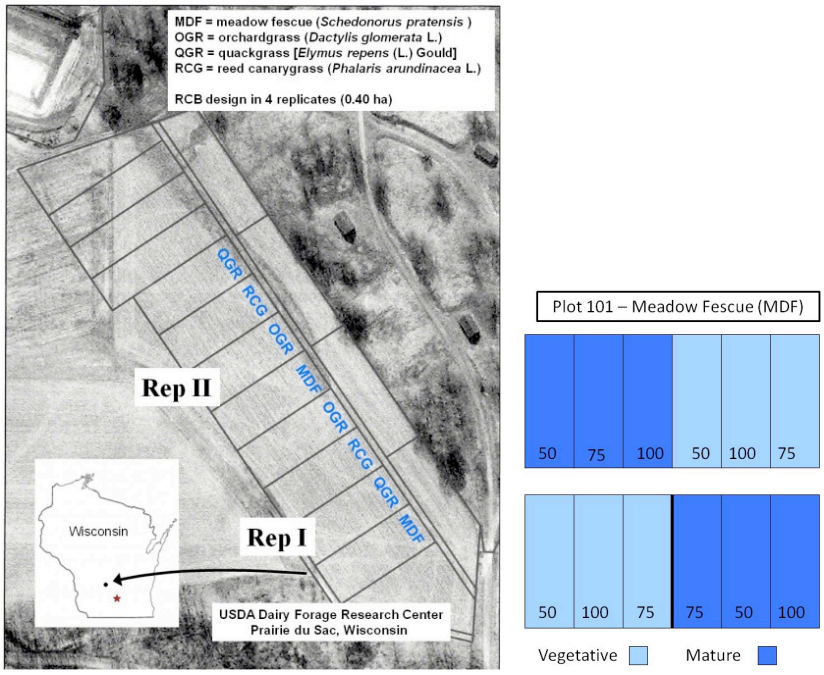

Fig. 1 Layout of Randomized Complete Block Design (RCBD) field experiment with two blocks (Rep I & II) of four cool-season grasses (MDF, OGR, RCG, and QGR) and four treatments per grass: (1) vegetative leaf stage at grazing – 50% biomass removal, (2) vegetative leaf stage – 100% biomass removal, (3) mature leaf stage – 50% biomass removal, and (4) mature leaf stage – 100% biomass removal. Treatment plots in which 75% of aboveground biomass was removed were not included in this thesis

Table 1. Grazing Schedule

(MDF = Meadow Fescue, QGR = Quackgrass, RCG = Reed Canarygrass, OGR = Orchardgrass)

	Growth Stage	Graze Number							Total # of	Graze Interval
Grass	% Biomass	1st	2nd	3rd	4th	5th	6th	7th	Graze Events	in Days
MDF	Vegetative 50	4/28	5/18	6/14	7/20	8/23	9/21	10/19	7	29
	Vegetative 100	5/18	6/21	8/2	9/14				4	40
	Mature 50	5/25	7/15	8/30					3	49
	Mature 100	6/7	7/27	9/21					3	53
QGR	Vegetative 50	5/11	6/7	6/28	7/27	8/23	9/28		6	28
	Vegetative 100	6/1	6/28	8/2	9/7				4	33
	Mature 50	6/7	7/27	9/14					3	49
	Mature 100	6/7	8/9						2	63
RCG	Vegetative 50	5/4	6/1	6/28	7/20	8/9	9/7	10/19	7	28
	Vegetative 100	5/25	6/21	7/20	8/16	9/21			5	30
	Mature 50	6/1	7/6	8/9	9/21				4	37
	Mature 100	6/7	7/20	9/7					3	46
OGR	Vegetative 50	4/28	5/18	6/14	7/12	8/9	9/7	10/19	7	29
	Vegetative 100	5/11	6/14	7/27	8/23	9/21			5	33
	Mature 50	5/18	6/28	8/9	9/21				4	42
	Mature 100	6/1	7/12	9/7					3	44

Table 2: Baseline Soil Carbon and Nitrogen

Grass	C:N Ratio	Carbon	Nitrogen
MDF	11.288838	2.75465	0.244551
QGR	10.461955	2.654285	0.256027
RCG	11.372885	2.661631	0.228765
OGR	10.668877	2.644843	0.249136

1.3 RESULTS

1.3.1 Aboveground Net Primary Productivity

The effect of grazing management on annual aboveground net primary productivity (ANPP) was species dependent ($p = 0.05$; Table 3). Reed canarygrass and orchardgrass behaved most similarly, however, with leaf stage at grazing having a significant effect at both levels of extent of defoliation ($p<0.01$ and $p=0.0005$ respectively; Table 4). Total ANPP was greater for both species in treatment plots grazed at a mature versus a vegetative leaf stage (Fig.2a and 2b). For meadow fescue and quackgrass, there were significant leaf developmental stage at grazing by extent of defoliation interactions on ANPP (Fig. 2c and 2d; Table 4). Meadow fescue produced significantly less forage ($p=0.001$) when grazed at the mature leaf stage with half the biomass removed, while quackgrass produced less forage ($p=0.005$) when grazed at the mature leaf stage with 100% of the biomass removed.

1.3.2 Belowground Net Primary Productivity

Grazing management had no effect on annual belowground net primary productivity (BNPP) of orchardgrass and quackgrass (BNPP averages for both species were 477 g/m^2; Fig. 3). Leaf stage at grazing had a marginal ($p=0.11$) effect, however, on the BNPP of meadow fescue. Total BNPP was greater for meadow fescue in treatment plots grazed at a mature versus a vegetative leaf stage (Fig. 3). Average BNPP for meadow fescue was 480 g/m^2. Both extent of defoliation ($p=0.007$) and leaf stage ($p=0.03$) at grazing had an effect on BNPP of reed

canarygrass plants. BNPP increased in reed canarygrass treatment plots grazed at a vegetative stage (Fig. 4a) and in plots in which 100% of the aboveground biomass was removed during grazing (Fig. 4b). Average BNPP for reed canarygrass was 433 g/m².

ANPP was negatively correlated to BNPP in reed canarygrass plots ($p = 0.06$; Fig. 5a), but showed a marginally positive correlation to BNPP in quackgrass plots ($p = 0.15$; Fig 5d). ANPP was not significantly correlated to BNPP in both orchardgrass and meadow fescue plots ($p = 0.54$ and $p = 0.40$; Fig. 5b and 5c respectively).

1.3.3 Root-shoot Ratios

The effect of grazing management on root-shoot ratios was species dependent as well (Table 4). There was no effect of grazing on the root-shoot ratios of orchardgrass and quackgrass (root-shoot ratio averages were 0.58 and 0.85 respectively). A moderately significant effect ($p=0.06$) of leaf stage at grazing on root-shoot ratio was observed for meadow fescue. Root-shoot ratio was determined to be greater in meadow fescue treatment plots grazed at a mature versus a vegetative leaf stage (Fig. 6). Both extent of defoliation ($p=0.007$) and leaf stage ($p=0.01$) at grazing had an effect, however, on the root-shoot ratio of reed canarygrass plants. Root-shoot ratio increased in reed canarygrass treatment plots grazed at a vegetative leaf stage (Fig. 7a) and in plots in which 100% of the aboveground biomass was removed during grazing (Fig. 7b).

1.3.4 Environmental Factors

The effect of each grazing management treatment on the four environmental factors recorded – soil moisture, soil temperature, available nitrogen, and leaf area index – differed by species (Table 4). There were significant leaf stage at grazing by extent of defoliation interactions on percent soil moisture in both reed canarygrass ($p = 0.09$; Fig. 8a) and meadow fescue ($p = 0.01$; Fig. 8b) plots. Percent soil moisture was significantly lower for both species in treatment plots grazed at the vegetative leaf stage with 100% of the biomass removed. There was no significant effect of grazing management on percent soil moisture observed, however, in either quackgrass or orchardgrass plots. There was no effect of grazing management on soil temperature across all species.

Net nitrogen mineralization and nitrification did not change significantly across different species or management regimes. However, there was a significant leaf stage at grazing by extent of defoliation interaction on net ammonification for meadow fescue ($p = 0.01$; Fig. 9). Net ammonification was significantly lower in meadow fescue treatment plots grazed at the vegetative leaf stage with 50% of the biomass removed.

A significant effect of leaf stage at grazing on pregraze leaf area index (LAI) was observed in orchardgrass plots ($p = 0.005$). Pregraze LAI was determined to be greater in orchardgrass treatment plots grazed at a mature versus a vegetative leaf stage (Fig. 10b). Both extent of defoliation ($p=0.002$) and leaf stage ($p=0.002$) at grazing had an effect, however, on the pregraze LAI of reed canarygrass plants. LAI increased in reed canarygrass treatment plots

676 grazed at a mature leaf stage (Fig. 10a²) and in plots in which 50% of the aboveground biomass
677 was removed during grazing (Fig. 10a¹).

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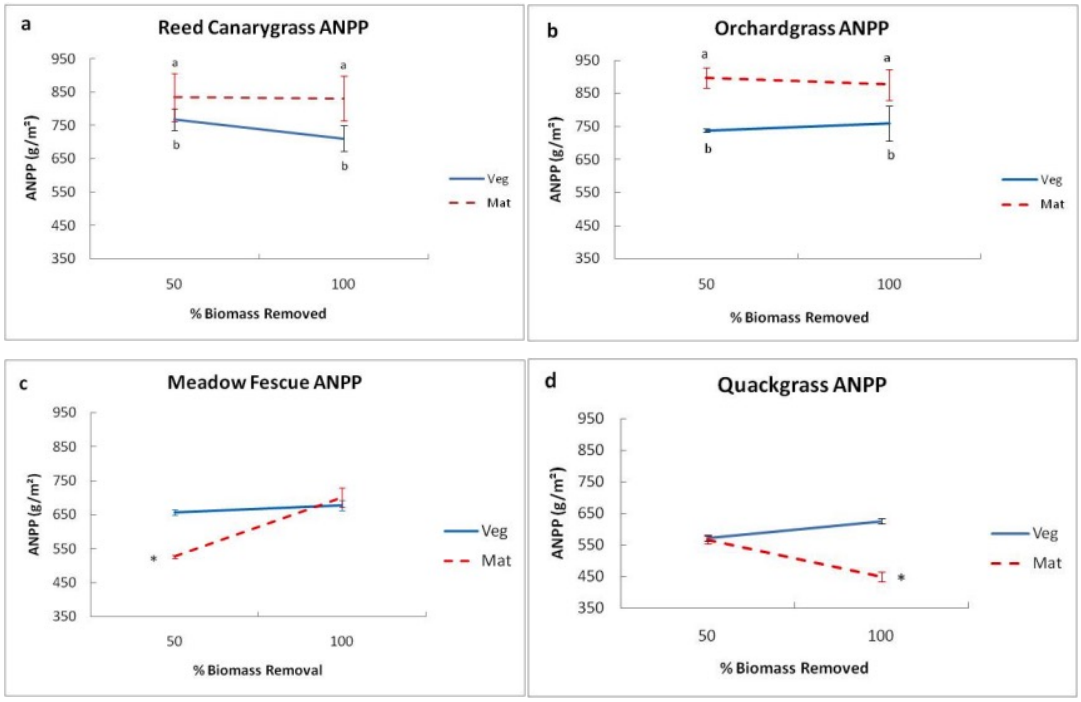

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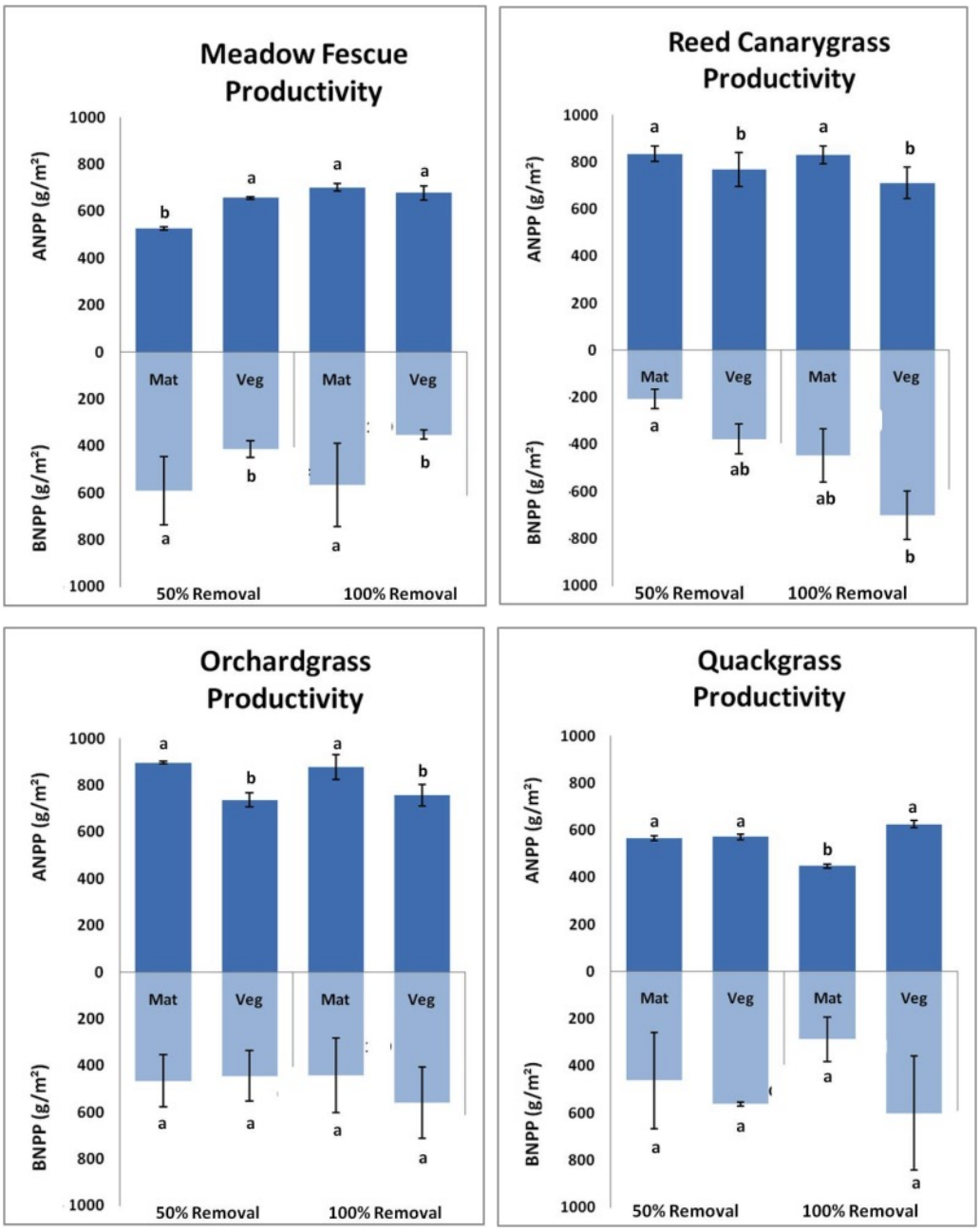
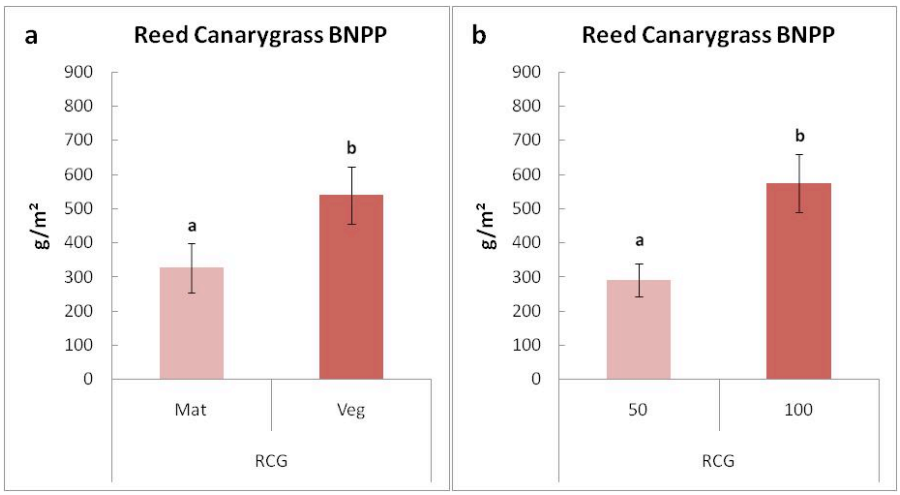
681

682 **Fig. 2** Effects of leaf stage at grazing (Mature and Vegetative) and extent of defoliation (50 and 100%) on annual
683 aboveground net primary productivity (ANPP in g/m²) of reed canarygrass **(a)** orchardgrass **(b)** meadow fescue **(c)**
684 and quackgrass **(d)**. Error bars represent ± 1 SE. Means of ANPP shown with different letters (p≤0.01) and asterisks
685 (p≤0.005) were determined to be significantly different using ANOVA linear mixed-effects model selection.



686
687 **Fig. 3** Effects of leaf stage at grazing (Mature and Vegetative) and extent of defoliation (50 and 100%) on ANPP
688 and BNPP in g/m² of each grass species. Error bars represent ± 1 SE. Means of ANPP and BNPP shown with
689 different letters were determined to be significantly different using ANOVA linear mixed-effects model selection:
690 meadow fescue (ANPP *p=0.001*; BNPP *p=0.11*), reed canarygrass (ANPP *p=0.01*; BNPP *p<0.03*), orchardgrass (ANPP
691 *p=0.0005*; BNPP *N.S.*), and quackgrass (ANPP *p=0.005*; BNPP *N.S.*) – see Table 4.



692
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694
695 **Fig. 4** Effects of **(a)** leaf stage at grazing (Mature and Vegetative) and **(b)** extent of defoliation (50 and 100%) on
696 annual belowground net primary productivity (BNPP) of reed canarygrass. Error bars represent ± 1 SE. Different
697 letters denote significant differences ($p < 0.03$) using ANOVA linear mixed-effects model selection.
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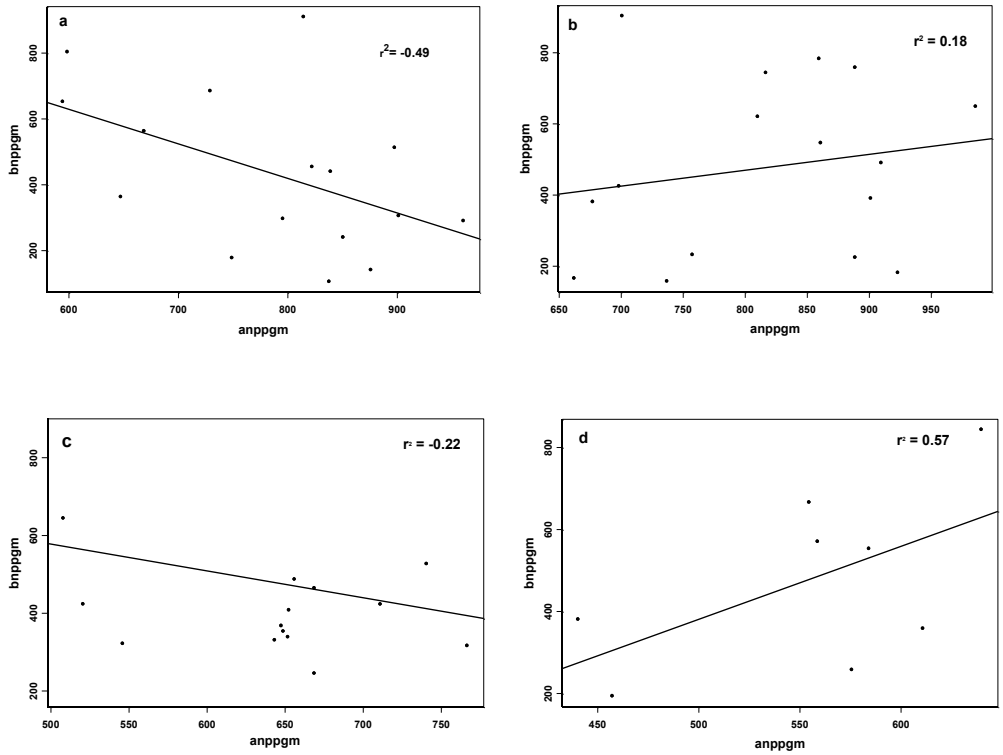

700
701
702 **Fig. 5** Root biomass (BNPP in g/m²) as a function of aboveground production (ANPP in g/m²) for **(a)** reed
703 canarygrass, *y = -1.05 + 1259.19x, r² = -0.49*; **(b)** orchardgrass, *y = 0.446 + 112.97x, r² = 0.18*; **(c)** meadow fescue,
704 *y = -0.69 + 922.81x, r²* = -0.22; and **(d)** quackgrass, *y = 1.78 – 508.99x, r² =0.57.*
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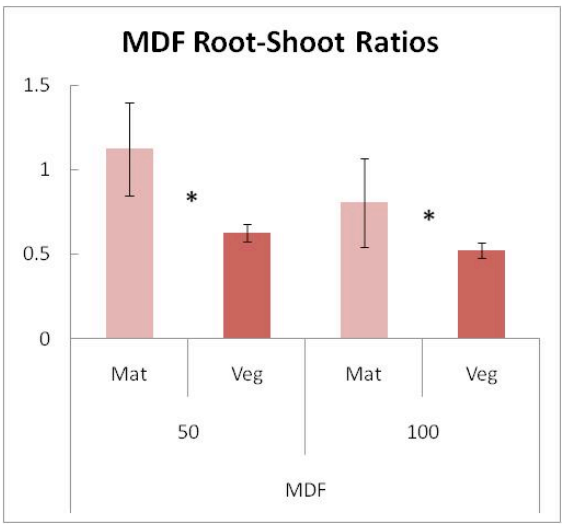


Fig. 6 Effects of leaf stage at grazing (Mature and Vegetative) and extent of defoliation (50 and 100) on root-shoot ratios of meadow fescue. Error bars represent ± 1 SE. Means of root-shoot ratios shown with asterisks ($p = 0.06$) were determined to be significantly different using ANOVA linear mixed-effects model selection.

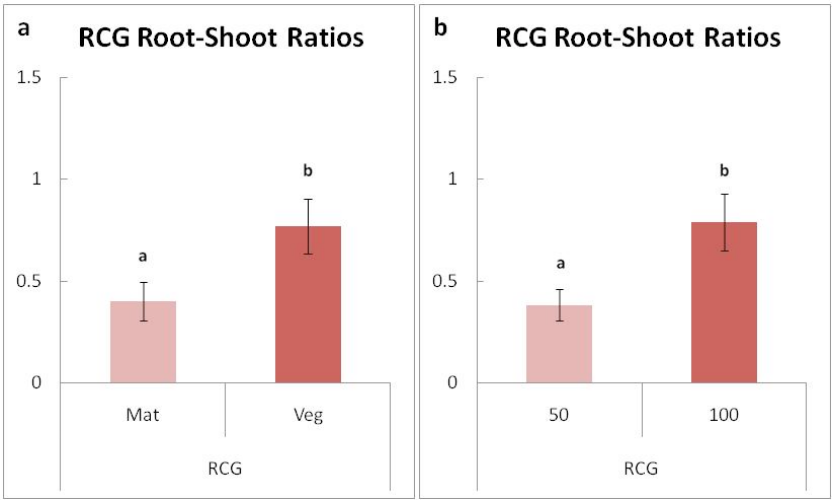


Fig. 7 Effects of leaf stage at grazing (Mature and Vegetative) and extent of defoliation (50 and 100) on root-shoot ratios of reed canarygrass **(a)** and **(b).** Error bars represent ± 1 SE. Means of root-shoot ratios shown with different letters ($p \leq 0.01$) were determined to be significantly different using ANOVA linear mixed-effects model selection.

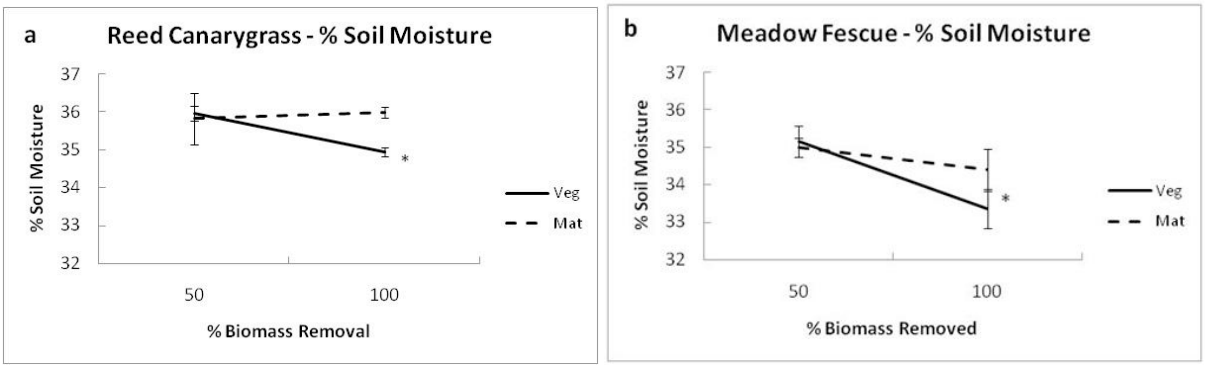


Fig. 8 Effects of leaf stage at grazing (Mature and Vegetative) and extent of defoliation (50 and 100) on percent soil moisture of reed canarygrass **(a)** and meadow fescue **(b)** plots. Error bars represent ± 1 SE. Means of % soil moisture shown with asterisks were determined to be significantly different using ANOVA linear mixed-effects model selection, $p<0.10$.

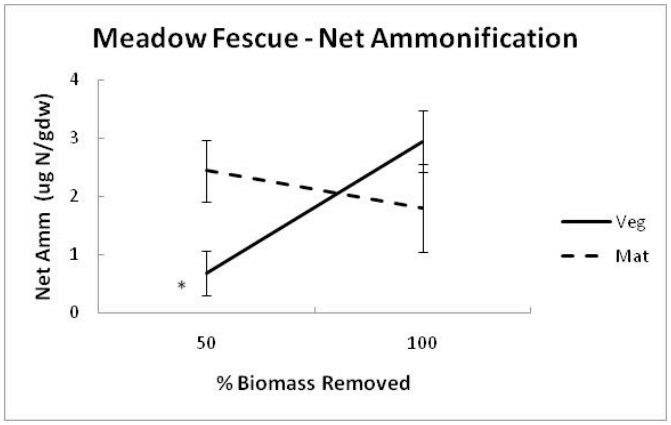
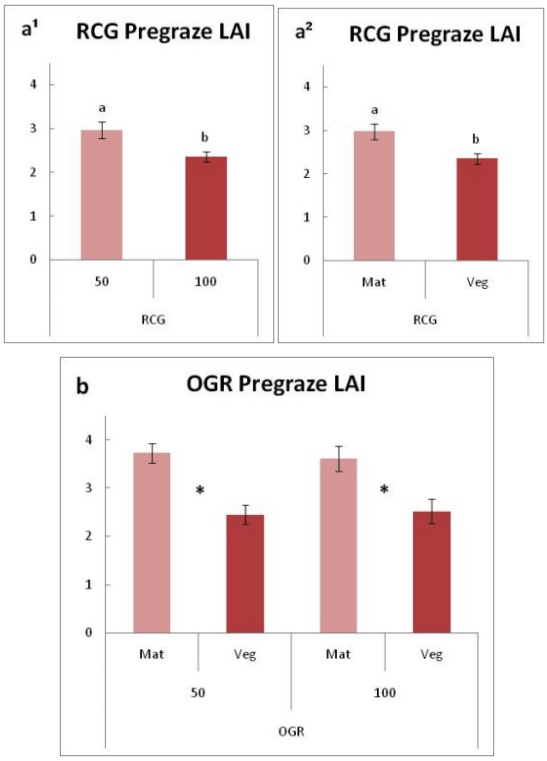


Fig. 9 Effects of leaf stage at grazing (Mature and Vegetative) and extent of defoliation (50 and 100) on net ammonification (ug N/gdw) of meadow fescue. Error bars represent ± 1 SE. Mean of net ammonification shown with an asterisk was determined to be significantly different using ANOVA linear mixed-effects model selection, $p<0.05$.



743
744
745 **Fig. 10** Effects of leaf stage at grazing (Mature and Vegetative) and extent of defoliation (50 and 100) on pre-graze
746 leaf area index (LAI) of **(a)** reed canarygrass and **(b)** orchardgrass. Error bars represent ± 1 SE. Means of pre-graze
747 LAI shown with asterisks ($p = 0.005$) and different letters ($p = 0.002$) were determined to be significantly different
748 using ANOVA linear mixed-effects model selection.
749

Table 3:

Variable	anpp~Grass Species (GS)	bnpp~GS	rootshoot~GS	soilH20~GS	soiltemp~GS	Pregraze LAI~GS	NetMin~GS	NetNit~GS	NetAmm~GS
P - value	0.05	0.93	0.35	0.35	0.27	0.095	0.48	0.57	0.75

Table 4:

Grass	ANPP Best Model	ANOVA p-values	BNPP Best Model	ANOVA p-values	Root-shoot (RS) Ratio	ANOVA p-values	Environmental Factors*	ANOVA p-values
MDF	anpp~Extent x Leaf	E x L = 0.0013	bnpp~Leaf	L = 0.11	RS~Leaf	L = 0.0639	NetAmm~Extent x Leaf	E x L = 0.0099
							SoilH20~Extent x Leaf	E x L = 0.0104
OGR	anpp~Leaf	L = 0.0005	bnpp~Leaf	L = 0.71	RS~Leaf	L = 0.32	PreLAI~Leaf	L = 0.005
QGR	anpp~Extent x Leaf	E x L = 0.005	bnpp~Leaf	L = 0.21	RS~Leaf	L = 0.37	<none>	N.S.
RCG	anpp~Leaf	L = 0.0097	bnpp~Extent + Leaf	E = 0.007, L = 0.028	RS~Extent + Leaf	E = 0.007, L = 0.011	PreLAI~Extent + Leaf	E = 0.002, L = 0.002
							SoilH20~Extent x Leaf	E x L = 0.094

* Only those environmental factors that were significantly effected by treatment are listed, by species, in this table. In QGR plots <none> were significant.

1.4 Discussion

1.4.1 Aboveground Production Response to Grazing Management was Species Specific

In the production of forage, the regrowth ability of individual pasture species is of crucial importance. Considerable differences exist among species in their production potential, resource allocation, and tolerance to grazing, which in turn affects aboveground net primary productivity (Willms and Jefferson, 1993). Our study demonstrates that ANPP is strongly influenced by grazing management as well as plant species. Results suggest that effects of leaf stage at grazing (mature vs. vegetative stage) and extent of defoliation (50 vs. 100% biomass removal) on ANPP are species dependent.

Reed canarygrass and orchardgrass

The lower ANPP observed in reed canarygrass and orchardgrass treatment plots grazed vegetatively suggests that leaf stage at grazing influences grazing tolerance for these two species. Grazing at a mature leaf stage allowed for a longer recovery period than typically recommended for tall-growing cool-season grasses (Undersander, 2002), but substantially increased aboveground productivity for both species. Earlier studies have also demonstrated that reed canarygrass and orchardgrass significantly increase re-growth as a percent of total production if grazed at a mature stage of development rather than at an earlier growth stage (Decker, 1967; Hall et al., 2005; Washko, 1967). With regards to lengthening recovery intervals,

773 to increase persistence of bulbous canarygrass (*Phalaris aquatica*) in Australian pastures the
774 implementation of rotational grazing techniques with longer rest-periods was highly
775 recommended (Chapman et al., 2003; Cullen et al., 2005; Lodge et al., 2003).

776 In New Zealand, the story for orchardgrass was similar. It was reported that in
777 comparison to perennial ryegrass (*Lolium perenne*), aboveground production of orchardgrass
778 increased by 50-60% when rotationally grazed every 30-60 days, with intervals between grazing
779 events varying depending on seasonal re-growth rates. Under continuous grazing, however,
780 two orchardgrass cultivars failed to persist, presumably due to the lack of rest periods. The
781 authors recommended that for orchardgrass only 50% of leaf blades be removed if frequent
782 defoliation was desired so that less physiological stress and increased tiller density would occur
783 (Brock et al., 1996). Agronomists in the U.S. have also found that ANPP and tiller density of
784 orchardgrass declined as clipping height was reduced (Volesky and Anderson, 2007).

785

786 ***Meadow fescue and quackgrass***

787

788 Although reed canarygrass and orchardgrass had increased aboveground productivity
789 when allowed to reach maturity before defoliation, this was not the case for meadow fescue or
790 quackgrass. Significant leaf stage at grazing by extent of defoliation interactions for ANPP of
791 meadow fescue and quackgrass suggest that these management variables are interdependent
792 for both species. For meadow fescue, when 50% of the aboveground biomass was defoliated
793 leaf stage was significant and mature grasses actually exhibited a decrease in yield. When 100%
794 of the aboveground biomass was defoliated, however, leaf stage was not significant. For

quackgrass, when 100% of the aboveground biomass was defoliated, leaf stage was significant and mature grasses again exhibited a decrease in yield. When 50% of the aboveground biomass was removed, however, leaf stage was not significant.

One factor influencing tiller survival and thus growth potential for forage species is number and status of meristems (Crawley, 1983). The tillers of most cool-season grasses elongate after the plant has shifted to the reproductive stage, lifting active apical meristems above defoliation height and causing them to be removed with grazing. Meadow fescue, on the other hand, not only tillers profusely early in the growing season, but has stems that do not elongate after initial heading. As a result it may be grazed more aggressively than other pasture grasses (Undersander, 2002). Having evolved with ungulate herbivory, it has a high level of stress tolerance (Fjellheim and Rognli, 2005) and has been found to increase both regrowth rates and cumulative yield when grazed at a vegetative leaf stage (Virkajarvi, 2003). Barnes et al. (2003) also noted that meadow fescue ANPP increased when a short residual stubble height was maintained. Our results support this conclusion since significantly lower ANPP was documented in experimental plots in which the highest stubble height (25cm) was maintained.

1.4.2 Belowground Production Response to Grazing Management was Species Specific

Aboveground production alone, however, does not accurately reflect total carbon assimilation of grassland species since belowground production can be of equal or greater magnitude (Mokany et al., 2006; Titlyanova et al., 1999). Results suggest that BNPP is significantly influenced by grazing management as well as plant species and relationships

between ANPP and BNPP can be particularly useful for explaining species specific responses to defoliation.

There is evidence that root structure differences across North American grassland species can drive ecosystem functions such as net primary productivity. For example, rhizomatous species in particular have a relatively large investment in shallow rhizomes in comparison to belowground carbon allocation of bunchgrasses (Craine et al., 2003). Our research demonstrates an apparent dependence of BNPP on ANPP and vice versa for both rhizomatous species, whether negative or positive in relationship. In contrast, ANPP was not significantly correlated to BNPP in both bunchgrass species: orchardgrass and meadow fescue.

Quackgrass, reed canarygrass, and meadow fescue

ANPP demonstrated a marginally positive correlation to BNPP in quackgrass plots. The positive correlation exhibited by ANPP and BNPP of quackgrass could conceivably have been much stronger had one experimental replicate not been removed from the study, due to thistle (*Cirsium vulgare*) and crabgrass (*Digitaria ischaemum*) invasion of this replicate. A strong positive correlation (r^2=0.73) between root and shoot dry weight of quackgrass has been found in previous research, supporting the conclusion that rhizome production of this forage species increases with shoot production (Westra and Wyse, 1981). This morphological characteristic could have allowed quackgrass a high level of stress tolerance and increased aboveground productivity even when 100% of its biomass was grazed at the vegetative leaf stage.

While quackgrass demonstrated a positive correlation between ANPP and BNPP, management strategies that significantly increased ANPP actually reduced BNPP in experimental plots seeded with reed canarygrass and meadow fescue, the latter species having marginal significance. This trend supports existing experimental evidence that in most temperate grasslands, root-shoot ratios decrease as shoot biomass (ANPP) increases (Mokany et al., 2006). It is generally believed that when all or most of the leaves are grazed from a graminoid plant, root growth slows or stops and the plant uses its carbohydrate reserves in those roots or stubble for the energy needed to grow new leaves and stems (Murphy, 1998).

Orchardgrass

Since there was no relationship between grazing management and belowground production of orchardgrass, we can conclude that extent of defoliation and leaf stage at grazing have less of an effect on belowground carbon storage potential of this species. A previous study concluded that orchardgrass was most defoliation-tolerant, compared to several other temperate perennial grasses, and helps explain the lack of belowground response to grazing management. The authors proposed that a high sheath-stem ratio was the adaptation favoring orchardgrass most strongly, allowing it to maintain photosynthesis and a level of carbon supply sufficient to support continued aboveground re-growth, without depleting belowground carbon, throughout the grazing experiment (Cullen et al., 2006).

1.4.3 Production Response to Environmental Conditions was Species Specific

Both environmental and developmental factors have the potential to interact with grazing management to influence ANPP and BNPP. Developmental factors include inherent species specific characteristics and re-growth strategies after defoliation, while environmental factors include soil moisture and temperature, nutrient availability, and competition for light (Mokany et al., 2006; Strauss and Agrawal, 1999). Timing and extent of defoliation can change a plant's microenvironment of sunlight intensity, soil moisture, and soil temperature, just as environmental changes such as low soil moisture can cause slow re-growth of defoliated pasture. Species specific physiological and morphological characteristics can also influence re-growth response, however, significantly changing annual production in temperate perennial pastures where environmental resources are in ample supply (Murphy, 1998).

The effect of grazing management on the environmental factors measured in our study was species dependent. Reed canarygrass and meadow fescue were the only two species to have both significantly different above and belowground productivity and environmental factors across treatments. Thus, possible developmental and environmental mechanisms for differences in productivity of these two species will be the focus hereafter.

Reed canarygrass

Significant differences in ANPP and BNPP across reed canarygrass plots can be partially explained by the leaf stage at grazing by extent of defoliation interaction on soil moisture. Reed

canarygrass plots in which 100% of the biomass was grazed at the vegetative leaf stage had both significantly lower ANPP and significantly higher BNPP and root-shoot ratios. These same experimental plots also had significantly lower soil moisture than all the others. Thus, it can be concluded that a particular management strategy of reed canarygrass (grazing 100% of the biomass at the vegetative leaf stage) influenced an environmental factor – soil moisture – which in turn influenced ANPP negatively and BNPP positively. Since reed canarygrass is a helophytic species known for its morphological plasticity (Lavergne and Molofsky, 2007), there is high potential for it to adjust its morphological characteristics depending on soil water levels. With less soil moisture, reed canarygrass would conceivably increase its root biomass relative to shoot biomass to compensate (Coops et al., 1996).

Even though BNPP and root-shoot ratios did not change significantly with soil moisture across all four grasses in this study, there are existing hypotheses and experimental evidence supporting the theory that root-shoot ratios become lower as water availability increases (Chapin et al., 1993; Gower et al., 1992; Schenk and Jackson, 2002). The 2010 growing season in Wisconsin did have one of the top five highest annual rainfalls, however, since 1960. Excess water could help explain why root-shoot ratios were generally low (<1.2) for a temperate grassland (Mokany et al., 2006; Titlyanova et al., 1999) across all treatments, as well as why in reed canarygrass experimental plots with significantly lower soil moisture there was an increase in BNPP. It should be noted that in these same experimental plots, where 100% of aboveground biomass was grazed at the vegetative leaf stage, considerable amounts of bare ground were evident. Significantly reduced soil moisture, quite possibly caused by increased evaporation rates, could have been driven by the drastic decrease in aboveground biomass.

Meadow fescue

Grazing management strategies had interactive effects on the environmental factors measured in meadow fescue plots, but these environmental responses to treatment do not correlate well to changes in productivity. Even though there was a significant leaf stage at grazing by extent of defoliation interaction for percent soil moisture in meadow fescue plots, the interaction pattern does not help explain subsequent changes in ANPP and BNPP. There was no significant effect of treatment on soil temperature or available nitrogen across all four grass species in this study, with the exception of a leaf stage at grazing by extent of defoliation interaction on net ammonification in meadow fescue plots. Once again, however, the interaction pattern does not help explain subsequent changes in ANPP and BNPP for this species.

Thus, in contrast to reed canarygrass, ANPP and BNPP of meadow fescue seem to depend more on developmental and management related factors, such as extent of defoliation and leaf stage at grazing, than on environmental factors such as resource availability. Previous studies have also found dry matter yields of both meadow fescue and orchardgrass to be highly dependent upon the phenological stage of development at harvest. The relative growth rate of meadow fescue was found to be highest after being cut at the vegetative leaf stage versus later in the growth cycle (Bonesmo and Skjelvag, 1999). For orchardgrass, on the other hand, actually delaying harvest beyond the boot stage (which falls directly between vegetative and reproductive leaf stages and was classified as part of the mature leaf stage for the purposes of our study; Moore et al., 1991) increased annual yields (Hall et al., 2005).

926

927 **1.4.4 Management Implications**

928

929 Even though forage quality is slightly greater (an increase of 1-7% digestibility) during
930 the vegetative leaf stage, stand persistence is best achieved for reed canarygrass and
931 orchardgrass when harvests are delayed until mature leaf stages. Cutting the first growth
932 between boot and early anthesis stages provides a good compromise for yield and persistence
933 for these two species, while still providing quality forage for most classes of livestock. Reed
934 canarygrass plants cut close and frequently may make slightly better quality forage, but yield
935 will be greatly reduced (Stannard, 2003). Orchardgrass responds especially well to rotation-
936 deferred grazing systems as well, in which paddocks are allowed to mature and produce seed,
937 at least periodically, for continuation of the stand (Bush, 2006).
938 When reed canarygrass, in particular, is grazed too extensively soil moisture levels are
939 also compromised. Experimental plots in which 100% of the biomass was grazed at the
940 vegetative leaf stage had both decreased aboveground production and significantly low soil
941 moisture. Unlike other forage species in our study, the combination of repeated extensive
942 defoliation and low soil moisture put noticeable stress on reed canarygrass and its root-shoot
943 ratio increased significantly to compensate (Titlyanova et al., 1999). For both these reasons,
944 reed canarygrass plants should be allowed to grow past the vegetative leaf stage before being
945 grazed. This may result in a slightly thinner sward and forage with more stems present, but will
946 allow for pasture recovery, especially during drought (Murphy, 1998).

In contrast to reed canarygrass and orchardgrass, however, meadow fescue and quackgrass demonstrated an increase in aboveground production when grazed vegetatively. These species specific responses to defoliation allow for deliberate planting of forage with offset "maturities", critical growth stages, and stress tolerance in order to schedule optimal harvest and/or grazing times. For example, orchardgrass and meadow fescue complement each other well. The former has increased productivity and persistence when grazed at the mature leaf stage and actually matures first, while the latter has increased production when grazed at the vegetative stage and matures second (Murphy, 1998).

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