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—to develop an understanding of range ecosystems and of the principles applicable to the management of range resources;

—to assist all who work with range resources to keep abreast of new findings and techniques in the science and art of range management;

—to improve the effectiveness of range management to obtain from range resources the products and values necessary for man's welfare;

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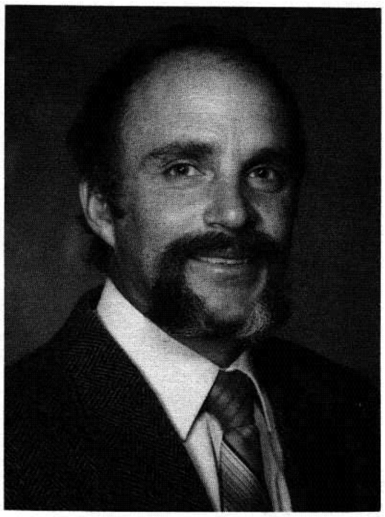
Invited Synthesis Paper



The Editorial Board of the *Journal of Range Management* invited Frederick D. Provenza to prepare this synthesis paper.

Fred Provenza was born in Colorado Springs, and raised in Salida, Colorado. He attended college at Colorado State University in Fort Collins, and obtained a B.S. degree in Wildlife Biology in 1973. He worked on a ranch near Salida while attending college, and for nearly two years after college.

Fred moved to Logan, Utah in 1975 and began work on M.S. degree in Range Science, which was obtained in 1978. He subsequently worked on a Ph.D. in Range Science, which was completed in 1982. In 1982 Fred began working on the faculty in the Range Science Department at Utah State University. He is currently a professor in the Department of Rangeland Resources. Fred has taught 3 courses since becoming a member of the Range Science Department; (RS 298, Summer Camp; RS 300, Range Principles; RS 703, Plant-Herbivore Interactions). He also received a grant from the Soil Conservation Service to teach RS 703 as part of their efforts in continuing education.This course was taught for the first time during the summer of 1991, and will be taught on an annual basis for the foreseeable future. The course takes place during a 2-week period and involves field work, lectures, and discussions.

Fred's research interests are in plant-herbivore interactions, with specific interests in how learning affects food and habitat selection by herbivores.

Postingestive feedback as an elementary determinant of food preference and intake in ruminants

FREDERICK D. PROVENZA

Abstract

Ruminants select nutritious diets from a diverse array of plant species that vary in kinds and concentrations of nutrients and toxins, and meet their nutritional requirements that vary with age, physiological state, and environmental conditions. Thus, ruminants possess a degree of nutritional wisdom in the sense that they generally select foods that meet nutritional needs and avoid foods that cause toxicosis. There is little reason to believe that nutritional wisdom occurs because animals can directly taste or smell either nutrients or toxins in foods. Instead, there is increasing evidence that neurally mediated interactions between the senses (i.e., taste and smell) and the viscera enable ruminants to sense the consequences of food ingestion, and these interactions operate in subtle but profound ways to affect food selection and intake, as well as the hedonic value of food. The sensation of being satisfied to the full (i.e., satiety) occurs when animals ingest adequate kinds and amounts of nutritious foods, and animals acquire preferences (mild to strong) for foods that cause satiety. Unpleasant feelings of physical discomfort (i.e., malaise) are caused by excesses of nutrients and toxins and by nutrient deficits, and animals acquire aversions (mild to strong) to foods that cause malaise. What constitutes excesses and deficits depends on each animal's morphology, physiology, and nutritional requirements. This does not mean that ruminants must maximize (optimize) intake of any particular nutrient or mix of nutrients within each meal or even on a daily basis, given that they can withstand departures from the normal average intake of nutrients (i.e., energy-rich substances, nitrogen, various minerals, and vitamins). Rather, homeostatic regulation needs only some increasing tendency, as a result of a gradually worsening deficit of some nutrient or of an excess of toxins or nutrients, to generate behavior to correct the disorder. Extreme states should cause herbivores to increase diet breadth and to acquire preferences for foods that rectify maladies. From an evolutionary standpoint, mechanisms that enable animals to experience feedback, sensations such as satiety and malaise, should be highly correlated with nutritional well being, toxicosis, and nutritional deficiencies, which are directly related with survival and reproduction.

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How wisely ruminants select their diets is a contentious issue. On the one hand, there is little evidence that ruminants can directly sense nutritional components in foods, and it is difficult to accept that liking or disliking the flavors of particular foods enables animals to select foods that are nutritious and avoid those that are toxic. In addition, ruminants occasionally die from overingesting substances (e.g., certain toxic plants, grain, lead plates from broken batteries), and they sometimes fail to ingest appropriate minerals which are offered cafeteria style. Given these observations, and the lack of a mechanistic framework to understand food selection, it is difficult to discern how ruminants might ingest foods to meet their nutritional requirements.

On the other hand, studies during the past decades have established ruminants generally select diets higher in nutrients and lower in toxins than the average food available (Arnold and Dudzinski 1978, Provenza and Balph 1990, Rosenthal and Janzen 1979, Raupp and Tallamy 1991, Rosenthal and Berenbaum 1992). Selection occurs even though ruminants' requirements vary with changing environmental and physiological conditions (Church 1988). Thus, ruminants apparently possess some degree of nutritional wisdom such that they are able to select foods that meet nutritional needs and to avoid foods that cause toxicosis.

Young ruminants can learn from mother and peers what is and is not appropriate to eat, and this apparently plays a critical role in the transmission of nutritional wisdom among generations (Provenza 1994a,c). Learning from mother increases efficiency of learning about nutritious foods and reduces risk of overingesting toxic foods. Lambs learn quickly (i.e., 5 min/day for 5 days) to avoid a "harmful" novel food lithium chloride (LiCl) that their mothers were trained to avoid, and to select a nutritious novel alternative, when they were with their mothers who exhibited the appropriate behavior (Mirza and Provenza 1990, 1992, 1994).

There is also evidence that food selection involves interactions between the senses of taste and smell and mechanisms to sense the consequences of food ingestion, such as satiety (experienced when animals ingest adequate kinds and amounts of nutritious foods) and malaise (experienced when animals ingest excesses of nutrients or toxins or experience nutrient deficits). Much remains to be learned concerning how taste and smell are integrated with postingestive feedback. The objective of this paper is to discuss how these factors may be related, thereby identifying some of the mechanisms that may underlie the nutritional wisdom of ruminants. Some of the views are speculative, and are offered in the hope that they will stimulate research on the interaction between the nutritional and behavioral bases of food selection in ruminants.

Models of Food Selection

Four models have emerged regarding food selection of ruminants: (1) euphagia, (2) hedyphagia, (3) body morphophysiology and size, and (4) learning through foraging consequences (Provenza and Balph 1990). Euphagia, the innate ability to taste and smell specific nutrients and toxins in plants, supposedly lets animals select nutritious foods and avoid harmful foods. Nonetheless, it is not likely that animals directly taste and smell most nutrients and toxins in foods because the taste, smell, and texture of each food results from a unique concoction of chemical compounds that make the flavor of each food unique (Bartoshuk 1991, but see conclusions of Provenza and Balph 1990 and Sclafani 1991a). Proponents of hedyphagia argue that animals select foods that are immediately "pleasing" to olfactory, gustatory, and tactile senses and avoid those that are not. According to the argument, evolution operates such that those plant compounds that are nutritious taste good and those that are toxic taste bad. Models based on body morphology and physiology assume that ruminant species differ in their ability to ingest forages with different physical and chemical characteristics. Proponents of these models argue that as a result of evolving in different environments, different ruminant species possess different morphological and physiological characteristics that cause them to ingest forage that differs in physical and chemical characteristics.

The fourth model, learning through foraging consequences, involves feedback mechanisms that provide the flexibility to select nutritious diets in environments where forages vary in concentrations of nutrients and toxins (Provenza and Balph 1990, Provenza and Cincotta 1993). Learning encompasses prominent aspects of the other 3 models. The learning model of foraging assumes that diet selection is a result of positive and negative consequences of foraging. The nutritional and toxicological consequences of food selection are related to an individual's morphology and physiology, which is the essence of the morphophysiology model. Neurally mediated interactions between the senses (i.e., taste and smell) and the viscera enable ruminants to sense the consequences of food ingestion, and these interactions can operate in subtle but profound ways to affect the hedonic value of food (i.e., pleasurable and unpleasurable sensations experienced through taste and smell), which is the gist of the hedyphagia model. Finally, feedback from nutrients and toxins can enable animals to select nutritious foods and limit intake of toxic foods, which is the essence of the euphagia model of food selection.

Evidence of Feedback in Ruminants

In the following discussion of how excesses and deficits of nutrients and excesses of toxins affect food selection and intake, I relied on 3 kinds of evidence to argue that interactions between the senses (i.e., taste and smell) and postingestive feedback are consequential. (1) Esophageally fistulated animals sham-fed various foods or purified compounds show that food flavor (i.e., taste and odor) and postingestive feedback both affect food selection and intake. (2) Other experiments in which animals receive a food or a purified compound, by gavage or ruminal infusion, that causes either aversive or positive postingestive effects, show the importance of feedback. (3) Similar experiments in which animals eat a new food (or a food containing a purified compound), and subsequently decrease or increase intake of the food, provide evidence for the importance of aversive and positive postingestive feedback in food selection and intake.

Excesses of Toxins

Mammals have mechanisms to digest foods, to assimilate nutrients (Church 1988), and to counter toxins (McArthur et al. 1991). The capacity of these systems is seldom exceeded because animals quickly experience internal malaise and limit intake before toxicosis ensues. Blood flow through the ruminal artery increases within 30 to 60 sec after feeding begins, and peaks about 15 min later (Barnes et al. 1986). Thus, ruminants probably sense many toxins (and nutrients) in the cardiovascular system early in a meal. Sheep acquire aversions to foods containing the toxicant LiCl within 1 hour (Provenza et al. 1993b). Goats learn to limit intake of twigs containing tannins within 1 hour (Provenza et al. 1994c), and learn to limit intake of various sources of dietary nonprotein nitrogen within minutes (Conrad et al. 1977).

Animals eat nutritious plants that contain toxins, but they generally limit intake in accord with the concentration of the toxin. Toxins cause malaise, which in turn causes animals to eat small amounts of a variety of plants (i.e., to increase diet breadth) (Bryant and Kuropat 1980, Bryant et al. 1991). For example, goats prefer older twigs (OG) to current season's twigs (CSG) from the shrub blackbrush *(Coleogyne ramosissima)*, even though CSG contains more nitrogen (1.04% vs 0.74%) and is more digestible (48% vs 38%) (Provenza et al. 1983). CSG contains a condensed tannin that causes aversive postingestive feedback (Provenza et al. 1990), and as a result, goats eat less CSG than OG within a meal (Provenza et al. 1994c).

Aversive postingestive feedback causes cattle, sheep, and goats to decrease intake of foods containing toxins like the alkaloids in larkspur (Olson and Ralphs 1986) and tall fescue (Aldrich et al. 1993, Thompson and Stuedemann 1993), condensed tannins in shrubs like blackbrush (Provenza et al. 1990), glucosinolates in brassica crops (Duncan and Milne 1992, 1993), saponins, coumarins, furocoumarins and anthraquinones in sacahuiste (Rankins et al. 1993), and lithium chloride added to foods (Provenza et al. 1990, 1993a, Lane et al. 1990, duToit et al. 1991, Ralphs and Cheney 1993). Aversive feedback also causes a decrease in intake of poor-quality silage (Buchanan-Smith 1990), leafy spurge (Kronberg et al. 1993), larkspur (Pfister et al. 1990), ponderosa pine (Pfister et al. 1992), bitterweed (Calhoun et al. 1981), and sagebrush (Johnson et al. 1976, Ngugi et al. 1994).

An aversion to a food increases with severity of the illness (Fig. 1), and decreases the longer the delay between food ingestion and illness (Garcia et al. 1974, duToit et al. 1991, Ralphs and Cheney 1993). The longer aversive postingestive feedback is delayed (Burritt and Provenza 1991), and the greater the positive feedback from the food during the delay (Thorhallsdottir 1991, Burritt and Provenza 1992, Ralphs et al. 1995, Villalba and Provenza unpublished), the more likely ruminants will ingest the food. Thus, malaise and satiety can interact across a broad and subtle continuum to affect food selection and intake.

Ruminants often eat nutritious foods containing toxins, an apparent anomaly which may be caused by 2 factors. Enhanced nutrient status may increase their ability to eat foods containing toxins (Illius and Andrews 1994). In addition, ruminants can limit intake to minimize toxicity (Provenza et al. 1994c, Ngugi et al. 1994). For instance, sheep maintain intake of LiCl at approximately 40 to 60 mg/KG body weight, and intake increases as toxicity diminishes (duToit et al. 1991, Launchbaugh et al. 1993). Thus, animals can use food resources whose chemical characteristics vary.

Intake of nutritious foods containing toxins is often cyclical, with sharp declines followed by gradual increases in intake (Pfister et al. 1994). A cyclical pattern of intake also occurs when ruminants eat grain. Production of organic acids from starch digestion evidently causes malaise, which causes intake to decline (Huber 1976, Britton and Stock 1987, Provenza et al. 1994d). Nonetheless, any negative feedback is ultimately followed by positive feedback (i.e., opponent-process theory of motivation of Solomon and Corbit 1974). Thus, when food ingestion is followed by aversive feedback, the aversion to the food diminishes as time passes because the recuperative process gradually counter-conditions the aversion (Garcia 1989).

Considering the millions of bites of food taken by ruminants each day, there are relatively few instances of toxicosis, most of which are probably the result of the failure of feedback and (or) sensory (i.e., taste and smell) systems (Provenza et al. 1992). For instance, toxicosis may occur when phytotoxins circumvent feedback mechanisms responsible for malaise, and when malaise is delayed temporally (several years with some pyrrolizidine alkaloids, Cheeke and Shull 1985). Animals may also be unable to discriminate slight changes in concentrations of a highly toxic compounds, to avoid interactions between toxins in 2 or more plants, and to differentiate nutritious and toxic plants when placed in unfamiliar environments.

Excesses of Energy or Nutrients

Low concentrations of nutrients limit intake, intermediate concentrations cause intake to increase, and excessive rates and amounts of nutrient release cause intake to decrease (Fig. 1, Arnold and Hill 1972). Levels of portal and jugular blood metabolites (e.g., volatile fatty acids, VFAs) that may enable ani-

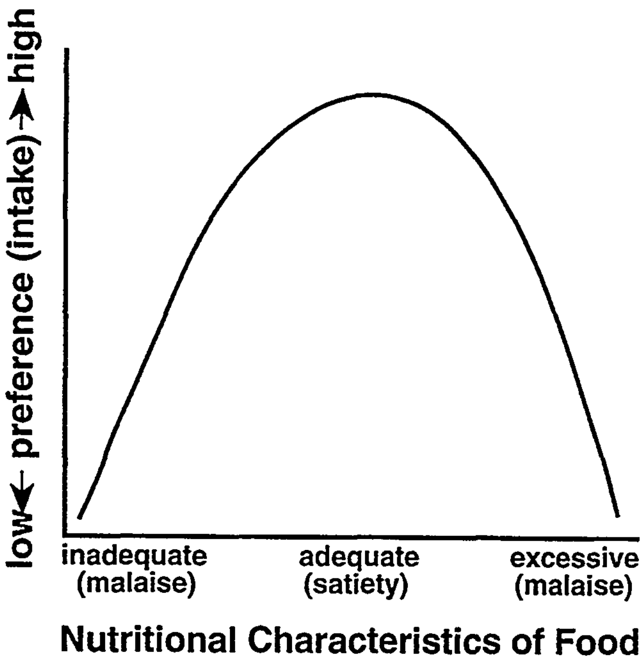

Fig 1. Low concentrations of nutrients adversely affect preference (intake), intermediate concentrations cause preference (intake) to increase, and excessive rates and amounts of nutrient release can cause preference (intake) to decrease. Accordingly, excesses or deficits of nutrients (and excesses of toxins) set a limit on the amount of a particular food that can be ingested within a particular time frame. Feedback enables animals to sense the consequences of food ingestion, which affects preference (intake) for particular foods.

mals to sense the effects of nutrient intake increase within 15 min after ruminants begin to eat (Thye et al. 1970, Evans et al. 1975, Chase et al. 1977, deJong 1981). An excess of energy or nutrients in a food causes ruminants to limit intake of the food, and in turn, can cause an increase in diet breadth. For example, ruminants prefer high-energy foods like grains, but they limit intake of grain and increase intake of alternative foods, once grain is overingested (Britton and Stock 1987, Ortega-Reyes et al. 1992, Phy and Provenza 1994 and unpublished). The decrease in intake is due to postingestive malaise, evidently caused by an excess of byproducts from microbial fermentation (e.g., VFAs like lactate and propionate) (Provenza et al. 1994d). An excess of propionate causes sheep to acquire strong aversions to foods (Ralphs et al. 1995). Thus, byproducts of microbial fermentation such as propionate and lactate can influence food selection and intake.

Excessive nitrogen in food can also adversely affect intake (Barker et al. 1988). Ruminants eating foods high in rumen-degradable protein experience high levels of ruminal ammonia, suffer malaise, and decrease intake (Prins and Beekman 1989). Microbial fermentation of nitrogen can result in inordinately high amounts of ammonia, which escape from the liver and pass into peripheral circulation where excessive ammonia is toxic (Chalupa et al. 1970, Prior et al. 1970, Fernandez et al. 1990, Schelcher et al. 1992). Ammonia toxicity is mediated by various mechanisms in the brain (Felipo et al. 1993). Toxicosis associated with excessive ammonia explains why intake quickly declines as concentrations of compounds (e.g., urea) that are readily converted to ammonia increase in food (Conrad et al. 1977, Choung et al. 1990). Aversive postingestive feedback causes animals to limit intake of foods paired with excessive amounts of urea (Kertz et al. 1982, see Grovum and Chapman 1988 for discussion related to the taste of urea), and sheep regulate silage intake to maintain blood ammonia nitrogen levels below 2 mg/L (Nicholson et al. 1992).

Aversive feedback from excessive (or inadequate) nitrogen helps to explain how lambs can select a diet that maximizes growth from isocaloric foods that vary in protein (Cropper et al. 1986, Kyriazakis and Oldham 1993, Fig. 2), and why they consume less protein as they age (Cropper et al. 1985). Excessive (or inadequate, see next section) nitrogen content in different foods likely causes various degrees of malaise, which will vary with the concentration of protein and the physiological requirements of the animal. What causes satiety for an animal at one age (e.g., young) may be excessive and cause malaise for another (e.g., older). Young growing animals, as well as adults deficient in protein, probably select diets in direct accordance with their protein requirements (Webster 1993). Changes in food selection likely occur as a result of continuing experience of the effects of foods on the internal milieu (Kyriazakis and Oldham 1993), which could be ascertained on a meal-to-meal basis (Provenza 1994b, Provenza et al. 1994c).

Ruminants also respond to concentrations of minerals in food. For instance, sheep fed an oat hay-lupine mixture containing either 0, 1.7, 3.3, 6.3, 12, or 21% of a mineral mix ate less as the concentration of the minerals increased; most of the sheep in the groups containing the highest concentrations eventually refused to eat the food (Masters et al. 1992). The decrease in intake is mediated by postingestive feedback resulting from increasing osmolality (Bell 1984, Grovum 1988, Grovum and Chapman 1988, Carter and Grovum 1990, Forbes et al. 1992, Anil et al. 1993), which depends on minerals in food and VFAs produced by microorganisms (Bennink et al. 1978). Intake also decreases when NaCl, KCl, Na-acetate, Na-propionate, and PEG are added to the rumen before feeding (Ternouth and Beattie 1971, Grovum and Bignell 1989), which indicates that many osmotically active particles can reduce intake (Carter and Grovum 1990).

Deficits of Energy or Nutrients

Animals acquire aversions to nutrient-deficient diets (Richter 1943), evidently because the effects of nutrient deficiencies resemble those of slow-acting toxins (Rozin 1976). The onset of malaise, and the degree to which it occurs, will depend on the particular nutrient and the severity of the deficiency. Malaise from nutrient-deficient diets should cause animals to increase diet breadth and to acquire preferences for foods that rectify deficits. This is evidently what occurs when cattle increase consumption of supplemental protein when forage is low in protein (Provenza et al. 1983). This may also explain why Angora goats consumed woodrat (*Neotoma lepida*) houses, made of juniper (*Juniperus osteosperma*) bark and twigs soaked with urine (nitrogen), when

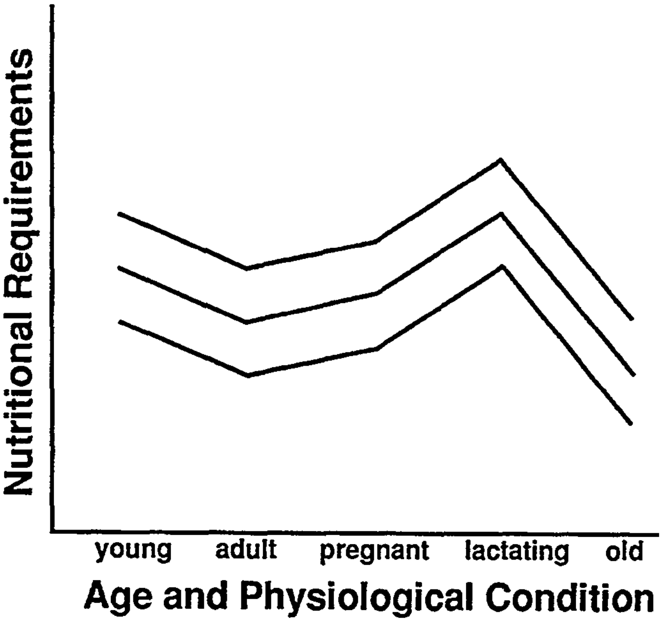

Fig. 2. Animals require various nutrients in amounts and proportions that vary with age, physiological condition, and environment. The ideal nutritional state (center line) occurs when all nutrients are obtained simultaneously. It is dynamic and multidimensional, with as many dimensions as there are functionally relevant nutrients (Emmans 1991, Simpson and Raubenheimer 1993). Nonetheless, ruminants need not maximize (optimize) intake of any particular nutrient or mix of nutrients within each meal or even on a daily basis, given that they can withstand departures from the normal average intake of nutrients (i.e., energy-rich substances, nitrogen, various minerals, and vitamins) (Booth 1985). Rather, homeostatic regulation needs only some increasing tendency, as a result of a gradually worsening deficit of some nutrient (lower line) or of an excess of toxins or nutrients (upper line), to generate conditions (i.e., malaise) to correct the disorder (i.e., cause animals to change food selection). Malaise causes animals to increase diet breadth, to acquire preferences for foods that rectify states of malaise, and to exhibit state-dependent food selection.

they browsed blackbrush, a shrub low in nitrogen (0.67%) (Provenza 1977).

Digestibility and intake are positively correlated, and they are closely related to the energy requirements of ruminants (Baile and Forbes 1974, Anil and Forbes 1980, Anil et al. 1993). Animals do not prefer poorly digestible foods low in energy, whereas they generally select highly digestible foods that are a source of energy when offered alternatives. The postingestive basis for this is illustrated experimentally when lambs ingest flavored foods (e.g., onion- or oregano-flavored straw) or solutions (e.g., grape or orange) paired with (e.g., glucose or starch) or without (e.g., saccharin) a readily available source of energy. Following conditioning, lambs show a strong preference for the flavors paired with the energy source (Thorhallsdottir 1991, Burritt and Provenza 1992, Ralphs et al. 1995, Villalba and Provenza unpublished).

Deficits or imbalances of amino acids also cause decreases in intake and food aversions in liquid-fed (Rogers and Egan 1975) and solid-fed (Egan and Rogers 1978) lambs. Conversely, sheep increase intake of a protein-deficient diet following infusions of protein into the duodenum (Egan 1977). Rats acquire strong aversions to amino-acid-imbalanced diets, but if no alternative is available, they will eat an imbalanced diet for energy and adapt to ad libitum intake over 7 days (Gietzen 1993). Nonetheless, this does not reflect the extinction of an aversion to the food because rats strongly prefer a protein-free diet to an amino-acid-imbalanced diet (Rogers and Leung 1977). Several amino acids (e.g., sulfur containing amino acids, lysine, histidine, and possibly threonine, valine, and isoleucine) may be co-limiting in different foods ingested by ruminants (reviewed by Merchen and Titgemeyer 1992, Oldham 1993). When lambs are fed low-protein diets, compensatory effects (e.g., nitrogen recycling) increase abomasal nitrogen flow to a level similar to that of lambs fed diets containing up to 30% more protein; nevertheless, lambs fed low-protein diets have lower nitrogen retention, which may reflect changes in profile and absorption of amino acids (Sultan and Loerch 1992). The quantity and quality of protein that enters the small intestine of ruminants depends largely on the amino acid composition of microbial protein. Ruminally produced microbial protein may not meet the amino acid needs of the animal when microbial protein production is limited, when amino acid requirements are high, or when nitrogen comes primarily from non-protein nitrogen sources.

Intake also decreases when diets are deficient in minerals. For example, cattle, sheep, and goats eventually decrease their intake of phosphorus-deficient diets. The reduction in food intake depends on the severity of the deficiency (Ternouth 1991), and is exacerbated because animals no longer meet requirements for energy and protein. As mineral concentrations increase or as electrolyte balance (e.g., Na+K-Cl) improves, intake increases linearly but then declines as concentrations increase further or as balance changes (Ross et al. 1994). Sheep rectify mineral deficits (e.g., phosphorus, sulphur, selenium) by ingesting mineral supplements (White et al. 1992), and the pica exhibited by cattle foraging on heathlands is evidently a response to a phosphorus deficit (Wallis de Vries 1994). Although it is not known whether recovery from mineral deficiencies causes acquired preferences for foods, sheep apparently prefer food flavors associated with a mineral (i.e., phosphorus) which caused recovery from deficiency (Welch 1980).

Ruminants experiencing nutrient deficits sample new foods and increase intake of particular foods that can rectify deficits, including substances other well-fed animals avoid. For instance, cattle with mineral deficiencies eat rabbit flesh and bones, whereas non-deficient animals may sniff or lick the flesh, but never eat them, and they ignore the bones (Wallis de Vries 1992, 1994). Deer and other ungulates experiencing deficits eat antlers (Sutcliffe 1977). Angora goats foraging on nitrogen-deficient blackbrush pastures ingest woodrat houses high in nitrogen (Provenza 1977), and bighorn sheep use rodent middens as mineral licks (Coates et al. 1991). Ruminants experiencing deficiencies eat live and dead lemmings, rabbits, birds (caribou, red deer, sheep: Kelsall 1968, J.P. Bryant, personal communication, Furness 1988), ptarmigan eggs (caribou: D. Swanson, personal communication), arctic terns (sheep), and fish (white-tailed deer) (Bazely 1989). Cattle ingesting mineral-deficient forages lick urine patches of rabbits and man, chew wood, consume soil, eat fecal pellets of rabbits, and ingest non-food items such as plastic, feathers, bones, cinders, sacks, tins, and even dead rabbits (Green 1925, Wallis de Vries 1992, 1994).

The study by Gordon et al. (1954), in which sheep and cattle apparently did not rectify phosphorus deficits, does not provide strong evidence that ruminants can not rectify deficits. In the study, 90 cattle and 500 sheep grazed on 5,500 acres that contained 8 groups of troughs (3 troughs per group), 2 containing calcium carbonate and 1 containing equal parts of calcium carbonate and dicalcium phosphate. It was not known how many animals visited the troughs, the consumption of the compounds by individuals that frequented the troughs, and the phosphorus status of animals that did and did not frequent the troughs. Animals ingested little of either substance throughout the yearlong study (2.3 g/animal/day). Consumption may have reflected avoidance of unfamiliar substances by the animals (Distel and Provenza 1991, Provenza et al. 1994b), and the reluctance of sheep to ingest food offered in unfamiliar containers (Chapple et al. 1987).

Finally, ruminants need not maximize (optimize) intake of any particular nutrient or mix of nutrients within each meal or even on a daily basis, given that animals can withstand departures from the normal average intake of nutrients (i.e., energy-rich substances, nitrogen, various minerals, and vitamins) (Booth 1985). Rather, homeostatic regulation needs only some increasing tendency, as a result of a gradually worsening deficit of some nutrient or of an excess of toxins or nutrients, to generate behavior to correct the disorder (Figs. 1 and 2). Extreme states should cause herbivores to increase diet breadth and to acquire preferences for foods that rectify maladies. Nutrients required in the greatest amounts should have the most consistent and compelling influence on food selection. Energy is important because it is required in large amounts, but other nutritional needs may take precedence at times. For instance, young lambs and rats select diets that meet their protein requirements for growth (Kyriazakis and Oldham 1993), even when that means overingesting energy in the case of rats (Webster 1993). Nutrients like phosphorus, required in lower amounts, may often be ingested as a result of meeting other nutrient requirements. If not, animals search for foods to rectify the deficit (e.g., Wallis de Vries 1994).

Fermentation and Feedback

Feedback mechanisms let ruminants sense the consequences of food ingestion. Aversive feedback or a lack of positive feedback from the gut to the central nervous system (CNS) probably causes animals to reduce intake if foods are too high or low in energy or nitrogen; the effect would be opposite if these nutrients were adequate (Fig. 1). Responses are probably mediated by a lack or an abundance of by-products of microbial fermentation (e.g., propionate, acetate, ammonia, amino acids). The microbes in the reticulo-rumen play an essential role in the nutrition of the ruminant. Nutrient deficiencies and toxins can adversely affect microbes (Owens 1988, Bryant et al. 1991), thereby reducing the production of byproducts of microbial fermentation and growth required by the ruminant. The same thing is probably true for other essential nutrients, and how they affect food selection will depend on nutrient requirements and availability in the forage (Emmans 1991).

Food nutritional quality and intake rate (i.e., bite size and bite rate) affect the rate of nutrient release in the gut (i.e., postingestive feedback). The preference for foods that can be eaten quickly (Kenney and Black 1984) probably reflects high rates of positive postingestive feedback, which in turn means it is important to define the relationship between intake rate and feedback from nutrient ingestion (Illius and Gordon 1990, Gross et al. 1993). Chewing facilitates feedback because it promotes the rapid release of nutrients (Beauchemin 1992). The speed and duration of nutrient release during microbial fermentation depend on the physical and chemical characteristics of the food. Feedback should be greater and more rapid from foods that are high in nutrients and highly digestible (e.g., soluble carbohydrates, protein), which can help to explain the well-known relationship between digestibility and intake. Animals should prefer meals of foods that rapidly provide positive feedback followed by a steady release of nutrients, which would quickly cause and subsequently maintain satiety. Sheep show a strong diurnal preference for clover (high rate of digestion) early in the day, after an overnight fast, and grass (slow but steady release of nutrients) later in the day, even though clover and grass have similar gross energy contents and ultimate digestibilities (Parsons et al. 1994).

Food selection and intake are not necessarily restricted by digesta load in the intestines or rumen or by rate of passage. Physical factors in the intestines do not limit intake of roughages because the intestines have a large excess capacity to transport bulk (Grovum 1987). Moreover, ruminants immediately increase intake to meet increased demands for nutrients during lactation (Ketelaars and Tolkamp 1992), and dramatic increases in forage intake and rumen fill postpartum are not limited by rumen capacity or distension (Stanley et al. 1993). Likewise, digesta load changes in response to energy deficit when sheep are fed a single roughage (Gherardi and Black 1989), such that the digestible energy consumed remains constant on a high- (i.e., 50% alfalfa pellets 50% corn) or a low-energy (100% fescue hay) diet (Quigley and Heitmann 1991). Rumen capacity remains relatively constant during the year, but digesta load increases with food intake in red deer (Francoise Domingue et al. 1992). In addition to changes in digesta load, rumen volume can increase to accommodate different forages when the rumen is distended for long periods (e.g., with water or air balloons, Mowat 1963). For instance, rumen tissue mass and volume are significantly greater when goats are reared on a poorly nutritious shrub (blackbrush) than when they are reared on a nutritious diet (alfalfa and calf-manna) (Distel and Provenza 1991). Increases in intake with increasing digestibility are commonly attributed to reductions in rumen fill and increases in rate of passage (Van Soest 1982). But rumen fill increases until digestibility is about 70% and then declines, even though intake continues to increase (Ketelaars and Tolkamp 1992). Finally, crude protein concentrations below 6 to 8% decrease microbial fermentation rates thereby reducing intake, presumably by decreasing rate of passage. But ruminants quickly (< 1 hour) increase intake of nutritious foods when consuming poorly digestible foods low in nitrogen (Baumont et al. 1990, Distel and Provenza 1991). The range (2 to 35%) of crude protein concentrations over which intake can be stimulated far exceeds limitations on fermentation in the rumen (Ketelaars and Tolkamp 1992).

Finally, changes in the rumen during a meal (e.g., distension, production of VFAs, changes in pH, osmolality) are likely integrated in the central nervous system to cause eating to stop. Satiety within a meal is presumably mediated by tension receptors, and stimulation of tension receptors in the reticulum (Grovum 1979, 1987, 1988) and in the rumen (Mbanya et al. 1993) can decrease intake. Nevertheless, feedback from tension receptors differs from feedback of nutrients and toxins. Ruminants that responded only to tension receptors could easily ingest poorly nutritious and toxic forages. Instead, ruminants are extremely selective among plant species and plant parts as well, even when foraging in monocultures (e.g., see Parsons et al. 1994 and references therein). Accordingly, feedback from nutrients and toxins is likely to be more important than stimulation of tension receptors in food selection and intake. Intraruminal infusions of acetate and propionate depress hay intake in cattle (Anil et al. 1993) and in sheep (Ternouth 1967, Baile and McLaughlin 1970, Bergen 1972), and a combination of acetate, propionate, and distension of the rumen increases satiety (Mbanya et al. 1993). Sheep respond more to propionate than to acetate (Farningham and Whyte 1993). The mechanisms underlying the response are not known, but it does not appear to involve osmotic pressure changes or insulin. As discussed below, byproducts of fermentation like propionate and neuropeptides like cholecystokinin (CCK) interact to cause satiety and to affect food selection (Farningham et al. 1993). CCK also enhances constriction of the pyloric sphincter, thereby slowing the rate of gastric emptying and increasing gastric distention (Baile et al. 1986). Thus, satiety is probably due to mildly aversive feedback from chemo-, osmo, and mechano-receptors in the body to the central nervous system (Mbanya et al. 1993, Anil et al. 1993).

Feedback Mechanisms that Relate Nutrition to Behavior

Affective and Cognitive Processes

Neurally mediated interactions between the senses (i.e., taste and smell) and postingestive feedback cause changes in preference (affective value), and changes in preference cause changes in food selection (Garcia 1989). Taste (the gustatory system specifically, Garcia 1989) plays a prominent role in both processes. Affective processes integrate the taste of food and its postingestive consequences, aversive or positive, thereby causing changes in incentive to eat particular foods; they involve neurally (i.e., primarily brain stem and limbic system) mediated interactions between the sense of taste and the body and they are noncognitive. (Fig. 3). Cognitive processes involve use of the senses of smell, sight, and hearing to select foods that cause satiety and to avoid foods that cause malaise; they involve interac-

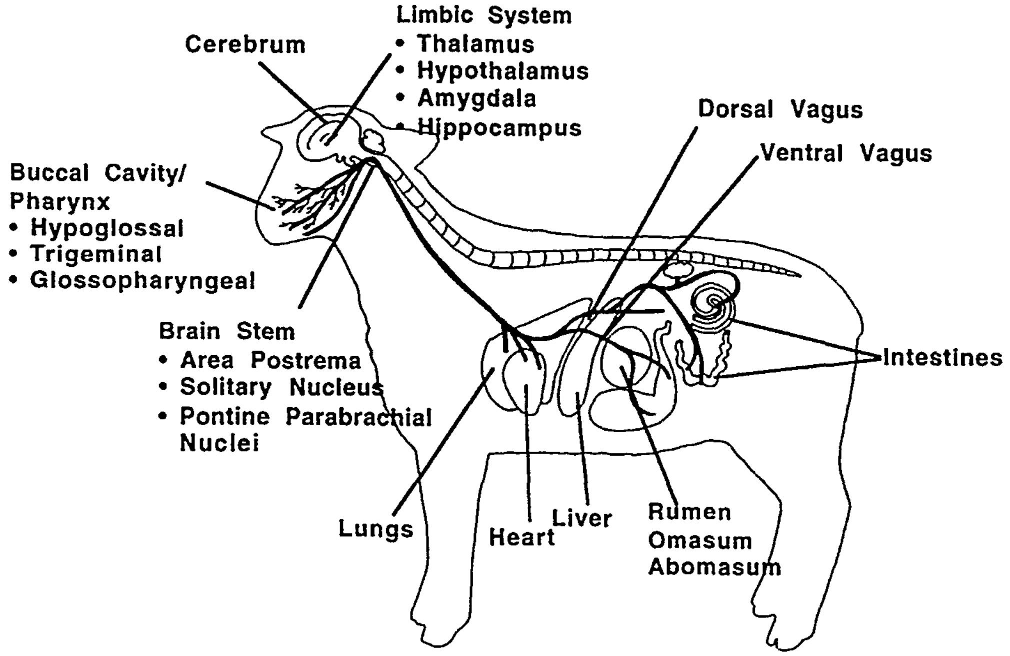

Fig. 3. The senses, visceral nerves, the brain stem, limbic system, and higher cortical centers interact through neuronal fibers that can facilitate or inhibit behavior. Gustatory and visceral afferent nerves that first synapse in the brain stem (involved with visceral, cardiac, and respiratory functions) proceed to the limbic system (concerned with emotional memory). Feedback from the gut to the brain stem and limbic system causes changes in preference for particular foods, which are non-cognitive and depend on the food's effect on the internal environment. On that basis, higher cortical centers (involved with declarative memory) interact with the limbic system to facilitate changes in food selection behavior.

tions between higher cortical centers, the limbic system and brain stem. Affective and cognitive processes are mediated by different brain systems, but they operate in parallel to regulate the internal environment. Thus, preference for food is adjusted according its effect on the internal environment, and on that basis animals select foods that are nutritious and avoid those that are toxic.

The Senses and Feedback

Taste, smell, and sight help animals identify and discriminate among foods, but these senses play somewhat different roles in food preferences and food selection. When animals are made ill following audiovisual and taste cues, they show much stronger aversions to the taste than to the audiovisual stimuli. In contrast, if they receive foot-shock following the same cues, they show much stronger aversions to the audiovisual than to the taste cues (Garcia and Koelling 1966, Lett 1985). This phenomenon is illustrated experimentally with hawks (Brett et al., 1976). Hawks fed white mice, and occasionally given a black mouse followed by an injection of LiCl, do not eat either black or white mice, presumably because both mice taste the same. But when a distinctive taste is added to the black mice, hawks learn to avoid black mice on sight after a single black mouse-toxicosis event. The taste cue potentiates the color cue. As Garcia (1989) suggests, "taste is the most powerful arbiter of what is fit to eat, smell comes next."

Differences in neuroanatomy help explain the different functions of the senses. For instance, neurons associated with taste receptors converge with neurons from the viscera in the most primitive part of the brain (i.e., the solitary nucleus of the brain stem); these gustatory and visceral neurons then relay to other parts of the brain stem, limbic system, and cortex (Fig. 3). Placement of the nose just above the mouth is beneficial in foraging, but olfaction has additional functions. For instance, olfactory receptors have direct and extensive connections with the part of the brain that affects emotion and motivation (i.e., the limbic system), and the part of the limbic system (i.e., the amygdala) which forms the basis for fear (Barinaga 1992, Davis 1992, LeDoux 1992, 1994). Thus, smell is involved in protecting animals from hazards like predation as well as noxious foods.

Taste and smell operate across different scales of time. Learning with long delays is characteristic of the taste-feedback system, which integrates information about food over a scale of minutes to hours; digestion and absorption are relatively slow processes (Garcia 1989). Thus, animals can acquire aversions even when feedback is delayed for many hours (Rozin 1976, Zahorik and Houpt 1981, Burritt and Provenza 1991). In contrast, a novel odor must be followed immediately by aversive postingestive feedback to produce strong aversion to the odor. In odor-taste-feedback conditioning, the odor-taste interval must be a matter of seconds or minutes. When odor is paired with taste, the conditioning of the odor is greatly enhanced. The ability of taste to enhance the conditioning associated with odor is called potentiation (Garcia 1989).

Cognitive and Non-cognitive Aspects of Food Selection

When nausea follows a meal, people often acquire aversions, and they generally rationalize why they no longer like particular foods (e.g., one of the foods made them sick in the past, they ate too much of a particular food, one of the foods was a novel, the food had a salient taste). In that sense, food aversions seem cognitive and rational. Nonetheless, affective processes involving taste and postingestive feedback do not involve cognitive associations. For instance, many of us remember acquiring an aversion to a particular food, even though we know the illness was not related to food (e.g., flu, reaction to a vaccine, seasick, chemotherapy). This knowledge does not alter the newly acquired aversion to food. Thus, interactions between the senses and postingestive feedback are not readily changed by cognitive ruminations.

Nonruminants and ruminants evidently do not differ in the non-cognitive aspects of how feedback is processed, for instance, in the origins and destinations of afferent neural signals, even though they differ in the sites and modes of nutrient absorption, kinds of digestive enzymes, and tissue metabolism (Church 1988). For instance, sheep that ate a familiar food, and were then anesthetized and given an intraruminal injection of LiCl, subsequently acquired an aversion to the food (Provenza et al. 1994a). Likewise, food aversions have been conditioned in nonruminants when they were anesthetized (Roll and Smith 1972, Bermudez-Rattoni et al. 1988), deeply tranquilized (Forthman Quick 1984), and when their electrocortical activity was depressed (Davis and Bures 1972, Buresova and Bures 1973).

These results bring into focus cognitive and non-cognitive (affective) aspects of learning and memory. Memory is generally thought of as the process by which earlier conscious experiences are recalled (LeDoux, 1992). The original learning and remembering are both conscious events. Such declarative (cognitive) memory is mediated by the hippocampus and the cortex. In contrast, emotional (non-cognitive) memory is mediated by the thalamus, amygdala, and cortex, and in all likelihood operates independently of conscious awareness. Nevertheless, emotional information may be stored within declarative memory and retrieved in parallel, "their activities joined seamlessly in conscious experience" (LeDoux, 1994). The mechanisms of emotional and declarative memories thus provide an explanation for the fact that animals in deep anesthesia acquire food aversions. More generally, acquired preferences and aversions are part of emotional memory; postingestive feedback and memory of the event occur whether or not animals are conscious. The emotional memory is stored within declarative memory of specific foods and the context in which they were eaten.

Variables That Control Taste-Feedback Associations

The particular food(s) that come to be associated with malaise (or satiety) in nonruminants and ruminants depend on several factors that probably interact. For instance, the volume of each food eaten in a meal affects acquired aversions in both groups of animals (Bond and DiGuisto 1975): Following administration of LiCl, goats reduced consumption of the food previously consumed in the largest amount (Provenza et al. 1994c). The novelty of the food item also affects these associations (Revusky and Bedarf 1967): When sheep that consumed 4 familiar foods and one novel food in a meal subsequently received LiCl, they avoided only the novel food (Burritt and Provenza 1991). The strength of aversion also depends on how soon toxicosis occurs after a food is ingested (Garcia et al. 1974, Cannon et al. 1985): Sheep acquire an aversion to the food eaten just prior to toxicosis (Provenza et al. 1993b). The concentration of a compound also affects aversions (Kalat and Rozin 1970, Cannon et al. 1985): Sweet (sodium saccharin) or bitter (aluminum sulfate) flavors, regardless of concentration, did not affect lambs' consumption of barley. But after a mild dose of LiCl, the lambs preferred the barley with the lowest concentration of either flavor (Launchbaugh et al. 1993). Goats had a similar response to blackbrush twigs (Provenza et al. 1994c). Finally, salient flavors affect the relationship (Kalat and Rozin 1970, 1971): For example, lambs with an aversion to cinnamon-flavored wheat also avoided cinnamon-flavored rice (Launchbaugh and Provenza 1993).

Preference and Feedback

Animals may express preferences for foods based on a change in liking for the flavor of the food or based on anticipated consequences from eating the food (Rozin and Zellner 1985). For instance, a human may avoid eating strawberries, because they cause hives, but still like their flavor. Conversely, the person is likely to acquire an aversion for the flavor of strawberries if their ingestion is followed by aversive postingestive feedback (i.e., nausea caused by a toxin). The same process occurs for acquired preferences. A person may ingest medicine, because of anticipated benefits (e.g., relief of a headache), but not like its flavor. On the other hand, the person is likely to acquire a liking for the flavor of the medicine if its ingestion is followed by positive postingestive feedback (e.g., satiety caused by calories).

Decreases in Preference

Lower- and upper-gastrointestinal distress evidently have different effects on preference. Lower intestinal discomfort (e.g., cramps, diarrhea, flatulence) may cause discerning animals to decrease intake of foods, but they evidently do not cause a decrease in liking for the food (Pelchat and Rozin 1982, Pelchat et al. 1983, Garcia et al. 1985, Garcia 1989). The same is true for respiratory distress, rashes, and allergies. Conversely, foods that cause upper-gastrointestinal distress (i.e., nausea from stimulation of the emetic system, Coil et al. 1978, Provenza et al. 1994d) cause negative hedonic shifts. Alternatively, upper gastrointestinal discomfort may simply cause more of a hedonic shift than lower gastrointestinal distress. The difference between hedonic shift and discomfort caused by distension may explain why livestock sometimes over-ingest nutritious foods that cause bloat (e.g., alfalfa). Positive feedback from nutrients may cause a strong liking for the food (i.e., a positive hedonic shift) that overrides any physical discomfort caused by stimulation of tension receptors in the reticulum and rumen.

Increases in Preference

Lambs acquire preferences for flavors paired with nutrients. For instance, when lambs consumed either grape- (group 1) or orange- (group 2) flavored glucose solutions on some days and orange- (group 1) or grape- (group 2) flavored saccharin solutions on alternate days, they subsequently preferred (96% to 4%) the flavor paired with glucose (Burritt and Provenza 1992). This acquired preference for a flavor reflected the nutritive properties of the solutions because lambs consumed the same amount of nutritive and non-nutritive solutions during conditioning and did not exhibit any preference when allowed to choose between unflavored solutions of glucose and saccharin in short-term tests (i.e., 5 min). Lambs exhibited similar preferences in experiments involving flavored straw paired with starch, propionate, or glucose (Thorhallsdottir 1991, Ralphs et al. 1995, Villalba and

Provenza, unpublished data).

The fact that lambs that are not deprived of nutrients exhibit a preference for certain flavors, even when the nutrient is no longer present suggests hedonic shifts are important (Villalba and Provenza, unpublished data). Rats also learn to like flavors paired with calories (i.e., they experience positive hedonic shifts), whether or not they initially like the flavor (Mehile 1991), and they acquire a strong preference (>95%) for bitter and sour tastes paired with nutritional consequences, even though these flavors were not preferred initially (Sclafani 1991c). These preferences persist for weeks in the absence of nutritional feedback, they occur whether or not rats are food deprived, and they are manifest in different environments, which suggests that rats acquire preferences for flavors on the basis of nutrient feedback.

Animals may also consume particular flavors because they anticipate the benefits, rather than because they prefer the flavors. For example, lambs evidently rectify acidosis by drinking a solution containing sodium bicarbonate (Phy and Provenza 1994 and unpublished data). But when lambs are given a choice between plain water and water with sodium bicarbonate, they prefer water. Thus, lambs drink the sodium bicarbonate solution (i.e., the medicine) because they anticipate its positive consequences (i.e., attenuate malaise caused by acidosis, Provenza et al. 1994d), not because they like the flavor. Likewise, rats prefer flavors associated with recovery from threonine deficiency (Gietzen et al. 1992), but only when they are deficient in threonine (Gietzen 1993).

Dependence on Internal State

Hedonic responses depend on the needs of the organism, positive if it ameliorates malaise and negative if it causes malaise. Sucrose or glucose tastes pleasant to fasted humans, but their tastes become unpleasant after they are consumed (Cabanac 1971). Non-ruminants can discriminate between foods, even when the differences in energy content are relatively small (Post 1993), and people given differently flavored medium- and low-carbohydrate snacks prefer the flavor paired with low-carbohydrate snacks when satiated but not when food deprived (Booth and Toase 1983). Flavor preferences conditioned using protein (Gibson and Booth 1986) or carbohydrates (Gibson and Booth 1989) also depend on the state of an animal.

State-dependent food selection generally has not been studied experimentally in ruminants, but their food selection changes within meals (Arnold and Dudzinski 1978), and there is no reason to believe they do not exhibit state-dependent foraging within and among meals (Jung and Koong 1985, Newman et al. 1994, Parsons et al. 1994). It is also likely that diet will vary with age, physiological condition, and environment (Fig. 2). For instance, the required protein:carbohydrate should decrease when animals cease growing, increase when animals are reproducing, and increase when energy requirements are high during winter.

Evolutionary Significance

Feedback is a process in which the factors that produce a result are themselves modified, corrected, and strengthened by that result. Accordingly, feedback adjusts hedonic value commensurate with the food's utility to the animal, and it enables animals to survive in an everchanging world. From an evolutionary standpoint, mechanisms that enable animals to experience feedback, sensations such as satiety and malaise, should be highly correlated with nutritional well being, toxicosis, and deficiencies. That is different from saying that food ingestion is reinforcing because food tastes good or bad, or because postingestive feedback from food ingestion is aversive or positive (Skinner 1976). These hedonic sensations merely accompany the conditions responsible for food selection, the nutritional and physiological well being of the animal. Accordingly, behavior and nutrition are directly related through feedback mechanisms.

Aspects of the Neural Basis for Food Selection

Neural Convergence

Visceral afferents probably interact with gustatory and olfactory afferents to facilitate or inhibit food ingestion (Fig. 3). Although there is little evidence to support or refute this hypothesis, because of a lack of research, there are anatomical and physiological mechanisms that might underlie such interactions (Novin 1983, Norgren 1983). The neural pathways of gustatory and visceral afferents have been fairly well established (e.g., gustatory and visceral afferents that first synapse in the nucleus of the solitary tract project through the pontine parabrachial nuclei (PBN) to the area postrema, to the thalamic gustatory relay (which in turn projects to the neocortex), and to ventral forebrain structures including the hypothalamus, amygdala, and red nucleus of the stria terminalis, Glenn and Erickson 1976, Spector et al. 1992). Lesions at various points along the pathway (e.g., vagotomy Louis-Sylvestre et al. 1983, Anil and Forbes 1980, 1988; abdominal vagus, solitary nucleus, midbrain, paraventricular nucleus, Crawley et al. 1984; ventromedial hypothalamic lesions, Cox and Smith 1986; PBN, Spector et al. 1992) make it impossible for animals to integrate taste and visceral signals to appropriately modify food selection and ingestion. This illustrates that gut-brain-gustatory interactions allow nutrients and toxins to be sensed. In the following section, I explain how the brain may actually sense excesses and deficits, and in turn provide feedback which causes an animal to alter food selection.

Acquired Aversions

Animals may acquire aversions to excesses of toxins and nutrients when the emetic system is stimulated (Coil et al. 1978, Provenza et al. 1994d). The emetic system is very sensitive to low doses of most toxins (Davis et al. 1986), and involves complex interactions between several areas in the brain stem including the area postrema and the chemoreceptor trigger zone (Seynaeve et al. 1991, Mitchelson 1992; Fig. 3). The area postrema is a circumventricular organ lying outside the blood-brain barrier, and the chemoreceptor trigger zone is a chemosensitive region in the area postrema. These regions of the emetic system can be stimulated directly by toxins in the cardiovascular system and cerebrospinal fluid (Borison and Wang 1953), and through visceral afferents (i.e., neurons that carry sensory information to the brain), primarily vagal afferents, and to a lesser extent, splanchnic afferents (Borison, 1986; Davis et al., 1986; Grahame-Smith, 1986; Kosten and Contreras, 1989). Efferent impulses (i.e., neurons that provide motor input to innervated structures) from the emetic system to effector organs travel through the hypoglossal, glossopharyngeal, and trigeminal nerves (innervating the buccal cavity and pharynx), through the vagal nerve (innervating the pharynx, respiratory and gastrointestinal tracts), from the respiratory center to the phrenic and intercostal nerves, and through some sympathetic efferents in the gastrointestinal tract (Seynaeve et al., 1991). These pathways to and from the emetic system clearly show how ingestion of an excess of a toxin or nutrients can cause upper gastrointestinal malaise, thereby causing the animal to decrease (intake), and how impulses from the emetic system to the gastrointestinal tract can cause a decrease in gut motility and rate of absorption of toxins (Stricker and Verbalis 1990, Bernstein et al. 1992) or nutrients (Baile et al. 1986).

Little research has concerned the role of the emetic system in food selection and intake of ruminants. In one study, antiemetic drugs (diphenhydramine, metoclopramide, dexamethasone) attenuated LiCl-induced aversions in sheep (Provenza et al. 1994d). Moreover, mild aversive feedback apparently caused sheep to limit their intake of grain. In another study, ergopeptide alkaloids (primarily ergovaline), produced by the endophytic fungus *Acremonium coenophialum*, reduced the intake of tall fescue by sheep (Aldrich et al. 1993). Daily dosages of an antiemetic drug (metoclopramide, which acts on serotonin ($5HT_3$) receptors) significantly increased intake of endophyte-infected tall fescue, but not intake of endophyte-free fescue. The ability of antiemetic drugs to increase intake of foods that cause aversive feedback is consistent with the hypothesis that antiemetic drugs cause intake to increase primarily by attenuating food aversions, not by increasing the rate of passage of food from the gut (Mitchelson 1992).

Lambs acquire aversions to foods that they eat when they experience imbalances in many essential amino acids (Rogers and Egan 1975, Egan and Rogers 1978). The neural mechanisms that enable ruminants to recognize an amino acid imbalance have not been identified. Neural mechanisms let rats recognize an imbalance as soon as 28 min. after ingesting a deficient diet (Gietzen et al. 1986), and similar mechanisms probably operate in ruminants. Rats avoid foods that are imbalanced in amino acid content when there is a decrease in the concentration of the limiting amino acid in the prepyriform cortex, as well as decreases in norepinephrine and cyclic AMP, and altered protein synthesis (Gietzen and Beverly 1992, Gietzen 1993). Rats then acquire an aversion to the diet, which is mediated by undetermined structures in the central nervous system and the neurotransmitter serotonin ($5HT_3$) (Hammer et al. 1990, Gietzen et al. 1991b). Blocking of $5HT_3$ receptors (by ICS 205-930) attenuated the aversive response of rats to an amino acid imbalanced-food (Gietzen 1993), and to LiCl (Gietzen et al. 1991a). Blocking $5HT_3$ receptors also attenuates chemotherapy-induced vomiting in humans (Costall et al. 1988).

Acquired Preferences

Much of the research concerning conditioned food preferences has involved rats. Rats eat more foods or non-nutritive flavors (foods) paired with calories (Messier and White 1984, Booth 1985, Mehiel and Bolles 1984, 1988, Simbayi et al. 1986, Mehile 1991, Sclafani 1991a,b), during recovery from nutritional deficiencies (Garcia et al. 1967, Zahorik et al. 1974), and during recovery from postingestive distress (Green and Garcia 1971, Sherman et al. 1983). Many mechanisms are likely to be involved in acquired preferences, as is the case with acquired food aversions (Grahame-Smith 1986) and with the control of food intake (deJong 1985). Accordingly, a single nutrient, compound, hormone, or organ is not apt to have a dominant role in the acquisition of food preferences, considering the variety of nutrients needed by animals. Nonetheless, all are likely to operate on a continuum, as outlined below for calories.

Acquired preferences caused by calories may be mediated by neuropeptides like CCK. Rats acquire preferences for flavors of noncaloric solutions when their ingestion is followed by intraperitoneal injections of CCK. Likewise, when exogenously administered CCK is given along with a calorie-paired flavor, CCK further increases rats' preference for the flavor (Mehile 1991). Conversely, high doses of CCK can condition food aversions (Deutsch and Gonzalez 1978, Stricker and Verbalis 1990, Perez and Sclafani 1991). These seemingly contradictory findings suggest there is a fine line between satiety (satisfied to the full) and surfeit (filled to nauseating or disgusting excess), which is to be expected if preferences and aversions to energy and nutrients are points along a continuum.

Behavioral observations also suggest a fine distinction between satiety and malaise, and that malaise operates in subtle ways to control food selection. For instance, when a person eats a food to satiety, the pleasantness of the flavor of the food is reduced more than other foods that were not eaten, which enhances intake of different foods offered later (Rolls et al. 1981, 1984). The more subsequent foods differ in taste, smell, appearance, texture, and nutrient content, the more intake of these foods is likely to increase (Rolls et al. 1984). Thus, a person can apparently acquire mild aversions to the flavors of particular foods, which eventually extends to all foods eaten during a meal. Such an aversion may last well beyond the end of the meal. When sheep on a pelleted diet are infused with propionate, their consumption of pellets over a 24 hour- period decreases as the dose of propionate increases (Farningham and Whyte 1993). Furthermore, sheep given low or moderate doses of propionate during a meal, acquire a strong preference for the food (Villalba and Provenza unpublished data), whereas sheep given a high dose of propionate during a meal, acquire a persistent aversion to the food (Ralphs et al. 1994). All of these observations are consistent with the hypothesis that preference and aversion are points along a broad and sensitive continuum.

Acquired preferences and aversions may involve many of the same mechanisms, which respond in a dosage-dependent fashion to nutrients and toxins alike. These may involve several brain regions (e.g., solitary nucleus, PBN, area postrema, and hypothalamus) and neurotransmitters. For instance, the area postrema, which is thought to be involved in acquired preferences and aversions, has receptors or binding sites for neurotransmitters (i.e., histamine, dopamine, serotonin ($5HT_3$), norepinephrine, CCK, enkephalins, and acetylcholine) that play roles in satiety (Baile 1974) and malaise (Seynaeve et al. 1991, Mitchelson 1992). Also, peptides involved in satiety and malaise mediate interactions between snakes and toxic frogs: Peptides in the frog's mucous produce satiety at low doses and toxicosis at higher doses in snakes. As Garcia (1989) suggests, "That may be the way chemical protection gradually evolves; those organisms which can quickly induce satiety in foragers stand a better chance of having their kind survive. Perhaps it is no accident that many phytochemicals such as caffeine, nicotine and digitalis cause a loss of appetite in vertebrates including humans, thus providing an excellent protection against continued munching by foragers."

In ruminants, visceral afferents probably interact with gustatory and olfactory afferents, and these effects are likely modulated through byproducts of microbial fermentation and by neurotransmitters within the CNS. For instance, the VFA propionate is a major source of energy in ruminants, and its role may be similar to that of hepatic glucose in the control of food intake in nonruminants. Portal flow of propionate can control food intake in ruminants (Farningham and Whyte 1993). Food intake during spontaneous meals was decreased by about 40% in goats and sheep by injections of propionate into the ruminal vein, but not decreased by infusions into the jugular vein (Baile 1971). Intraportal administration of propionate depresses food intake in sheep only if the vagal or splanchnic nerve supply from the liver to the central nervous system is intact (Anil and Forbes 1988). Afferent nerve signals from the liver to the central nervous system may cause the release of peptides like CCK, which cause satiety in a dose-dependent fashion when administered within the central nervous system in sheep (Della-Fera and Baile 1979, 1981, Grovum 1981). Low doses of propionate or CCK do not affect food intake in sheep, but they interact and decrease intake by 44% over a 2- hour period (Farningham et al. 1993). These data suggest that byproducts of fermentation like propionate and neuropeptides like CCK interact to cause satiety and affect food selection.

There are 2 types of receptors for CCK in the area postrema, one for CCK in cerebrospinal fluid and one for axonally transported CCK (Moran et al. 1986). CCK receptors on vagal axons innervating the liver proceed rostrally to the area postrema, a circumventricular organ that receives input from both blood and synaptic transmission (Sankaran et al. 1979, Zarbin et al. 1981). The CCK pathway runs from the area postrema through the midbrain to at least three nuclei of the hypothalamus: the paraventricular nucleus, the ventromedial nucleus, and the dorsomedial nucleus (nuclei in the amygdala are also involved). Within the hypothalamus, CCK may modulate endorphins and norepinephrine (Baile et al. 1986), thereby affecting preferences for flavors paired with calories.

Varied Diets

Some believe animals ingest an assortment of foods to increase the likelihood of ingesting the necessary nutrients (Westoby 1978), whereas others believe they do so to reduce the potential of overingesting toxins (Freeland and Janzen 1974). Both factors are important. Plants contain a bewildering array of secondary metabolites, many (perhaps most) of them toxic (Cheeke and Shull 1985, Bryant et al. 1991). Secondary metabolites cause ruminants to limit intake of even the most nourishing foods, which in turn causes ruminants to ingest a diverse array of plants to minimize toxicosis. Energy and primary nutrients such as nitrogen and phosphorus often co-vary in their availability and they are often concentrated in young plant parts. Nonetheless, it may be difficult for animals to meet requirements when energy and nutrients are not equally distributed among resources. This can occur when habitats vary in soil fertility (Wallis de Vries 1994), or with an imbalance in nutrient contents, such as an excess of protein in young growth (Prins and Beekman 1989). Thus, varied diets also reflect availability of nutrients in plants and nutritional requirements of animals.

Mild aversions caused by excesses of nutrients and toxins and by nutrient deficits cause animals to eat different foods. Moreover, eating to the point of satiety is likely to be mildly to strongly aversive. Accordingly, malaise is probably an important reason why ruminants eat varied diets (Provenza 1994b). Several factors likely act synergistically to cause animals to acquire mild aversions to foods within and among meals. Aversions are acquired on the basis of interactions between sensory receptors (taste and odor of particular foods) and postingestive feedback (e.g., amount and frequency of malaise) which depends on the nutritional and toxicological characteristics of the diet. The more foods differ in taste, smell, appearance, texture, and nutrient content, the more each food is likely to contribute to the diet. The more closely a food matches the nutritional requirements of the animal, the more likely the food will be a staple in the diet. Nevertheless, ingestion of any food to satiety is likely to cause animals to temporarily decrease their preference for the food. For instance, sheep show a strong preference for clover early in the day and for grass later in the day (Parsons et al. 1994), which may reflect mild aversions to both clover and grass (Provenza 1994b). The time required for the onset of an aversion, the degree to which the aversion is manifest, and the duration over which a particular food is avoided will depend on the flavor of the food and the amount and frequency of malaise. Accordingly, aversions produced by satiety are likely a result of interactions between the senses and postingestive feedback, and not simply a result of sensory-specific satiety.

Sensory-specific satiety is the decrease in preference for a food as it is eaten within a meal and over longer periods (Rolls 1986). Such decreases in preference occur in ruminants (e.g., Baumont et al. 1990, Ramos and Tennessen 1993, Newman et al. 1992, 1994, Parsons et al. 1994) and nonruminants (Rolls 1986). The phenomenon has been attributed to sensory properties of foods, rather than to postingestive feedback, because the preference for ingested food tends to decrease soon after a meal (i.e., 2 to 20 min) and then gradually increases during the next hour (Rolls et al. 1981, 1984). Satiety occurs whether flavors are nutritive or non-nutritive (Wooley et al. 1972) and in foods of varying nutritional value (Birch and Deysher 1986). Other evidence that suggests the response is mediated by taste and smell is the fact that pleasantness of the sweetest sodas, containing the most calories and potentially the most satiating, declines even when they are tasted and not swallowed (Drewnowski et al. 1982).

Nonetheless, these changes in preference as a result of consumption do not rule out interactions between the senses (taste and smell) and postingestive feedback. Postingestive effects (e.g., release of saliva and digestive enzymes, release of most gastrointestinal and pancreatic hormones, release of neurotransmitters involved in satiety) occur upon initiation of a meal and can begin upon experiencing the flavor of a familiar food (i.e., they are Pavlovian processes). For instance, after a flavor is paired with a caloric solution, the flavor alone elicits the release of CCK, a peptide that moderates hedonics within a meal (Fedorchak and Bolles 1988, Mehile 1991). In addition, feedback from nutrients and toxins can begin rapidly following initiation of a meal, as discussed previously. Finally, when an animal only tastes a food or ingests a food of low nutrient density, the lack of a positive postingestive effect may be aversive. For example, the cephalic-phase responses to sweet substances can, if followed by ingestion of noncaloric solutions, reduce preference for the taste (Tordoff and Friedman 1989). Thus, it is more reasonable to assume that the senses and postingestive feedback interact during foraging to constantly modulate the hedonics of food ingestion, within a meal and from meal to meal. Eating a variety of foods has several benefits, such as obtaining a more balanced diet, reducing consumption of toxic foods, sampling of foods, and maintaining a diverse microflora in the rumen. But malaise, rather than benefits, is the cause of varied diets.

Opportunities for Research

Ruminants discriminate among foods with their senses and sense the consequences of food selection through feedback mechanisms, both of which are integrated within the central nervous system. Several facets of this interaction merit further study. Studies of ruminants have focused on the effects of VFAs like propionate and peptides like CCK on suppression of feeding. These compounds probably mediate acquired preferences and aversions, and should be studied to determine how they affect the acquisition of preferences and aversions in ruminants. Administration of high concentrations of propionate to sheep not only caused satiety, but they also conditioned strong food aversions (Ralphs et al. 1995).

Calories cause positive hedonic shifts and toxins cause negative shifts, but it is not clear if the same is true for foods or flavors paired with other nutrients (e.g., nitrogen, phosphorus), with recovery from nutrient deficits, or with recovery from excesses of nutrients or toxins. It would also be interesting to know if ruminants sense the effects of toxins in the same way, and by the same mechanisms, as they sense states like acidosis (Ortega-Reyes et al. 1992), amino acid imbalances (Egan and Rogers 1978), and deficits of phosphorus (Ternouth 1991). Do ruminants sense all diet-related maladies in the same manner and by the same physiological mechanisms (Grant 1987, Galef 1991), or do they differ in how they sense satiety caused by carbohydrates (Miner 1992), amino acids (Egan and Rogers 1978), and other nutrients? If ruminants can distinguish among maladies (satieties), can they also learn to ingest substances that rectify different internal states? If so, this information would be valuable in preventing toxicosis and in rectifying nutritional deficits.

Positive and negative hedonic shifts occur as a result of experiences early in life, but it is not clear how experiences early in life cause hedonic shifts. Ruminants acquire strong preferences for foods consumed early in life, and prefer those foods as adults, whereas they are reluctant to eat foods they have not experienced (e.g., Distel and Provenza 1991, Ramos and Tennessen 1992, Walker et al. 1992, Biquand and Biquand-Guyot 1992). Mother and peers influence the dietary habits of young ruminants (Provenza 1994a, Provenza and Balph 1987, 1988, Provenza 1994a,c), and experiences with mother appear to be especially influential (e.g., Thorhallsdottir et al. 1990, Mirza and Provenza 1990, 1992, 1994, Nolte et al. 1990). It is not known if hedonic shifts simply reflect flavor-feedback conditioning over a long period, or if there are additive effects resulting from interactions between age of exposure, mother, and postingestive feedback.

Finally, it is important to determine how ruminants acquire dietary habits and the basis for varied diets within and among meals. Goats first introduced to blackbrush-dominated rangelands sample all foods in the area during the first few hours, including potentially toxic plants like *Juniperus osteosperma* (bark and green leaves), *Gutierrezia microcephala* (a forb), and *Marrubium vulgare* (a forb), as well as non-toxic shrubs like *Prunus fasciculata* and *Purshia tridentata*. They also sample both CSG and OG from blackbrush. Goats evidently eat small amounts of each food, and during the next few days they limit intake of the potentially toxic foods and ingest meals composed primarily of blackbrush OG and *Prunus fasciculata*. It is important to understand how ruminants acquire aversions and preferences in such a complex environment.

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Vegetation and soil responses to grazing simulation on riparian meadows

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Abstract

Riparian areas have not responded consistently to grazing systems, suggesting that more knowledge is needed to explain how different areas respond to specific stresses. Several studies were conducted to determine herbaceous plant response to simulated grazing on riparian areas. One low-elevation redtop (*Agrostis stolonifera* L.) site in Oregon and 2 high-elevation sedge (*Carex* spp. L.) sites in Idaho were studied for 3 years. Several combinations of defoliation, compaction, nutrient return, and season of use were examined. The redtop community responded to spring, fall, or spring-fall defoliations by maintaining or increasing the following year's aboveground biomass production. The sedge communities maintained or decreased the following years's biomass production after spring, mid summer, or late summer defoliations. An increase in forbs occurred in 1 sedge community following spring defoliations to 1- or 5-cm residual stubble heights. The most consistent plant response among areas was reduction in height growth and biomass production following compaction treatments. When both defoliation and compaction are considered, it appears that spring, fall, or spring and fall grazing to a 5-cm stubble height on the redtop site would not decrease riparian herbage production. In contrast, when defoliation, compaction, and nutrient return effects are considered in the mountain meadow sedge-dominated communities, grazing once annually during the growing season to a 5-cm stubble height in the spring, or to a 10-cm stubble height in late summer, or at a utilization rate exceeding 30% of the total annual biomass production can reduce herbage production significantly. Results suggest that many of the land management agency riparian guidelines would maintain biomass productivity in these sedge-dominated communities.

Key Words: *Agrostis stolonifera*, *Carex* spp., *Alopecurus pratensis*, defoliation, compaction, nutrient return

Riparian areas have reacted erratically to the application of many traditional upland grazing systems (Skovlin 1984, Platts 1991). The lack of consistent results is largely a reflection of the differences in plant species, environmental conditions, and livestock concentrations found in riparian areas. Improved information is needed concerning the response of riparian forage plants to grazing animals if riparian grazing systems are to experience consistent success (Platts and Raleigh 1984).

Grazing animals primarily affect foraging areas by defoliating plants, trampling soil and plants, and excreting wastes that may nourish plants (Heitschmidt 1990, Matches 1992). Reviews by Heitschmidt (1990) and Matches (1992) have pointed out that in mesic grazing lands, plant communities may produce more herbage as a result of some degree of defoliation, while plant communities in arid situations may produce less herbage as a result of almost any amount of defoliation. A major effect of soil compaction by hoof action is reduced macropore space, that reduces infiltration, percolation, root growth, and overall plant production (Lull 1959, Bryant et al. 1972). The response of plant growth to nutrient return via excreta of grazing animals may be less than is often assumed. Nearly all of the N in urine and feces can be lost to volatilization or leaching (Watson and Lapins 1969, Floate 1970, Woodmansee 1978). The amount recovered in plant tissue may be only 22% (Ball et al. 1979). Perhaps the most complete study of combined defoliation, trampling, and excreta effects was conducted on a perennial ryegrass-white clover (*Lolium perenne* L.-*Trifolium repens* L.) pasture grazed by sheep (Curll and Wilkins 1983). Overall, as stocking rates increased, herbage growth was decreased, since the benefits of increased N transfer were outweighed by the negative effects of trampling and increased intensity of defoliation (Curll and Wilkins 1982, 1983).

Studies of simulated livestock grazing have advantages over studies using livestock; they cost less and require less space, and they provide the opportunity to examine the various individual effects of grazing. There has been some question whether defoliation by clipping duplicates the effects of grazing in upland situations where grazing may be patchy (Stroud et al. 1985, Wallace 1990); however, there should be less concern in meadow situations where cattle tend to graze to a relatively uniform stubble height (Bartolome 1984). The simulation of trampling combined with defoliation should result in a plant response closely paralleling the response to livestock grazing (Bryant et al. 1972), particularly when nutrient return is added. This paper reports 3 different, but related, simulation studies. The objective of these studies was to simulate and evaluate livestock grazing on herbaceous riparian

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meadows including the effects of defoliation, compaction, nutrient return, and season of treatment.

Study Areas

Heavy to very heavy grazing use had occurred for many years previous to fencing of the study areas. Each area had several years of recovery before the treatment sequences were initiated.

Willow Creek Area

This area is located about 16 km north-northwest of Brogan, Ore., along Willow Creek in section 19, T14N, R42E. Elevation of the study area is 927 m. The flow of Willow Creek is controlled by Malheur Reservoir about 6 km upstream; therefore, the area rarely experiences flooding in the spring. The valley is V-shaped with a narrow riparian area. Most of the study quadrats were within 3 m of the streambank. At the time the area was fenced in 1987, the closely grazed vegetation appeared to be predominantly Kentucky bluegrass (*Poa pratensis* L.). Redtop (*Agrostis stolonifera* L.) became the predominant species within 2 years after fencing. The vegetation on the surrounding uplands is typical of the sagebrush (*Artemesia* spp. L.) ecosystem (Garrison et al. 1977).

Soils are formed in mixed alluvial sediments derived from basalt and volcanic ash on benches and terraces. The surface 15 cm of soil is a sandy loam to loamy sand with 10% cobble and gravel. At 15 to 28 cm a cobbly sandy loam to very gravelly loam horizon occurs with 22 to 52% cobble and gravel. Below 51 cm is very gravelly coarse sand overlaying streambed cobble and gravel (Jack R. Wenderoth, Vale District, BLM, Vale, Ore., personal communication 1992).

Annual precipitation at the nearby community of Brogan was 30.4 cm, 18.0 cm, and 18.2 cm for water years 1989, 1990, and 1991, respectively. Mean annual precipitation at Brogan for the period 1987-1993 was 23.4 cm. The nearest reporting weather station, Vale, approximately 48 km south and about 120 m lower in elevation than Brogan, has a long-term average annual precipitation of 24.5 cm. Growing season at Vale averages 139 days, frost to frost.

Valley Creek Area

This area is located about 6 km northwest of Stanley, Ida., along Valley Creek near the border of sections 24, T11N, R12E and 19, T11N, R13E. The elevation is 1,950 m. The area was fenced in 1986 and is representative of the mountain meadows ecosystem containing wet to intermittently wet sites in the forest zone of the mountain West (Garrison et al. 1977). This reach of Valley Creek flows through an open valley. Typical plants at the study site were water sedge (*Carex aquatilis* Wahl.), slenderbeak sedge (*C. athrostachya* Olney), smallwing sedge (*C. microptera* Mack.), meadow foxtail (*Alopecurus pratensis* L.), and thickstem aster (*Aster integrifolius* Nutt.).

Soils are formed in alluvial sediments derived primarily from granite. The upper 11 cm has a loam texture with very high organic matter. From 11 to 27 cm is a silty loam, and from 27 to 58 cm is a very gravelly loamy sand with 45% gravel. Below 58 cm are stones and small boulders in free water (David R. Gilman, Sawtooth National Forest, Twin Falls, Ida., personal communication 1992).

Annual precipitation at the nearby community of Stanley was 31.4, 39.3, 32.6, and 28.7 cm for water years 1989 through 1992, respectively. The long-term average annual precipitation is 42.7 cm. Growing season at Stanley averages 12 days, frost to frost.

Stanley Creek Area

This area is located about 6 km northwest of Stanley along Stanley Creek in portions of section 29, T11N, R13E. The elevation is 1,950 m. The area was fenced in 1987. At the site of the experimental area, Stanley Creek flows through a broad, flat valley characterized by mountain meadows. Typical plants at the study area included water sedge, slenderbeak sedge, shortbeak sedge (*Carex simulata* Mack.), and Wolfs willow (*Salix wolfii* Bebb).

Soils are formed in alluvium and lacustrine sediments derived from granite. They have moderately rapid permeability. The upper 38 cm is typically a gravelly loam with 25% cobbles. Immediately below is a gravelly sandy clay loam with 30% cobbles (David R. Gilman, Sawtooth National Forest, Twin Falls, Ida., personal communication 1991).

Annual precipitation and temperature regimes are similar to nearby Valley Creek.

Methods

Willow Creek Area

Forty-eight 1-m^2 quadrats were established along Willow Creek in a completely randomized block design in the fall of 1988. The objective at Willow Creek was to study the effects of defoliation height (DH), soil compaction (C), and season of treatment (S) on herbaceous riparian vegetation height growth and biomass production, and on soil strength and compression. Seasons of defoliation and compaction treatments were spring (May), fall (September), and spring and fall. Phenological stages for the predominant species, redtop, were "vegetative" in May and "seed mature" in September. Treatments were applied from the fall of 1988 through the spring of 1991. All combinations of defoliation, compaction, and season were represented in the study. Each treatment combination had 2 replications. Plots assigned to either spring or fall treatments were defoliated and/or compacted once each year; those assigned to spring-fall treatments were subjected to defoliation and/or compaction twice each year. The mechanical defoliation treatments consisted of no defoliation (i.e., control), and defoliation to 10-cm, 5-cm, and 1-cm stubble heights. The compaction treatments consisted of compaction and no compaction. The soil was compacted by dropping a 14 kg steel impactor from a height of about 75 cm. The impact surface area was 100 cm^2. This procedure appeared to duplicate the impression depth of the hoof print of a mature cow. Each compacted quadrat was completely covered by impacts since typical stocking rates of 2+ aum/ha should result in an average trampling of 1 "m^2/m^2" (Scholl 1989). Observations of typical heavily grazed riparian areas show the entire area covered with hoof impacts. An area is normally covered several times over with hoof impacts in very heavily grazed areas. On upland sites it has been shown that cattle tend to step between grass plants with a tussock growth form (Balph and Malechek 1985). Results of Balph et al. (1989) show that as bunchgrass tussocks become shorter, cattle are more likely to step on them. On heavily grazed riparian areas with their characteristic sod-forming vegetation composition, the plants appear to be subjected to direct trampling that would not only compact the soil, but may also subject plant crowns to compression injury.

Standing crop of current green biomass was estimated by a disk meter (Karl and Nicholson 1987) in the fall of 1989 and 1990. The meter readings were calibrated to local vegetation conditions annually by selecting temporary plots with a range of biomass and determining the relationship between vegetation dry weight and disk meter reading. Twelve to 15 samples were utilized to calibrate the disk meter for each situation annually. A complete harvest of all dry matter, both current growth and litter, from the center 1/4 of the plots was conducted in the fall of 1991. All biomass measurements, therefore, occurred 12 months after fall treatments and 4 months after spring treatments. Average graminoid and forb heights were measured at the time of final harvest.

Soil strength was determined with a pocket penetrometer in the fall of 1989 and 1991. This method has been correlated with unconfined compressive strength of soil, and it is useful in comparing relative strengths and zones of compaction among similar soil types (Bradford 1986). Soil strength was measured in 2 opposing corners of the quadrats and averaged. The corners were selected to best represent mineral soil, that is, soil surface not covered by heavy litter or duff, or rock. Measurements of soil surface elevation was made from a reference device placed over 2 heavy stakes located on opposing corners of each quadrat. Three measurements from the reference bar over the 0.25-m^2 harvest area were taken before and after each treatment episode.

Valley and Stanley Creek Areas

Two sets of 32, 1-m^2 quadrats were established along Valley Creek in completely randomized block designs during the fall of 1989. The study continued through 1992. The objective was to investigate the effects of defoliation, soil compaction, nutrient return (NR), and season of treatment on herbaceous riparian vegetation. The treatments of defoliation and soil compaction were similar to those described for Willow Creek. Manure and urea solution were added to designated plots to approximate the nutrient return by grazing animals. Fifty-five g of dry current year's manure and 1 g of urea in 1 L of water were applied to the designated quadrats. The amounts applied were based on local production and consumption estimates, and on generalized values from Tiedemann et al. (1986).

All treatments were applied to 1 set of quadrats in spring (June) and to the other set in late summer (late August-early September). The phenological stages of the predominant sedges were "partially headed" in June and "seed mature" in late August-early September. Each plot received one treatment or treatment combination annually. Measures of treatment response were similar to those for Willow Creek apart from: 1) biomass production was expressed as seasonal standing crop except that final harvest in 1992 allowed percentage removed in 1992 to be calculated on total annual biomass production, and 2) measurements of soil surface level were not taken. All combinations of defoliation, compaction, and nutrient return were represented within seasons. Each treatment combination had 2 replications per season.

Twelve 0.25-m^2 quadrats were established along Stanley Creek in a completely randomized block design in the summer of 1989. The objective was to study the effects of defoliation during the first week of August on herbaceous riparian vegetation. Phenological stage of predominant sedges was "seed mature." The treatments were no defoliation, and defoliation to 10-cm, 5-cm, and 1-cm stubble heights. Each plot was subjected to a single defoliation annually. Each treatment had 3 replications. Average plant height was measured annually at the time of treatment. The dry weight of vegetation removed by each defoliation was determined. Complete harvest of the center 1/4 of each plot was completed in October 1991 to determine the defoliation effects on biomass production.

A summary of the treatment and measurement schedule for the 3 study areas is found in Table 1.

Analysis

Statistical analysis was by analysis of variance utilizing a General Linear Model. Significant differences among 3 or more means were identified by the use of a protected Fisher's LSD. All differences reported were signicant at $P < 0.10$.

Table 1. Annual treatment and measurement schedule for 3 years of study.

		Dates of activity	
	Annual treatment	Annual measurement	Final measurement
Willow Creek	Spring	Fall	Fall
	Fall	Fall	Fall
	Spring-Fall	Fall	Fall
Valley Creek	Spring	Spring	Late summer
	Late summer	Late summer	Late summer
Stanley Creek	Mid summer	Mid summer	Fall

Results

Willow Creek Area

Height Response

Compaction (C) reduced graminoid height growth by an average of 10.3% (Table 2), however, an interaction between compaction and season ($P = 0.004$) suggested graminoid height growth was reduced more from spring or spring and fall compaction than by fall compaction. The average reduction in graminoid height growth following spring or spring and fall treatments only was 19.8% (39.4 vs. 48.8 cm). No main effect of defoliation height (DH) or season (S) was apparent. Forb heights for defoliation treatments averaged only 51.4% of the control treatment heights (Table 2).

Biomass Response

Annual biomass production was related to DH, C, and year (Y) ($P = 0.048$, 0.003, <0.001, respectively). The 5-cm defoliation treatment produced more annual biomass than the control or the 1-cm defoliation treatment; the 10-cm defoliation treatment produced more biomass than the control (Fig. 1). None of the defoliation treatments decreased production, even though foliage removal was up to 90% of the total annual growth (Fig. 1, Table 2). Compaction reduced production by an average of 13.8% (122.2 vs. 141.7 g/0.25 m^2), but a strong interaction with season occurred ($P = 0.009$) wherein the primary compaction effect occurred in the spring. Spring and spring-fall compaction treatments reduced annual biomass production an average of 22.2% (114.7 vs. 147.4 g/0.25 m^2). Average annual production of all treatments declined through the study period (175.3 down to 98.9 g/0.25 m^2) as drought conditions became more severe and streamflow releases from the upstream reservoir decreased. Total standing crop biomass (including litter) at final harvest was significantly related only to DH ($P = 0.076$). The primary cause of the differences in total biomass was the variation in dead biomass (previous years' foliage and litter) ($P < 0.001$). The 1-cm and 5-

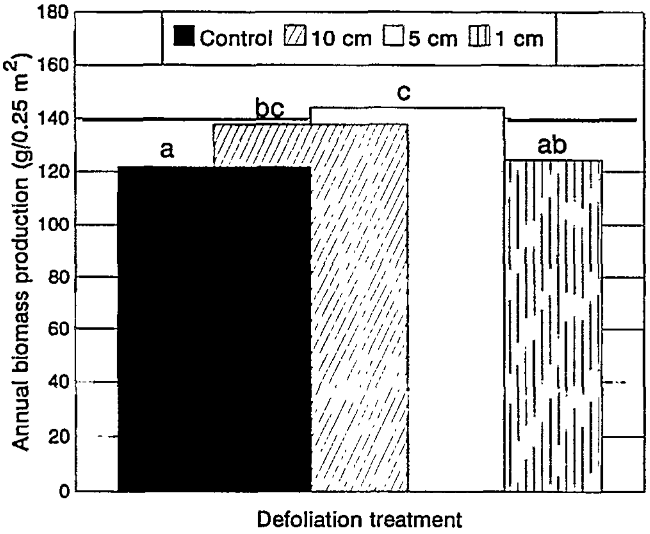

Fig. 1 Effect of defoliation to different stubble heights on annual biomass production at Willow Creek. Treatments with different letters are different at $P < 0.10$.

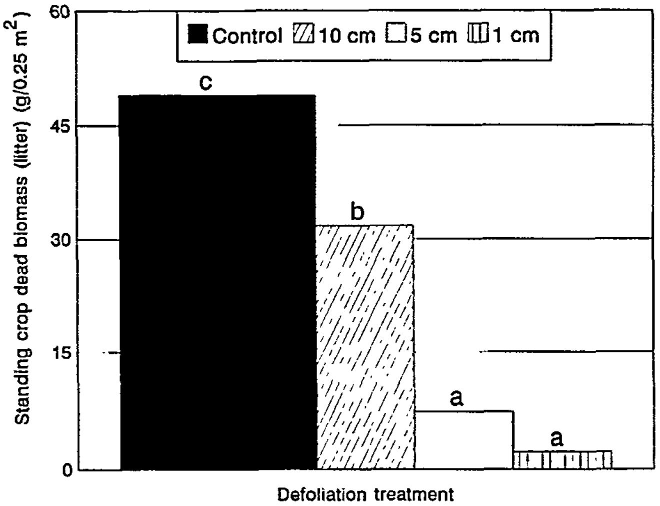

Fig. 2. Effect of defoliation to different stubble heights on the standing crop of dead biomass (litter) at Willow Creek. Treatments with different letters are different at $P < 0.10$.

cm treatments had little dead foliage and litter present (Fig. 2).

Botanical Composition

Redtop dominated all treatments throughout the study. The forb components included slender bird's-foot trefoil (*Lotus tenuis* Wadst. & Kit. ex Willd.), thistle (*Cirsium* spp. Mill.), meadow goldenrod (*Solidago canadensis* L.), and field horsetail (*Equisetum arvense* L.). Little relationship was apparent between treatment and individual forb species, except that slender bird's-foot trefoil appeared only on quadrats defoliated during the spring or during spring and fall. The mean proportion of forbs in the total biomass composition was 18.8%. No significant differences were found among treatments.

Soil Response

Compaction increased soil compressive strength by an average of 59.2% (Table 2). An interaction of C x S occurred ($P = 0.074$), reflecting a greater effect of the spring and fall compaction treatment as compared to the individual spring or fall treatments. The greatest soil strength was measured in the final year of treatment (Table 2). The compaction treatment also changed the elevation of the soil surface ($P = 0.001$). The control quadrats were appar-

Table 2. Various 1991 measures on the Willow Creek quadrats.

Treatment	Heights		Graminoid biomass Removed by defoliation			Soil
comparisons	Graminoids	Forbs	Spring	Fall	Sp/fall	strength
	-------cm-------			-----------%----------		-kg/cm^2-
Defoliation						
Control	45.4	60.9b[1]	--	--	--	2.01
10 cm	43.8	31.9a	15.1	46.7a	33.7a	1.93
5 cm	45.8	28.3a	22.6	62.4b	68.2b	1.98
1 cm	42.1	33.8a	23.4	73.5b	90.8c	2.22
P[2]	NS	0.002	NS	0.039	<0.003	NS
Compaction						
No	46.7	43.3	21.5	62.5	60.5	1.57
Yes	41.9	34.1	19.2	59.2	67.9	2.50
P	0.027[3]	NS	NS	NS	NS	<0.001
Season						
Spring	42.2	40.9	20.4	--	--	2.00
Fall	44.7	38.1	--	60.9	--	1.90
Spring and fall	45.9	37.1	--	--	64.2	2.20
P	NS[3]	NS	--	--	--	NS
Year						
1991	--	--	--	--	--	2.46
1989	--	--	--	--	--	1.61
P	--	--	--	--	--	<0.001

[1] Means within treatments followed by different letters are different at $P < 0.10$.
[2] Probability of random differences within the treatment comparisons.
[3] Interaction occurred between compaction and season. Primary reduction of graminoid height growth occurred following spring or spring-fall treatments.

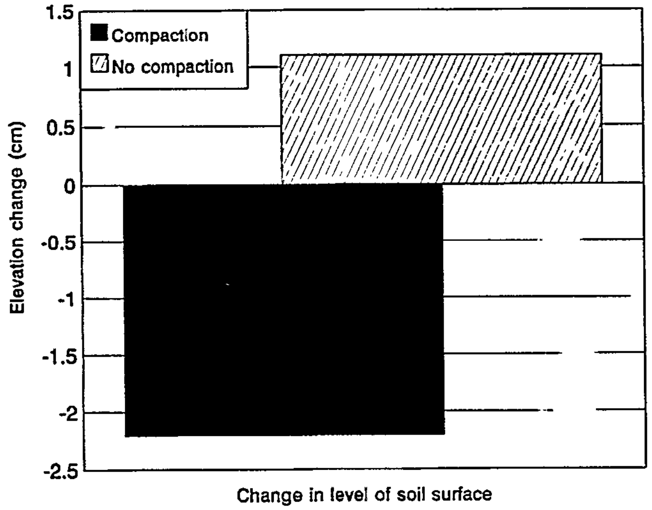

Fig. 3. Effect of compaction from 1988 to 1991 on soil surface elevation at Willow Creek.

ently still recovering from previous grazing impacts; the soil surface level rose more than 1 cm during the 3 years of study (Fig. 3). In contrast, soil surface of the compacted quadrats was lowered more than 2 cm.

Valley Creek Area

Height Response.

Graminoid height growth was reduced by both defoliation and compaction (Table 3). Perhaps the most important finding was the interaction among late summer DH and C treatments (P = 0.016); and by a similar, but nonsignificant, trend among spring treatments. Severe defoliation or compaction reduced height growth to a similar level, but the application of both treatments simultaneously did not increase the total effect. The effects were, therefore, not additive.

Biomass Response

Defoliation and C affected the following year's biomass (Table 3). An interaction of DH x C occurred for spring treatments (P = 0.064), and a similar nonsignificant trend occurred for late summer treatments. In these cases severe defoliation or compaction reduced biomass production to a similar level within seasons, however, the combination of both treatments did not reduce biomass production further–a strong nonadditive effect. Defoliation treatments that removed greater than 30% of the annual biomass production reduced the following year's biomass production below that of the control (Table 3). Compaction reduced the following year's standing crop biomass an average of 7.1 (spring) to 11.3% (late summer). Nutrient return in late summer increased the following year's biomass by 9.9%, but NR on spring plots showed no response (Table 3). A possible reason is that nutrients from the spring application can be used during the remainder of the growing season, after plant measurements are made; therefore, they would be less available for the following spring's growth. Nutrients from the late summer application would be potentially more available for the following growing season.

Graminoid biomass regrowth that occurred between the 1992 spring treatment and the final harvest in late summer 1992 was directly related only to the compaction treatment. Compaction reduced regrowth from 17.6 to 7.2 g/0.25 m2 ($P < 0.001$). No significant differences occurred in the amount of forb regrowth.

Botanical Composition

All of the quadrats were dominated by graminoids throughout the study. Twenty-nine spring treatment quadrats were dominated by sedges and 3 by meadow foxtail. Twenty-five late summer

Table 3. Various measures on the Valley Creek quadrats.

Treatment Comparisons	Graminoid height		Standing crop live biomass		Graininoid biomass harvested 1992		Soil strength	
	Spring	Lt sum	Spring	Lt sum	Spring	Lt sum	Spring	Lt sum
	-----cm-----		--g/0.25 m^2--		-------%-------		---kg/cm^2---	
Defoliation								
Control	20.6d[1]	27.9b	44.8b	74.2c	--	--	1.42	1.88
10 cm	18.9c	22.8a	42.8ab	66.4b	19.2a	32.7a	1.57	1.94
5 cm	16.8b	22.1a	41.3a	62.0ab	39.0b	55.3b	1.44	1.80
1 cm	14.0a	21.8a	40.1a	60.5a	54.1c	74.7c	1.56	2.15
P[2]	<0.001	0.001[3]	0.032[3]	<0.001	<0.001	<0.001	NS	NS
Compaction								
No	19.3	25.8	43.8	69.7	37.7	47.0	1.46	1.77
Yes	15.8	22.0	40.7	61.8	37.2	34.4	1.53	2.11
P	<0.001	0.001[3]	0.009[3]	0.001	NS	<0.001	NS	0.004
Nutrient return								
No	17.8	23.5	42.5	62.7	36.2	40.8	1.53	1.86
Yes	17.3	24.3	42.0	68.9	38.7	40.6	1.46	2.02
P	NS	NS	NS	0.010	NS	NS	NS	NS
Year								
92	18.1	22.2	44.6b	62.9a	--	--	1.95c	2.32b
91	17.0	25.6	34.1a	65.3ab	--	--	1.44b	1.79a
90	--	--	48.1c	69.1b	--	--	1.10a	1.72a
	NS	0.002	<0.001	0.094	--	--	<0.001	<0.001

[1] Means within treatments followed by different letters are different at $P < 0.10$.

[2] Probability of random differences within the treatment comparisons.

[3] Interaction occurred between defoliation height and compaction. The individual effects did not appear to be additive.

treatment quadrats were dominated by sedges, 6 by meadow foxtail, and 1 by Kentucky bluegrass. The second most abundant species, spring or late summer treatments, was usually meadow foxtail or Kentucky bluegrass. The third most abundant plant was often a forb—typically thickstem aster. The proportion of forbs in the total biomass composition averaged 17%, and was significantly related only to to the spring DH treatment ($P = 0.076$). The proportion of forbs in the 5-cm and 1-cm DH treatments was about 10% higher than the control.

Soil Strength

Soil compressive strength or resistance to penetration was significantly related only to Y (year) and to late summer C; although spring C produced a similar trend (Table 3). The highest values of soil strength were associated the driest year of the study.

Stanley Creek Area

Height Response

Midsummer height growth was affected by the 2 previous years of defoliation that removed 29-75% of the annual biomass production ($P < 0.001$) (Fig. 4). Graminoid height growth for the control and the 10-cm stubble height treatment were similar. In contrast, the 5-cm and the 1-cm stubble height treatments had reduced height growth. Plants subjected to the most severe defoliation (1-cm stubble height) had a height growth reduction of 42% in 1991 compared to 1989.

Biomass Response

Biomass was less responsive to the defoliation treatments than was height. After 3 treatment cycles only the 1-cm stubble height treatment had significantly reduced total annual production of herbage (Table 4). The reduced vigor in the 1-cm treatment resulted in no more foliage harvested than in the 5-cm treatment. This suggests no forage harvest benefit from continued severe grazing. As would be expected, the residual fall herbage was vastly different among treatments because of the limited regrowth on the defoliated quadrats (Table 4).

Discussion

The results of the different phases of this investigation demonstrate, in part, why riparian grazing approaches often seem to have inconsistent results. Different riparian areas respond differently. A growth response to grazing, as suggested by Tierney (1992) and reported by Bryant (1985), appears to have occurred in the redtop community on a site with a long growing-season, but not in the sedge-dominated communities in high mountain meadows sites where the growing season is short.

Table 4. Various 1991 measures on the Stanley Creek summer defoliated quadrats.

Treatment comparisons	Total biomass production	Biomass harvested	Fall biomass residual
	----------	g/0.25 m²	----------
Defoliation			
Control	32.0b[1]	0.0a	32.0c
10 cm	28.2b	8.2b	20.0b
5 cm	29.5b	14.9c	14.6b
1 cm	18.2a	13.7c	4.5a
P[2]	0.094	<0.001	0.001

[1] Means within treatments followed by different letters are different at $P < 0.10$.

[2] Probability of random differences within the treatment comparisons.

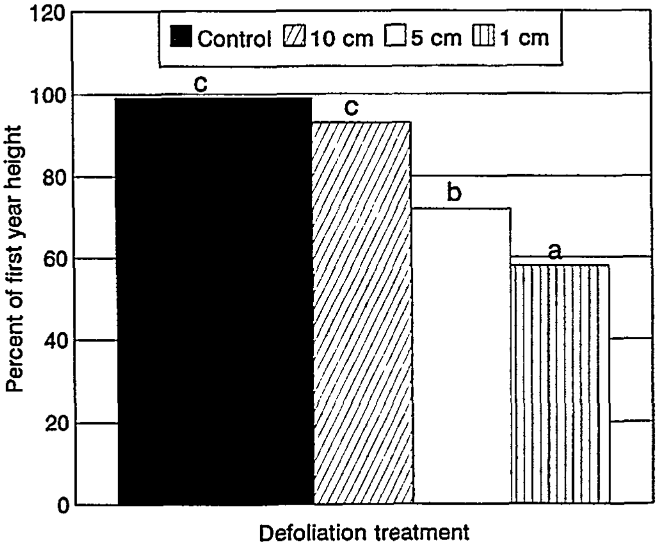

Fig. 4. Response to stubble height defoliation by graminoid plant height growth in 1991 at Stanley Creek. Treatments with different letters are different at $P < 0.10$.

It is not clear why the sites responded differently to defoliation since the average proportion of foliage removed was similar. The positive response to defoliation by the redtop plant community may have been a combination of tolerance to grazing (Raven 1986), reduction in litter buildup (Volland 1978, Branson 1985, Oesterheld and McNaughton 1991), longer growing season, or the lack of defoliation during the "boot" stage (Miller et al. 1990). In some cases redtop has been shown to decline in the absence of grazing, although this was apparently a result of increased competition from other plant species (Pehrsson 1988). Maschinski and Whitham (1989) concluded that compensatory plant response to defoliation varied with competition, nutrient levels, and timing of herbivory. Although Belsky (1987) seriously questioned the expression of overcompensation, or growth response to defoliation, she concluded that moderately grazed wetlands were the most likely situation for this to occur, assuming compaction was not severe.

Little information is available on the response to grazing by sedge species on high-elevation sites. Most of these species are assumed to be relatively resistant to grazing because of their rhizomatous growth habit (Hansen et al. 1988) although results have varied. Nebraska sedge (*Carex nebrascensis* Dewey) reduced spring height growth, but not shoot densities, following the previous summer's 64% utilization rate (Ratliff and Westfall 1987). One year after shorthair sedge (*Carex exserta* Mackenzie), shorthair reedgrass (*Calamagrostis breweri* Thurb.), and rock sedge (*Carex scopulorum* T.H. Holm) were defoliated, total root nonstructural carbohydrates were reduced by 20 to 40% (Debenedetti 1980). In contrast, grazing removal of 15 to 25% (June) and 41 to 44% (Sept.) of beaked sedge (*Carex rostrata* ex With.) shoot height for 2 years resulted in increased shoot density and no effect on shoot productivity (Allen and Marlow 1994). In the present study there appeared to be decreased height growth and biomass production by the sedge-dominated community in response to some of the 10-cm treatments, most of the 5-cm treatments, and all of the 1-cm defoliation treatments. This occurred even though the litter buildup on the mountain meadows was similar to that on Willow Creek. There was no indication that treatment in spring or mid summer was more detrimental than late summer treatment, at least when defoliating to stubble-height criteria. Although plants are often potentially more susceptible to defoliation in the spring particularly at the "boot" phenological stage (McLean and Wikeen 1985, Miller et al. 1990), a stubble-height removal results in a lower percent defoliation in the spring when plants have not reached full stature, than in the fall when plants are fully grown.

A relatively consistent effect among the sites was the reduction of plant growth by compaction. The reduction of height growth and biomass production at Willow Creek and Valley Creek averaged 12-13% when the quadrats were compacted annually. Bryant et al. (1972) found an 8 to 50+% reduction in Kentucky bluegrass yields after trampling treatments by mature cattle. The approximation of animal nutrient return on Stanley Creek suggested an increase in biomass production of about 10% in response to the late summer treatment. This was substantially less than that measured by Curll and Wilkins (1983) under intensive sheep grazing of a grass-clover sward.

An increase in the proportion of forbs in the composition only occurred on 1 sedge-dominated site. This followed spring defoliation treatments to 1- or 5-cm residual stubble heights. Additional changes may have appeared if the study had been longer, as 3 years is a short period for successional change. In wet meadows most changes in species composition apparently occur from grazing-induced changes in meadow hydrology and lowering of the water table rather than from defoliation or compaction (Bartolome 1984).

In recent years land management agencies have established a variety of forage utilization standards or guidelines for riparian areas. These typically include residual stubble height or utilization by weight criteria (Table 5). Grazing simulation studies described here suggest that all of the listed agency guidelines would be adequate to maintain the vigor of herbaceous riparian communities dominated by plants, such as redtop, adapted to disturbance. Our results infer that redtop will maintain vigor under defoliation to a 5-cm stubble height and the associated trampling compaction. In contrast, our results from mountain meadow communities indicate that defoliation to a 5-cm stubble height with the associated trampling damage and nutrient return will often reduce future sedge biomass production and may allow a greater proportion of forbs in the plant community composition. It appeared that a 10-cm or greater stubble height may be required to insure full biomass production in these high-elevation, sedge-dominated communities. If utilization guidelines are used, those

Table 5. Several land management agency riparian grazing utilization standards and guidelines.

Criteria	Where applied	Information source
Residual stubble height of herbaceous forage		
10 to 20 cm	Streams important to threatened and endangered fish species	BLM, Idaho, Erv Cowley, personal communication, 1994
10 to 15 cm	Carex communities in mountain riparian areas	USFS Region 2, Rangeland Ecosystem Inventory and Management Guide, 1994
10 to 15 cm	Highly sensitive riparian areas in unsatisfactory condition	USFS, Upper Ruby Final EIS, Beaverhead NF, Montana, 1992
5 to 8 cm	Relatively stable riparian areas in satisfactory condition	ditto
10 to 15 cm	Seasonlong riparian grazing	USFS, Region 4, Desk Guide, 1993; and Clary and Webster (1989)
10 cm	Rotation riparian grazing	USFS, Region 4, Desk Guide, 1993
Percentage utilization by weight of herbaceous forage		
30%	Riparian areas not meeting Sawtooth FLRMP[1] standards	USFS, Stanley Basin Final EIS, Sawtooth NF, Idaho, 1993
40 to 50%	Riparian areas meeting Sawtooth FLRMP standards	ditto
25%	Primary chinook salmon production areas	USFS, Bear Valley and Elk Creek, Biological Opinion, Boise NF, Idaho, 1993
45 to 60%	Rotation grazing systems	USFS, Land Resource and Management Plan, Boise NF, 1990
30 to 55%	Seasonlong grazing	USFS, Region 4, Desk Guide, 1993
50 to 65%	Rotation grazing	ditto

[1] Forest Land Resource Management Plans

rates that do not exceed 30% of the annual biomass production will likely maintain production the following year. Therefore, the majority of land management agencies' riparian (streamside) residual stubble height grazing recommendations in Table 5 appear to be adequate for maintenance of biomass production in our mountain meadow sedge-dominated communities. Some of the percentage utilization criteria, however, may be too liberal to maintain full productivity on high elevation sites, based on our Valley Creek data. The specific recommendations listed here, however, do not address the issues of streambank stability and channel maintenance.

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Bison selectivity and grazing response of little bluestem in tallgrass prairie

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Abstract

The perennial bunchgrass little bluestem (*Schizachyrium scoparium* [Michx.] Nash) was examined in a 5-yr study on tallgrass prairie to determine how fire influences its use by bison and its responses to grazing. On unburned prairie, bison grazed only 5% of the available little bluestem, selecting it only 30% as frequently as big bluestem, the dominant co-occurring species. On burned prairie, grazing frequency of little bluestem was over 3-fold greater and equal to that of its dominant neighbor. Grazing frequency of little bluestem was affected by plant size (basal area). On burned sites, plants of intermediate size classes were least abundant (<10% of total) but were grazed most frequently (>50%). Small plants were most abundant but were grazed least frequently. Density, tiller numbers, and basal area of little bluestem were significantly greater in annually burned compared to infrequently burned sites but were decreased by > 50% in grazed compared to ungrazed sites. Grazing shifted the population size distribution toward higher frequencies of smaller individuals (< 50 cm² basal area), whereas burning increased the frequency of large (> 200 cm² basal area) individuals. In unburned prairie, little bluestem accumulates a persistent clump of standing dead tillers that appear to serve as a physical deterrent to grazing. Although burning enhances its growth, it also removes its canopy of dead tillers exposing the plant to grazers. The shift in population structure toward a high frequency of smaller (and perhaps less drought- or grazing-tolerant) individuals may contribute to the decline of little bluestem populations under persistent grazing. Thus, plant growth form, population size structure, and fire interact to influence bison grazing patterns and responses of little bluestem to grazing on tallgrass prairie.

Key Words: bison, grazing, fire, bunchgrass, *Schizachyrium scoparium*

Studies of plant-grazer interactions have shown that numerous characteristics of the plant and the grazer may influence both the probability of a given plant being grazed and its response to herbivory (Dirzo 1984). Plant traits that reduce the probability of a plant being grazed (grazing avoidance) or those that increase its ability to recover following grazing (grazing tolerance) are 2 primary mechanisms by which plants cope with herbivory (Briske 1991). Plant characteristics such as growth form, size, morphology and nutritional status, and environmental factors such as resource availability, plant competition and fire may all be important in determining both the selection of species, plants, or plant parts by grazers and the subsequent growth, tillering, and reproductive responses of grasses following herbivory (e.g. Mueggler 1972, Archer and Detling 1984, Coppock and Detling 1986, Hartnett 1989, Ganskopp and Rose 1992, Ganskopp et al. 1992, Vinton et al. 1993). The spatial and species selectivity of grazers and plant responses to grazing patterns have important implications for the management of rangeland ecosystems.

In tallgrass prairie and other grassland communities, variation in growth form and size among co-occurring plants, and the occurrence of fire, may significantly influence grazing patterns and plant responses. For example, in tallgrass prairie little bluestem is an important bunchgrass and produces a high ratio of reproductive stems to vegetative tillers. Although it has a comparatively low tolerance to grazing (Butler and Briske 1988, Mullahey et al. 1990), its development of a persistent clump of dead reproductive tillers may be an effective grazing avoidance mechanism (Ruyle and Rice 1991, Brummer et al. 1993). Fire in tallgrass prairie removes this physical barrier and exposes the plants to grazers. This may significantly increase the frequency at which little bluestem is grazed relative to other dominant forage grasses such as big bluestem. Thus, the patterns of grazing of little bluestem, and its responses to grazing, may differ considerably between burned and unburned prairie.

Furthermore, recent studies indicate that, within monotypic pastures, cattle selectively graze bunchgrasses based on plant basal area (Ganskopp and Rose 1992). Whether such selectivity based on plant size occurs in diverse, multi-species grasslands such as tallgrass prairie is unknown.

The objectives of this study were to: 1) assess patterns of bison grazing of little bluestem in tallgrass prairie by quantifying both its grazing frequency (percentage of available plants grazed) and its selection by bison (use relative to its most abundant neighboring plant species), 2) assess the influence of plant size on the selection of plants by bison, and 3) assess the effects of fire on the relative grazing frequency of little bluestem and its responses

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to grazing. Previous studies in tallgrass prairie have examined the growth and tillering dynamics of some of the rhizomatous tall grasses (e.g. Peet et al. 1975, Knapp and Hulbert 1986, Forwood and Magai 1992, Vinton and Hartnett 1992), but the growth and dynamics of the bunchgrass little bluestem in relation to fire and grazing in tallgrass prairie have not been studied.

Materials and Methods

This study was conducted on the Konza Prairie Research Natural Area, a 3,487 hectare tallgrass prairie site located in the northern Flint Hills region of northeastern Kansas (39°05'N, 96°35'W). Average monthly temperature ranges from a January low of -2.7° C to a July high of 26.6° C and average annual total precipitation is 835 mm. The vegetation of Konza Prairie is predominantly tallgrass prairie, dominated by the C_4 grasses big bluestem (*Andropogon gerardii* Vitman), little bluestem [*Schizachyrium scoparium* (Michx.) Nash], Indiangrass [*Sorghastrum nutans* (L.) Nash], and switchgrass (*Panicum virgatum* L.), with numerous subdominant grasses, composites, legumes, and other forbs (Kuchler 1967, Freeman and Hulbert 1985). A few woody species, such as leadplant (*Amorpha canascens* Pursh) and New Jersey tea (*Ceanothus herbaceous* Raf.), are locally common. The vascular flora of Konza includes over 500 species representing over 60 families (Freeman and Hulbert 1985). The soils are Chase silty clay loams: fine, montmorillonitic, mesic Aquic Arguidolls. Bison were introduced onto a 1,000 ha portion of Konza Prairie in October 1987 at a stocking rate of 9 ha au^{-1}. The stocking rate was gradually increased to 5 ha au^{-1} by 1992. The animals are free to move among 10 watersheds (avg. size = 100 ha) that are subjected to prescribed April burning annually or at 2-yr, 4-yr or 20-yr intervals. For this study, we sampled in an annually burned watershed and a watershed burned at 4-yr intervals that had been grazed by bison since 1987, and nearby annually burned and 4-yr burn interval watersheds that were ungrazed. The 4-yr burn interval watersheds were last burned in 1990 and thus had not burned within 2 years of our sampling. For simplicity, these sites and the annually burned sites will hereafter be referred to as "unburned" and "burned" sites respectively.

Soil types, slopes, aspects, and previous land-use histories are similar among the watersheds studied. Prior to the introduction of bison in 1987, all watersheds sampled in this study had been ungrazed and similarly managed for approximately 20 yrs. The various prescribed burning frequency treatments were initiated on Konza Prairie in 1970. In addition, the Konza Prairie Long-Term Ecological Research Program plant community data (Data Set PVC-081, unpublished) indicate that there were no significant initial differences in botanical composition among the study sites.

Plants were marked at the beginning of the 1992 growing season, the fifth season after the initiation of the grazing treatments on the watersheds. Five 50-m transects were established in each of the treatment areas. At 1-m intervals along each transect, the nearest little bluestem bunch and big bluestem tiller was marked and mapped, for a total of 250 plants of each species in each watershed and 2,000 plants overall. Bunch size (for little bluestem) and distance from the transect sampling point were recorded. Basal area was determined by measuring the greatest basal diameter and a second diameter perpendicular to the first, and solving for the area of the ellipse. Little bluestem plants were stratified into 6 size classes based on basal area, ranging from less than 25 cm^2 to greater than 200 cm^2. All plants were censused every 2 weeks beginning 1 June and continuing until 15 August in 1992 and 1993 to determine grazing frequency. Also, during the first week of August, an additional 1,000 plants of each species were randomly sampled along the transects to determine whether they had been grazed or not during the season. Grazing frequency of big bluestem (*Andropogon gerardii* Vitman) was measured to provide a reference or comparison for assessing bison selection or avoidance of little bluestem and because it is the most abundant co-occurring species in these tallgrass prairie communities (accounting for >50 % of the total plant cover) and the most frequent nearest-neighbor of little bluestem.

Differences between grazing frequencies of big and little bluestem were determined using the 2-way analysis of variance procedure, and Fisher's Protected L.S.D. ($P < 0.05$) was used to separate means. Chi-square analysis ($P < 0.05$) was used to examine the hypothesis that the number of plants grazed was independent of the number available within each size class. Degree of association between class rankings based on the number of plants grazed and number of plants occurring within size classes was indexed with Spearman's rank correlation coefficient.

In early September, a total of approximately 300 little bluestem plants were randomly selected along the 50-m transects and harvested: 50 plants in each of the ungrazed watersheds, 50 grazed plants in each of the grazed watersheds, and 50 ungrazed plants in each of the grazed watersheds. The plants were oven-dried at 75° C for at least 3 days. The plants were separated into reproductive tiller and vegetative tiller components, counted, and weighed to the nearest mg.

The influence of fire and grazing on plant response variables was analyzed using 2-way analysis of variance procedures. Differences between means were tested with Fisher's Protected L.S.D. at a significance level of $P < 0.05$.

Results

Bison Selectivity

In unburned prairie, little bluestem was grazed far less frequently than its dominant neighbor, but the 2 species were grazed at equal frequencies on burned prairie (Fig. 1). Bison grazed little bluestem 3.3 times more frequently on burned prairie (26.5% of plants grazed) than on unburned prairie (6.9% of plants grazed) (Fig. 1).

The grazing frequency of little bluestem was also significantly affected by plant size (freq. of plants grazed in each size class was significantly different than freq. available [Chi-square significant at the $p < 0.05$ level]) (Fig. 2). In the burned watershed, plants in the 2 smallest size classes occurred most frequently but were grazed least frequently, while intermediate sized plants in the 100 cm^2 and 150 cm^2 size classes occurred least frequently and were grazed most frequently (Fig. 2). Bison grazed plants in the 50 to 200 cm^2 size classes most frequently. Spearman's rank correlation showed that the number of plants grazed within each size class was significantly inversely related to the relative number of plants available within each size class. In the unburned sites, the low grazing frequency of the plants precluded statistical comparisons of grazing frequency among size classes.

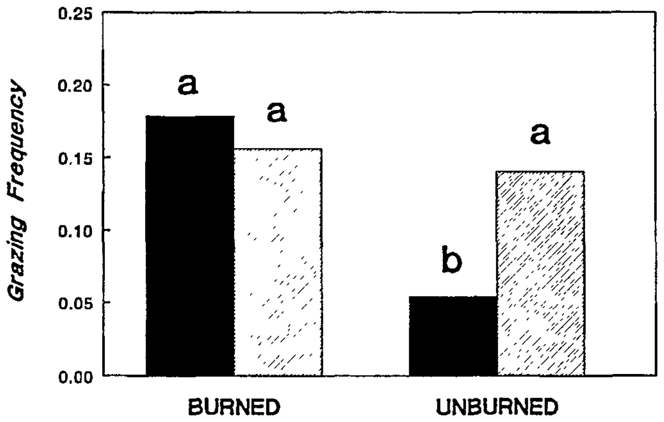

Fig. 1. Mean grazing frequencies of little bluestem (solid bars) and big bluestem (cross hatched bars) in burned and unburned prairie. Similar letters above bars indicates no significant difference in grazing frequency at the $p < 0.05$ level (ANOVA, LSD).

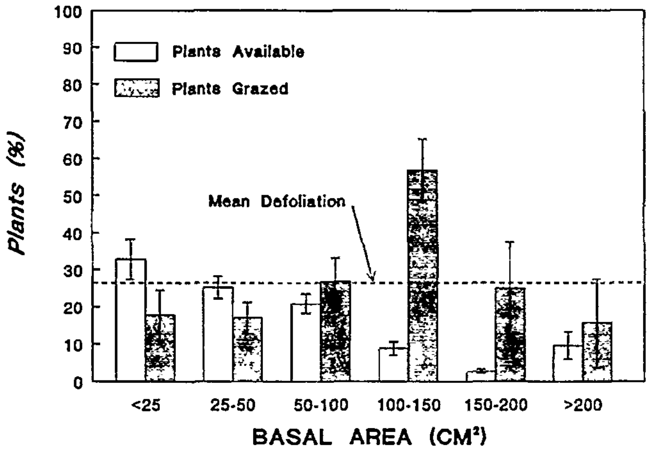

Fig. 2. Availability and percent of little bluestem plants grazed (mean + 1 SE) in 7 basal area size classes in annually burned tallgrass prairie. Dashed line indicates the mean percent of all plants defoliated.

Plant Responses to Grazing

Little bluestem plant (bunch) density was reduced by grazing and increased by annual burning (Fig. 3a). The average density of plants was 0.5 plants m^{-2} in grazed prairie and 0.9 plants m^{-2} in ungrazed prairie. On both grazed and ungrazed sites, little bluestem densities were nearly double on annually burned compared to infrequently burned sites (Fig. 3a). Mean basal area was reduced by grazing in both burned and unburned prairie. Burning alone increased mean basal area relative to that of unburned prairie and the largest mean bunch size was found in the ungrazed annually burned site (Fig. 3b). In general, grazing had a larger effect on average bunch size than did burning.

In addition to altering mean basal area, 5 years of burning and grazing shifted the size class distribution of little bluestem (Fig. 4). Annual burning resulted in a population with high frequency of large individuals (> 200 cm^2), while grazing by bison shifted the distribution towards the smaller size classes (Fig. 4). In the grazed watersheds, mean basal area was 72.6 cm^2 and 76.5 cm^2 in burned and unburned prairie, respectively. In grazed prairie, plants in the <25 to 100 cm^2 size classes occurred the most frequently, while those in the large (100 to >200) size classes were the least frequent in both burned and unburned sites (Fig. 4). In the ungrazed watersheds, mean basal area was 225.5 cm^2 and 168.6 cm^2 in burned and unburned prairie, respectively. Small individuals (<50 cm^2) were generally much less frequent and large individuals (> 200cm^2) were more frequent in ungrazed than in grazed sites (Fig. 4).

Table. 1. Mean biomass and densities of vegetative and reproductive tillers of little bluestem in burned/grazed (BU/GR), burned/ungrazed (BU/UNGR), unburned/grazed (UNBU/GR), and unburned/ungrazed (UNBU/UNGR) tallgrass prairie.

	BU/GR	BU/UNGR	UNBU/GR	UNBU/UNGR
Tillers plant^{-1}				
Vegetative	44.2a	73.5b	48.3a	55.9a
Reproductive	2.8a	11.3b	4.5a	7.8c
Tillers cm^{-2} Basal Area				
Vegetative	0.57a	0.66a	0.49a	0.55a
Reproductive	0.05ab	0.09c	0.03a	0.08bc
Tillers m^{-2}				
Vegetative	27.3a	79.0b	22.6a	34.7a
Reproductive	2.3a	12.3b	2.5a	4.9c
Total	29.5a	91.3b	25.1a	39.6a
Grams tiller^{-1}				
Vegetative	0.13a	0.19b	0.08c	0.14a
Reproductive	0.39a	0.43a	0.60b	0.81c
Grams m^{-2}				
Vegetative	3.6a	12.7b	2.8a	4.9a
Reproductive	1.3a	5.8b	1.7a	4.0c
Total	4.9a	18.5b	4.4a	9.0c

Values within a row with the same lowercase letter do not differ ($p < 0.05$).

Grazing reduced the number of little bluestem vegetative tillers per plant in annually burned prairie, but not in unburned prairie (Table 1). In the grazed watersheds, burning decreased the number of reproductive tillers per plant, while burning increased reproductive tillers in ungrazed areas. No significant differences were detected in tiller density within clumps (vegetative tillers cm^{-2} of basal area) among any treatments, but the number of reproductive tiller cm^{-2} of plant basal area was decreased by grazing in both burned and unburned prairie (Table 1). Grazing reduced the number of vegetative tillers m^{-2} and reproductive tillers m^{-2} in the burned areas, but not in the unburned areas (Table 1). Burning increased vegetative tiller biomass and reduced reproductive tiller biomass in grazed and ungrazed prairie. Grazing reduced biomass of all tillers except reproductive tillers in burned prairie. Grazing reduced both vegetative and reproductive tiller production (g m^{-2}) in the burned sites, but not in the unburned sites. Overall, little bluestem standing crop was dramatically increased by burning in ungrazed prairie but not in grazed prairie.

Discussion

The results reported here demonstrate that fire in tallgrass prairie alters grazing frequency of the bunchgrass little bluestem and its selection relative to the dominant co-occurring species. In addition, little bluestem plant size (bunch basal area) is an important basis for selection among conspecific plants. Previous studies have shown that fire frequency alters the spatial patterns of bison grazing at the landscape scale in grasslands (Coppock and

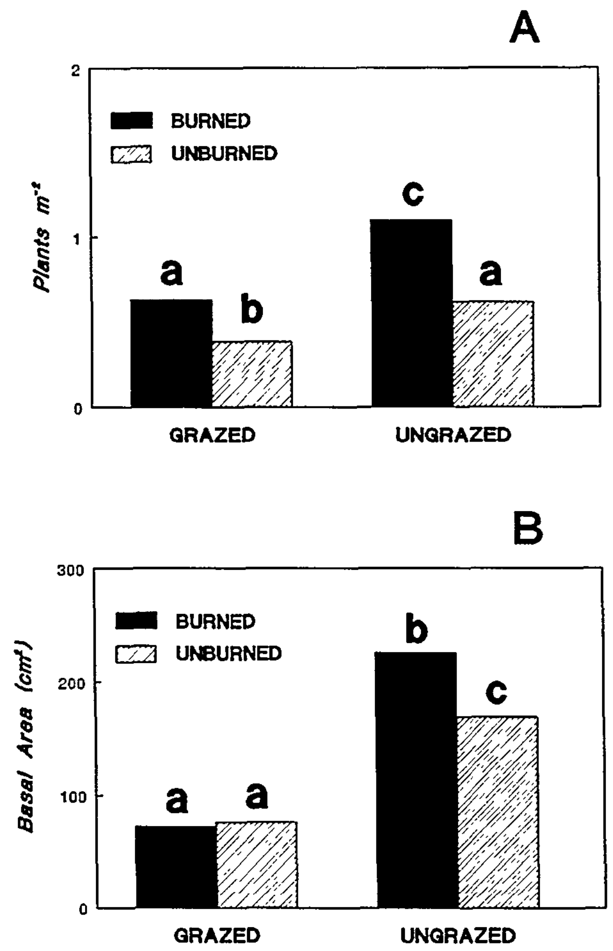

Fig. 3. a) Mean plant density of little bluestem plants (bunches) by treatment. b) Mean plant basal area of little bluestem plants by treatment. Similar letters above bars indicate no significant difference between treatments at the

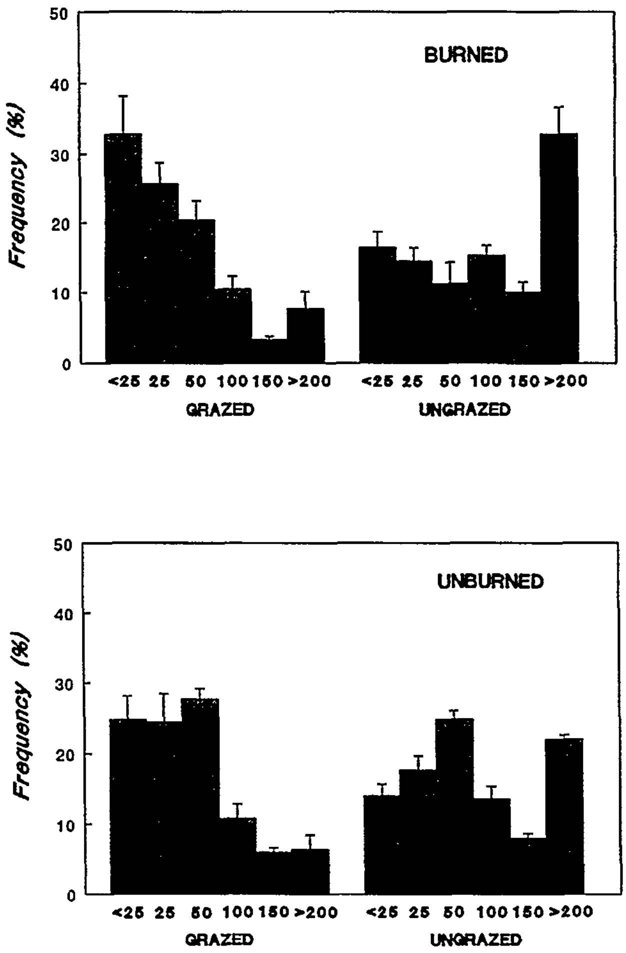

Fig. 4. Mean ± 1 SE) percent of little bluestem individuals in each of 6 size (basal area) classes in burned/grazed, burned/grazed, unburned/grazed, and unburned/ungrazed tallgrass prairie. Numbers on the x-axis indicate lower limit of each size class.

Detling 1986, Vinton et al. 1993). Thus, in addition to the documented direct effects of fire in tallgrass prairie (e.g. Hulbert 1986, Collins and Wallace 1990), fire may also influence these plant communities indirectly by altering patterns of large ungulate grazing at several scales.

In prairie that had not been recently burned, bison avoided little bluestem relative to its dominant neighbor, big bluestem, but this pattern of selectivity was eliminated by burning. The increased grazing frequency on little bluestem in the annually burned prairie compared to the site that had not burned for 2 years is most likely the result of the removal of its persistent standing dead tillers by burning. Recent studies have shown that the presence of standing dead stems deters grazing by cattle (Ganskopp et al. 1992, Brummer et al. 1993). The frequency at which neighboring big bluestem plants were grazed (a plant lacking persistent standing dead tillers) was unaffected by burning. With longer intervals between fires, bison might display even greater avoidance of little bluestem in favor of other co-occurring grasses, but only up to a point. The increase in standing dead biomass within bunches, and its deterrent effect on grazers, would be expected to reach an asymptote due to the gradual decomposition of dead tillers and reproductive culms.

An alternate hypothesis explaining the increased grazing frequency of little bluestem during the season after fire is that burning may alter its nutrient content or some other aspect of its forage quality, increasing its acceptability to bison. However, although burning generally increases the productivity of little bluestem (Towne and Owensby 1984, Svejcar and Christiansen 1986), it is unlikely that a change in plant tissue nutrient content alone could account for a 3-fold increase in its use after fire and such a large increase in its use relative to other co-occurring C_4 grasses.

Bison selectively grazed intermediate sized little bluestem plants and they avoided individuals in large and small size classes although they were available in greater numbers. This selectivity is most likely related to animal bite width and the efficiency with which animals harvest forage from bunchgrasses. Plants with diameters between 11 and 14 cm were grazed most frequently. Although we found no published data on the bite width of bison, Ganskopp and Rose (1992) reported that the mean bite width of 4+ year old Hereford X Angus cattle was 9 cm. Bison can be expected to have similar, or slightly larger, bite widths compared to cattle and the effective bite width is expanded somewhat by the use of the tongue. Ganskopp and Rose (1992) showed that cattle grazing monotypic stands of the caespitose grass *Agropyron* *desertorum* exhibited strong size preferences. Our results show that such size-based preferences also are evident in bison grazing and in mixed composition as well as monotypic communities.

Burning and herbivory acted to modify demographic characteristics of little bluestem at the plant and at the population level. Over the 5-yr period, bison grazing resulted in the shift in the little bluestem population size structure towards a high frequency of smaller plants. This shift is most likely caused by the fragmentation of intermediate and large plants (Briske and Anderson 1990). This change in population size distribution may result in greater mortality rates because smaller individuals of little bluestem may be less tolerant of drought conditions than large individuals (Butler and Briske 1988, Briske and Anderson 1990). This change in size structure may also result in reduced reproductive success because both seed production and vegetative reproduction are generally plant size-dependent in herbaceous perennials (e.g. Hartnett 1990). Thus, a grazing-induced shift to smaller size classes and resulting decrease in reproduction and/or survivorship may explain why little bluestem declines under persistent grazing, particularly in burned prairie, where it is more vulnerable to large grazers and more frequently grazed..

Density of little bluestem plants (bunches) was uniformly higher on burned prairie, but was significantly reduced by grazing. In contrast, Butler and Briske (1988) reported that herbivory results in increased plant density by fragmenting large individuals into a larger number of small individuals. In our study, we also observed the apparent fragmentation of large plants, but total plant density was reduced by grazing. This may be the result of significant mortality among the smaller plants due to more intense grazing, or higher levels of interspecific plant competition in our study site where little bluestem occurs in mixed stands with tall grasses (Butler and Briske conducted their study in monospecific stands of little bluestem). Grazing reduced vegetative tillers per plant by 39.9% and 13.6% in burned and unburned prairie, respectively, and reproductive tillers by 75% and 42.3% in burned and unburned prairie, respectively. The more pronounced effect of grazing in burned than in unburned prairie is most likely explained by the higher grazing intensity on little bluestem in the burned prairie relative to unburned sites. The larger effects of grazing on reproductive tiller numbers than on vegetative tiller numbers is consistent with earlier studies showing that reproductive responses are more sensitive to grazing stress than vegetative growth responses in big bluestem and switchgrass (*Panicum virgatum* L.) on tallgrass prairie (Vinton and Hartnett 1992). Plants in the grazed areas that were ungrazed during the current season had tiller numbers similar to grazed plants and had tiller weights similar to plants in the ungrazed areas. Thus, tiller number per plant appears to be related to previous seasons' grazing history, whereas tiller weight is influenced by current season's grazing. Intraclonal tiller densities (tillers cm^{-2} of plant basal area) were not different among any treatments. This is not unexpected given that bunchgrasses are characterized by the compact spatial arrangements of tillers within clones with strongly regulated intraclonal tiller densities (Williams and Briske 1991).

Previous work has indicated that bunchgrasses of the Great Plains are more poorly adapted to large herbivore grazing than are rhizomatous species (Mack and Thompson 1982, Mullahey et al. 1991). Bunchgrasses are known to decline in grassland communities as a result of long-term grazing. Although burning favors little bluestem in ungrazed tallgrass prairie, it also removes its protective canopy of standing dead tillers resulting in increased vulnerability to large grazers. Thus, even though burning apparently improves growth conditions for little bluestem, the increased grazing intensity it experiences and resulting suppression is enough to offset any fire induced increase in population growth potential. Thus, little bluestem (and likely other C_4 bunchgrasses) can be expected to exhibit opposite responses to burning in grazed compared to ungrazed prairie.

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Grazing influences on watering point vegetation in the Chihuahuan desert

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Abstract

Long-term influences of livestock grazing on vegetation around watering points was studied on 2 upland Chihuahuan desert ranges in southcentral New Mexico using regression analysis. One range had been conservatively stocked since the 1950's while the other was more heavily stocked. About 45% of the climax vegetation occurred on the heavily stocked range compared to 70% on the conservatively stocked range. During 3 years of study, both ranges were stocked conservatively so annual utilization of the key forage grasses was 30-35%. Regression analyses showed black grama (*Boueteloua eriopoda* Torr.), mesa dropseed (*Sporobolus flexuosus* Thurb, Rybd.), threeawn (*Aristida* sp.), and total perennial grass standing crop increased as distance from water increased on the good condition range ($P < 0.05$). However, black grama and threeawn standing crop showed no association with distance from water on the fair condition range. Broom snakeweed (*Xanthocephalum sarothrae* Pursh.), the primary poisonous plant found on both ranges, was associated ($r^2 = 0.35$) with distance from water only on the good condition range in April. Poisonous plants other than broom snakeweed decreased as distance from water increased with the exception of the fair condition range in October. No livestock losses from poisonous plants were noted on either range over the 3 years. We attribute this to the present conservative stocking rates. Our study supports the recommendation that downward stocking rate adjustments be made for the zone more than 1,600 m from water.

Key Words: rangeland, grazing management, forage, stocking rate, range condition

Livestock use forage plants more heavily around watering points compared to areas away from water (Valentine 1947, Holscher and Woolfolk 1953, Pinchak et al. 1991, Hart et al. 1991, 1993). However research documenting the long-term (over 30 years) interactions of livestock grazing and distance from water on forage productivity is lacking. This type of information would be useful in refining adjustments for distance from water in grazing capacity determinations, and in decisions regarding location and spacing of watering points. There is still reluctance for managers in government agencies and on private ranches to adjust stocking rates for distance from water and slope.

This study was designed to evaluate vegetation standing crop biomass and species composition at varying distances from water on 2 upland sandy ranges in different ecological condition in the Chihuahuan desert of southcentral New Mexico, with known grazing histories. The hypothesis tested was that after decades of livestock grazing production of desirable forage increased more rapidly on range in good condition than on range in fair condition as distance from water increased.

Study Area

The 2 study ranges are located 37 km north of Las Cruces, N.M. Their western boundaries are adjacent to Interstate Highway 25. The study area is on the southern end of the Jornada Del Muerte Basin. This area is bounded by the San Andres Mountains on the east and several isolated mountains on the west. Elevation varies from 1,188 to 1,371 m with level or gently rolling hills. There are no permanent streams.

The basin consists of unconsolidated Pleistocene detritus. This alluvial fill from the bordering mountains is as much as 100 m thick and the filling process is still active. Coarser sediments are found near the foothills with finer soil particles in the drainages. The soils show almost no organic matter and little change in texture between surface and subsurface layers. The lime content is high in all of the soil types, grading into a solid, calcareous substrata at variable depths in the coarser soils.

Study pasture soils are primarily shallow, fine sandy loams of the Simona-Cruces associations (fine loamy, mixed, thermic, typic Haplargids). The topography is relatively flat with all slopes under 5%.

The climate of the Jornada basin is typical of arid grassland regions. There is an abundance of sunshine, a wide range between day and night temperatures throughout the year, low relative humidity and low, extremely variable precipitation.

Seasonal patterns of precipitation are characterized by small amounts in spring and a peak in August with gradually reduced amounts during fall (Pieper and Herbel 1982). A smaller peak

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occurs in January. Summer precipitation originates in the Gulf of Mexico and occurs as intense local convectional thunderstorms of short duration. Winter precipitation originates from the Pacific Ocean and is characterized by gentle frontal storms.

Temperatures reach a peak in June and decline until December. Wind velocities are highest in March, April, and May and lowest in December. These winds cause much soil erosion and increase water stress on vegetation by increasing transpiration and reducing the soil moisture content by evaporation.

During the study (1988-1990), precipitation on the experimental area was about 17% above the long-term average (Fusco 1993). There were no temperature aberrations.

Vegetation on the Jornada Basin is classified as Chihuahuan desert grassland and shrubland (Brown 1982). Most of the grassland areas have been invaded by brushy species during the last 100 years (Brown 1950, Dick-Peddie 1966). The principal grassland type is black grama (*Bouteloua eriopoda* Torr.) with mesa dropseed (*Sporobolus flexuosus* Thurb. Rybd.) intermixed. The shrub type is mainly honey mesquite (*Prosopis glandulosa* Torr.) sandhills, with snakeweed (*Xanthocephalum* spp.) invading certain sites. Annual forbs include leather leaf croton (*Croton pottsii Lam.*), nightshades (*Solanum* sp.), globemallow (*Sphaeralcea* sp.) and Russian thistle (*Salsola iberica* L.). The presence of these forbs is dependent on seasonal precipitation.

Much of the grazing history is based on interviews with retired employees of the Animal and Range Science Department at NMSU. Before 1922 when the College Experimental Ranch was established, both study areas were mostly black grama grassland with a minor brush component (honey mesquite). Although some of the area was heavily grazed by cattle, watering points were widely spaced which minimized the number of zones of degradation. During the 1930's and the 1940's, the College Ranch range was stocked conservatively compared to the adjacent BLM ranges. Reports from this period show the College Ranch range used in our study produced about 360 kg of perennial forage per ha and was stocked at about 40 ha animal unit^{-1} (Neale 1937, Valentine 1947, Knox et al. 1959). Based on Valentine (1947), the utilization level on much of the College Ranch range averaged near 35%. In contrast accounts by retired College Ranch personnel and BLM records indicate the adjacent BLM study range was stocked at around 24 ha animal unit^{1}, and the utilization level averaged somewhere between 50 and 60%.

Extended drought during the mid-1950's reduced the black grama on both study areas. Following the drought, honey mesquite increased on both ranges. These changes are documented on the adjoining Jornada Experimental Range by Buffington and Herbel (1965). From 1954 to 1967 period, range condition appears to have declined severely on the College Ranch because of combination of drought and failure to adequately adjust stocking rate.

In 1967, the College Ranch study area was placed under intensive grazing management and the stocking rate was reduced from 41 to 67 ha animal unit^{1} (Beck 1978, Beck et al. 1987). Since then, utilization of the key forage species has averaged about 30 percent. The stocking rate has been increased from 67 ha per animal unit^{-1} to 45 ha per animal with no increase in degree of forage use or sacrifice in cattle performance (Beck et al. 1987, Beck and Kiesling 1991). Overall condition using the Soil Conservation Service approach (Dyksterhuis 1949) has improved from mid-fair to high-good during the 24 year period with 70% of the climax vegetation remaining (Tembo 1990).

The grazing history of the BLM range is unknown from 1950 to 1980 period, but detailed records have been kept since 1981. Before 1981, the general grazing plan was to remove about 50% of the perennial grass production using continuous grazing. The stocking rate from the late 1960's to 1981 was about 42 ha animal unit^{1}. In 1981 to 1990, the rancher destocked the range to an average rate of 72 ha animal unit^{1}. Poor cattle performance and recognition that the range was deteriorating were the reasons for the voluntary reduction in stocking rate based on interviews with the rancher.

BLM records show heavy use levels of 60 to 80% for the early 1980's but in the mid 1980's to 1990 use levels were considered to be between 20 and 40%. Range condition in 1982 based on BLM records was low-fair (32% of climax remaining). In 1990 condition had improved to high-fair with 45% climax vegetation. The USDA Soil Conservation Service procedure developed by Dyksterhuis (1949) was used for estimates of range condition.

Materials and Methods

One watering point each was selected on the College Ranch and BLM ranges and both had been in operation for 40-50 years, had a long history of continuous grazing, and were similar in topography. On the BLM range 44% of the area is within 1.6 km from water, 38% is between 1.6 and 3.2 km from water and 18% is over 3.2 km from water. On the College Ranch range 50% of the area is within 1.6 km from water, 45% is between 1.6 and 3.2 km from water and 5% is over 3.2 km from water.

Four transects were randomly selected originating from each watering point center. Two transects were oriented between 0° and 180° and the other 2 between 180° and 360°. Each transect was 1,700 m long. In October and April (1988-1990), vegetation inside a 0.5 m^2 quadrat was clipped to ground level at 50 m, 150 m and every 200 m from 300 up to 1,700 m from the watering point. These distances were used to represent the major zones of potential grazing influences on vegetation. Transects were terminated at 1,700 m because of changes in range site. The vegetation was hand separated by species in the field and oven dried at a constant temperature of 60° C. Only plant material produced during the previous growing season was included in standing crop evaluation.

Linear Regression analysis was used to evaluate standing crop data pooled across years (Neter and Wasserman 1974). The dependent variable was standing crop (g/m^2) and the independent variable was distance from water (50, 150, 400, 800, 1,300, 1,700 m). Standing crop data were pooled into these categories to improve the precision associated with each estimate. Separate regressions were determined for each range and month for each plant and plant category. Regressions for range and month within each plant and plant category were compared using the procedures of Neter and Wasserman (1974) and tested at the $P < 0.05$ level.

Results and Discussion

Regression analyses showed standing crop (g/m^2) was significantly related to distance from water for black grama, mesa

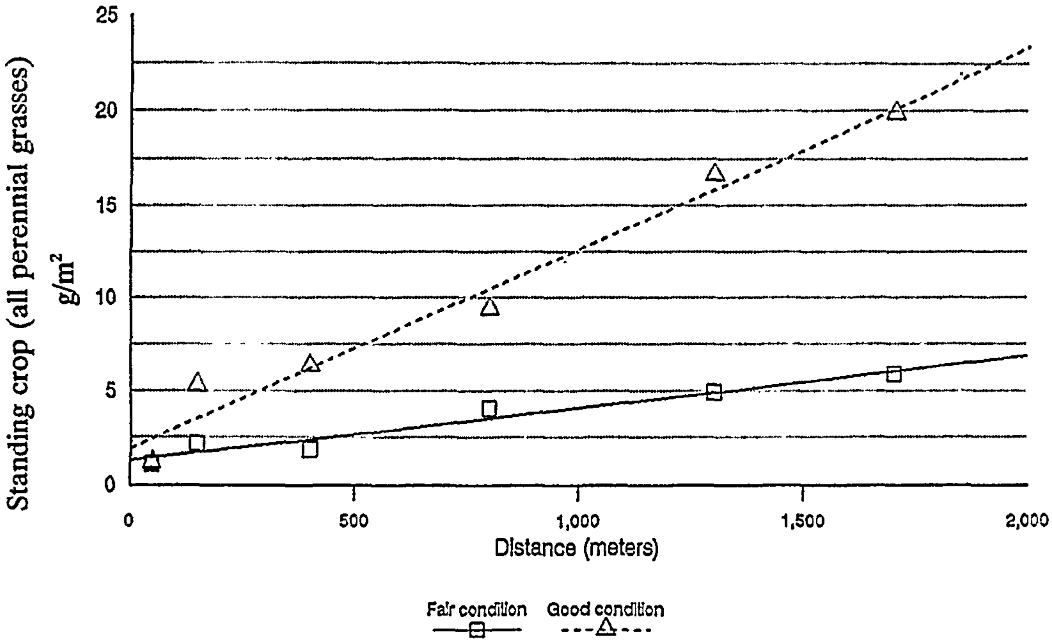

Fig. 1. Standing crop (g/m²) of all perennial grasses for data pooled across years on good and fair condition Chihuahuan desert ranges at 6 distances from water. (Regression equations are given in Table 2).

dropseed, threeawns, total grasses, poisonous forbs, broom snakeweed, and total poisonous forbs on the good condition range (Tables 1 and 2). However, this association was diminished or lacking for most plant categories on the fair condition range. Regression equations differed between seasons and ranges for the various plant categories with the exception of threeawn on the good condition range in October. Black grama and total grasses on the good condition range showed the highest associations with distance from water. However, black grama were nearly absent from the entire fair condition range, and therefore, showed no association with distance from water.

Perennial Grasses

Our data show that even long term conservative cattle grazing causes a reduction in perennial grass standing crop as distance from water decreases in the zone 1,700 m from water (Fig. 1). This effect is accentuated by heavy grazing intensities. Although it has generally been recognized that livestock grazing reduces desirable forage species around watering points (Lange 1969), actual documentation is restricted to Martin and Ward (1970) in Arizona, Foran and Bastin (1984) in Australia, and Soltero et al. (1989) in Mexico. In the Soltero et al. (1989) study the biomass of grasses in the zone under 600 m from water was reduced about 50 percent compared to the zone 600-1,500 m from water under a short-duration grazing system. Comparisons of distances between 900 and 1,500 m from water showed no differences in grass standing crop. Our study confirms that grazing effects are greatly diminished beyond 1,000 m from water.

Standing crop of the 3 main forage grasses were affected to different degrees by distance from water (Tables 1 an 2). Black grama showed the greatest reduction followed by mesa dropseed and then threeawn. Cattle food habits studies on desert grassland ranges in New Mexico by Rosiere et al. (1975), Hakkila et al. (1987) and Daniel (1991) show black grama to be most preferred followed by mesa dropseed and then threeawn. Black grama is considered to be a decreaser while mesa dropseed and threeawn are considered increasers in terms of grazing response (Soil Conservation Service 1979). Our results confirm this categorization.

Fluffgrass (*Erioneuron pulchellum* [H. B. K.] Tateoka) is the other important perennial grass found on the study area. It receives little grazing use by cattle (Daniel 1991), and showed no definite trend with distance from water (Fusco 1993). It tended to be more prevalent on the BLM compared to College Ranch range. This grass is highly fibrous and lower in nutritional value compared to the other perennial grasses (Nelson et al. 1970).

On the College Ranch range, forage was scarce (under 10 g/m²) in the zones under 500 m from water in the fall and under 900 m from water in the spring. On the BLM range forage was scarce in the zones under 1,700 m from water in the fall and over the entire study area in spring. Based on these data livestock would have to travel over twice as far between forage and water on the BLM compared to the College Ranch range.

Data on the impact of travel distance between feed and water on cattle performance is limited to Sneva et al. (1973) and Hart et al. (1993). On cold desert range in southeastern Oregon Sneva et al. (1973) found cows trailed 1,600 m to water in the spring-summer period had calves that gained less weight than those in pastures with water nearby. In the Shortgrass prairie of Wyoming Hart et al. (1993) found calves gained 20% more on moderately stocked pastures with 1.6 km maximum distance to water compared to a similarly stocked pasture with a 5.0 km maximum distance to water. Data from our study show forage on the BLM range was severely depleted in the zone under 1,700 m from water during the spring (Fusco 1993). In this period cows typically have young calves and are under stress from parturition, lactation and lack of green forage. Failure to adjust stocking rates downward for distance from water could drastically reduce calf

Table 1. Standing crop of plant species and species groups by distance from water, range condition, and month, 1988-1990.

			Distance m						
Plant category	Range condition	Month	50	150	400 (300-500)	800 (700-900)	1300 (1100-1500)	1700	Mean
							standing crop, g/m²		
Black grama	Fair	April	0.00	0.00	0.00	0.00	0.23	0.00	0.04
		October	0.00	0.04	0.03	0.01	0.16	0.04	0.05
	Good	April	0.00	0.13	0.51	2.77	5.48	8.08	2.83
		October	0.00	0.00	2.04	2.57	8.41	12.44	4.24
Mesa dropseed	Fair	April	0.27	0.32	1.36	2.35	1.91	1.59	1.30
		October	0.86	1.05	1.49	4.10	5.11	4.08	2.65
	Good	April	0.86	2.76	1.11	2.76	2.41	3.09	2.17
		October	0.17	1.86	2.57	6.07	5.63	6.59	3.82
Threeawn	Fair	April	0.74	1.41	0.24	0.33	0.74	0.53	0.67
		October	1.04	1.55	0.10	0.96	0.56	1.17	0.90
	Good	April	0.17	2.38	2.37	2.06	5.45	4.74	2.86
		October	0.00	2.07	3.81	2.21	5.25	3.84	2.86
Total perennial grasses	Fair	April	1.01	1.73	1.84	2.88	2.89	2.18	2.10
		October	1.23	2.63	1.91	5.20	6.95	9.54	4.59
	Good	April	1.03	5.44	3.99	7.63	13.71	16.37	8.03
		October	1.48	5.13	8.65	11.14	19.61	24.69	11.78
Palatable forbs	Fair	April	0.04	0.13	0.10	0.16	0.24	0.01	0.11
		October	0.24	0.50	0.89	0.63	0.41	0.21	0.48
	Good	April	0.48	2.21	2.07	1.84	1.56	0.76	1.49
		October	0.50	1.14	2.38	3.34	1.99	1.31	1.78
Poisonous forbs	Fair	April	0.10	0.06	0.15	2.09	0.07	0.03	0.42
		October	1.11	1.42	0.70	0.30	1.11	0.80	0.79
	Good	April	1.32	0.22	0.22	0.39	0.05	0.02	0.37
		October	4.17	3.39	0.13	2.70	0.28	0.31	1.91
Broom snakeweed	Fair	April	9.31	8.59	10.76	8.29	9.53	6.95	8.91
		October	18.11	10.63	15.84	10.69	10.04	9.74	12.51
	Good	April	6.16	2.03	5.83	7.99	4.46	3.55	5.00
		October	8.57	4.52	8.92	7.73	10.63	6.24	7.72
Total poisonous plants	Fair	April	9.41	8.65	10.91	10.38	9.60	6.98	9.32
		October	19.22	12.05	16.54	10.99	11.15	9.82	13.30
	Good	April	7.48	2.25	6.05	8.38	4.51	3.57	5.37
		October	12.74	8.11	9.05	10.43	10.91	6.55	9.63

performance particularly on ranges in fair or poor condition. Holechek (1988) recommends no stocking rate reductions for the zone under 1,600 m from water, a 50% reduction for the zone 1,600 to 3,200 m from water and that the zone over 3,200 m from water be considered ungrazable. These recommendations seem reasonable based on our study.

Research is needed in the Chihuahuan desert to evaluate how travel distance between water and forage affect cow-calf performance particularly in the spring-early summer stress period. It is likely calf performance would be more adversely affected by extended travel to and from water in the Chihuahuan desert than in the cold desert of Oregon. This is because of the higher temperatures and lack of spring green forage in the Chihuahuan desert.

Breed of cattle can affect range use and productivity. Brangus cattle have been superior to Herefords in productivity in the Chihuahuan desert (Winder et al. 1991). This appears to be at least partially explained by more efficient use of the range based on research presently in progress.

Poisonous Plants

Poisonous plant biomass (broom snakeweed excluded) showed a weak tendency to decline as distance from water increased (Tables 1 and 2). This tendency was more pronounced on the good than on the fair condition range. Broom snakeweed accounted for over 75% of the biomass of poisonous plants on both ranges. Other important poisonous forbs included redroot pigweed (*Amaranthus pubescens* [Uline and Bray] RYBO.), silverleaf nightshade (*Solanum triflorum* Nutt.), and desert senna (*Cassia bauhinioides* Gray).

Broom snakeweed standing crop averaged about 50% higher on the BLM range than on the College Ranch range for data pooled across season, years, and distances from water (Fusco 1993). Pieper et al. (1991), on Shortgrass-pinyon juniper range in south-central New Mexico, found higher levels of broom snakeweed under heavy compared to moderately stocked pastures. Early observers reported broom snakeweed to be found around livestock watering installations and other areas of livestock concentration (Jardine and Forsling 1922, Talbot 1926). However Jameson (1970) argued against the use of snakeweed as an indicator of range condition and suggested climatic factors were primarily responsible for snakeweed invasions. Research by McDaniel (1984) indicates that reductions in herbaceous cover by both drought and grazing followed by fall-spring precipitation favors snakeweed.

Over the 3 years of study, we observed no cattle death losses from poisonous plants on either the BLM or College Ranch ranges. We attribute the lack of death loss from poisonous plants

Table 2. Regression equations for predicting standing crop (g/m2), (y) plant species an species groups using distance from water (x) as the independent variable.

Plant category (dependent variable)	Range Condition	Month	Equation	r^2[1]
Black grama	Good	April	$y = -0.82593 + 0.0049831x$	.98
		October	$y = -1.238 + 0.007475x$	.95
	Fair	April	$y = 0.03833$	NS
		October	$y = 0.04667$	NS
Mesa dropseed	Good	April	$y = 2.16444$	NS
		October	$y = 1.150817 + 0.003633x$	0.3113
	Fair	April	$y = -0.043022 + 0.004291x - 0.000001994x^2$	0.3920
		October	$y = 0.639350 + 0.002739x$	0.4265
Threeawn	Good	April	$y = 1.201438 + 0.002266x$	0.3522
		October	$y = 1.201438 + 0.002266x$	0.3522
	Fair	April	$y = 0.66500$	NS
		October	$y = 0.89552$	NS
Total perennial grasses	Good	April	$y = 1.668590 + 0.008667x$	0.5616
		October	$y = 2.276296 + 0.012677x$	0.7443
	Fair	April	$y = 2.0866$	NS
		October	$y = 1.041934 + 0.004819x$	0.6143
Palatable forbs	Good	April	$y = 1.4847$	NS
		October	$y = 0.351329 + 0.005941x - 0.000003254x$	0.3538
	Fair	April	$y = 0.11333$	NS
		October	$y = 0.48000$	NS
Poisonous forbs	Good	April	$y = 0.718720 - 0.000474x$	0.2994
		October	$y = 3.451850 - 0.002097x$	0.3488
	Fair	April	$y = -0.287035 + 0.003343x - 0.000001941x^2$	0.2653
		October	$y = 0.79167$	NS
Broom Snakeweed	Good	April	$y = 1.63915 + 0.011691x - 0.00000645x^2$	0.3510
		October	$y = 7.71778$	NS
	Fair	April	$y = 8.90444$	NS
		October	$y = 12.50889$	NS
Total poisonous forbs	Good	April	$y = 2.573278 + 0.010392x - 0.000005961x^2$	0.2984
		October	$y = 9.63167$	NS
	Fair	April	$y = 9.32056$	NS
		October	$y = 13.295$	NS

[1] NS = Non-significant at $P < 0.05$.

to the conservative stocking rates presently used on the 2 ranges (30-35% use of perennial grasses). Annual death losses on Chihuahuan desert ranches average about 4% but on the conservatively stocked College Ranch pastures, annual death losses have been under 1% for the last 25 years (Holechek 1992). On the adjacent Jornada Experimental Range, Paulsen and Ares (1962) reported cattle death losses averaged 1.74% between 1939 and 1951 on conservatively stocked pastures. With the possible exceptions of larkspur (*Delphinium* sp.) and loco (*Astragalus* sp) elevated death losses of livestock (over 2% annually) from poisonous plants appears to be primarily a stocking rate problem. Long term stocking rate studies by Hutchings and Stewart (1953) in the salt desert of Utah, Klipple and Costello (1960) in the Shortgrass prairie of Colorado, and Taylor and Ralphs (1992) on chaparral range in Texas show heavy stocking rates greatly elevated livestock death losses compared to moderate stocking rates. During a three year study involving 400 head of cattle on several pastures on mountain range in northeastern Oregon, Holechek (1980) noted a death loss of only one animal, and it was not certain the animal died from poisonous plant consumption. These ranges were in high ecological condition and all pastures were conservatively stocked. Annual death losses on the Fort Stanton Experimental range in southcentral New Mexico have been under 2% over the last 20 years.

Wildlife Plants

Russian Thistle, redroot pigweed and broom snakeweed are primary foods for scaled quail, an important gamebird on the study area (Schemnitz 1961, Davis et al. 1975). Redroot pigweed is a key food plant for mourning doves in the Chihuahuan desert (Davis and Anderson 1973). Russian thistle and redroot pigweed were more prevalent crop in the zone under 500 m from water compared to the zones farther away (Fusco 1993). Highest numbers of mourning doves occur around degraded watering points where redroot pigweed is prevalent (Holechek and Saiwana 1991). Both scaled quail and mourning doves are important gamebirds in southcentral New Mexico and considerable money is spent in hunting related activities involving them. The development of watering points for livestock and the associated vegetation changes around these areas appears to benefit both scaled quail and mourning doves (Holechek and Saiwana 1991). Research is in progress to evaluate how watering points influence pronghorn foods and range use.

Management Implications

Our study shows that long term conservative continuous cattle grazing on upland sandy sites in the Chihuahuan desert severely reduces the biomass of perennial forage grasses in the zone less than 1,000 m from water. This effect is accentuated by heavier grazing intensities. Poisonous plants and annual forbs dominate the zone under 500 m from water. Many of these plants are reported to be important foods for scaled quail and mourning doves which are the two primary upland gamebirds in New Mexico. Therefore, from a multiple use standpoint, the vegetation changes caused by conservative livestock grazing around watering points may have some advantages.

Two practical approaches are available to minimize degradation and enhance productivity of perennial grasses around desert watering points. These involve adjustment of stocking rate for distance from water and rotation of access to watering points. So far there has been a reluctance by both public and private land managers to adopt these practices on Chihuahuan desert ranges.

Reducing stocking rate when distances exceed 1,600 m from water has long been advocated by range researchers (Valentine 1947). This appears to have benefits for both vegetation (Holechek and Pieper 1992) and livestock (Sneva et al. 1973, Hart et al. 1993). For cattle Holechek (1988) suggested no reduction for the zone under 1,600 m from water, a 50% reduction for the zone 1,600 to 3,200 m from water and that the zone over 3,200 m from water be considered ungrazable.

Our research supports this recommendation. However we believe that information on the influence of travel distance between feed and water on cow-calf and yearling cattle performance in the Chihuahuan desert would be useful in regard to possible refinements.

On Arizona semidesert ranges, Martin and Ward (1970) found regulating access to watering points could be an effective means of increasing perennial grass production, with little extra cost for labor or fence. Compared to continuous grazing, rotating access to watering points nearly doubled the yield of perennial grasses over an eight year period. Most of the improvement occurred within 300 m of the watering points. This approach appears to be sound for Chihuahuan desert ranges in New Mexico.

No livestock losses to poisonous plants were noted on either range in our study over the 3 year period of investigation. Poisonous plants accounted for over half the standing crop on the Bureau of Land Management range. The conservative stocking rate presently applied to this range during the period of study appears to explain the lack of poisonous plant death losses. Studies from other range types (Klipple and Costello 1960, Taylor and Ralphs 1992) indicate livestock losses to poisonous plants are more a function of stocking rate than range condition.

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Effects of buffer additions on fermentation of dormant range grasses

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Abstract

Replicated two-stage in vitro studies were conducted to determine the effects of single amino acid or branched-chain volatile fatty acid buffer additions on in vitro dry matter disappearance, neutral detergent fiber disappearance, and fermentation kinetics of dormant range grasses. Substrates consisted of separate samples of 2 cool season mid-grasses, western wheatgrass (*Agropyron smithii* Rydb.) and Japanese brome (*Bromus japonicus* Thunb.), and a mixture of warm season shortgrasses, buffalograss (*Bunchloe dactyloids* [Nutt.] *Engelm.*), and blue grama (*Bouteloua gracilis* [H.B.K.] Lag. ex Steud.), hand clipped from standing forage in mid-March. Isonitrogenous treatments included buffer containing urea with or without amino acids, branched-chain volatile fatty acids, sodium sulfate, or starch. Urea increased ($P<0.05$) in vitro dry matter disappearance and in vitro neutral detergent fiber disappearance of the cool season grasses over N free buffer. Methionine addition increased ($P<0.05$) in vitro neutral detergent fiber disappearance and rate of fermentation of both cool season grasses and in vitro dry matter disappearance of Japanese brome over urea alone. Sodium sulfate increased ($P<0.05$) in vitro neutral detergent fiber disappearance of Japanese brome compared to urea alone. None of the branched-chain volatile fatty acids tested increased dry matter disappearance, neutral detergent fiber disappearance, or rate of fermentation of the dormant range grasses. Addition of urea or amino acids did not increase in vitro dry matter disappearance or in vitro neutral detergent fiber disappearance of the shortgrass mixture. In vitro screening of amino acid and branched-chain volatile fatty acid buffer additions to dormant range grasses showed that methionine supplementation with urea offers the greatest potential, among the supplements evaluated, for improving digestibility and rate of fermentation of cool season grasses. None of the buffer supplements improved fermentation of the warm season grasses.

Key Words: gas production, fiber disappearance, urea, sulfur, starch

Urea based protein supplements typically limit performance of ruminants consuming mature low protein forages in comparison to animals fed oilseed meal supplements (Williams et al. 1969; Rush and Totusek 1976; Clanton 1978). Identification of constituents contained in natural protein supplements that benefit ruminal fermentation and ultimately enhance animal performance could lead to more effective nitrogen supplementation. Inclusion of amino acids (Maeng et al. 1976; Clark and Peterson 1985), branched-chain volatile fatty acids (Soofi et al. 1982; Mir et al. 1986), or minerals (Spears et al. 1976; Slyter et al. 1988) with urea have been shown to increase substrate digestibility and (or) rate of fermentation in vitro. The response to a given addition was not consistent for all fiber sources in those studies. The objective of this study was to screen amino acids and branched-chain volatile fatty acids as potential urea-grain supplement additions which would serve to increase forage utilization by cattle consuming dormant range grasses.

Materials and Methods

Three trials (replicated twice) utilizing two-stage in vitro fermentations (Tilleys and Terry 1963, as modified by Martin and Barnes 1980) were conducted for each of 2 cool season mid-grasses, western wheatgrass (*Agropyron smithii* Rydb.) and Japanese brome (*Bromus japonicus* Thunb.), and a mixture of warm season shortgrasses, buffalograss (*Buchloe dactyloids* [Nutt.] Engelm.) and blue grama (*Bouteloua gracilis* [H.B.K.] Lag. ex Steud.). In mid-March, grass samples were hand clipped from dormant standing vegetation pastures located at the South Dakota State University Range and Livestock Research Station near Cottonwood, S.D. Grass was clipped approximately 1 to 3 cm above ground level. oven dried at 60° C, ground through a Wiley mill (1 mm screen), and stored until used in the in vitro fermentations. Inoculum was obtained from ruminally fistulated cows provided ad libitum access to a mature prairie hay composed of 63% western wheatgrass, 35% Japanese brome, and 2% unidentified forage (sd = 10, 11, and 3% respectively) as determined by sorting 15 random subsamples. Analytical composition of the grass samples used as substrate and the prairie hay fed to fistulated cows are listed in Table 1.

Each of the 3 trials (western wheatgrass, Japanese brome, and shortgrasses) consisted of 2 individual 48 hour incubations (run). Nested within trial were isonitrogenous (50 mg supplemental N/deciliter buffer) treatments (Table 2) consisting of the following buffer additions: 1) urea, 2) to 6) urea and amino acid (argi-

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Table 1. Chemical composition of dormant range grasses and prairie grass hay[a]

Item	Western wheatgrass	Japanese brome	Shortgrass mixture	Grass hay
Dry matter, %	96.4	93.5	93.5	91.5
Crude protein, %	2.8	3.0	4.1	5.9
Ash %	8.7	6.8	15.2	10.2
Calicum, %	.33	.24	.47	.40
Phosphorus, %	.05	.04	.06	.11
Sulfur, %	.07	.05	.07	.10
Neutral detergent fiber, %	69.9	68.7	65.1	63.9
Acid detergent fiber, %	43.6	50.6	35.9	33.7
Lignin, %	2.7	2.0	3.2	2.4
Acid insoluble silica, %	7.02	5.44	12.06	5.7

[a]Dry matter basis.

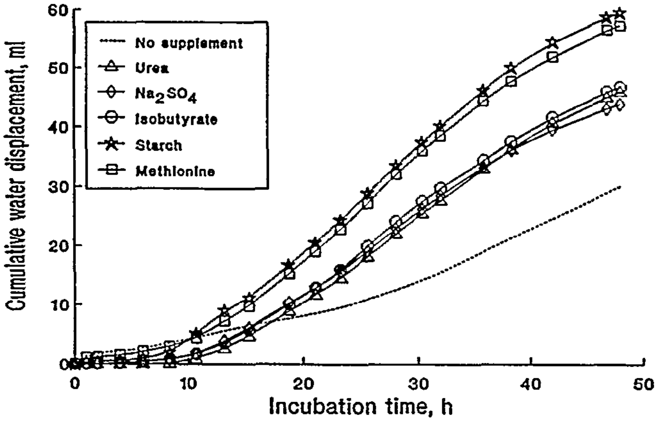

Fig. 1. Cumulative water displacement during 48 hour in vitro fermenttion of WWG with grass alone (no additions), urea alone, and urea plus Na_2SO_4, isobutyrate, starch, or methionine addition to the buffer solution.

nine, histidine, isoleucine, leucine, or methionine), 7) to 9) urea and branched-chain volatile fatty acid (isobutyric, isovaleric, or 2-methyl butyric), 10) urea and sodium sulfate (isosulfer to methionine, 28.56 mg sulfur/deciliter buffer), and 11) urea and corn starch (starch equal weight to methionine). Selection of amino acids and branched-chain volatile fatty acids was based on results from previous trials (Maeng et al. 1976; Clark and Peterson 1985) which indicated that these buffer additions may limit in vitro fermentation. Amino acid and branched-chain volatile fatty acid additions were isomolar (.88 mmol/deciliter buffer), amino acids provided approximately 25% of supplemental N/tube. Arginine and histidine could not be simultaneously isomolar and isonitrogenous, and therefore N levels for these treatments were higher.

Triplicate samples of western wheatgrass, Japanese brome, and shortgrasses (both with and without urea included in the buffer) and blank tubes containing ruminal fluid and N free buffer accompanied all 6 runs for the 3 trials. Ruminal fluid was collected at approximately 1000 each day, transported to the laboratory in a thermos at 39° C, and strained through 6 layers of cheese cloth. For each treatment, triplicate samples (.5g) of grass were placed in 50-ml polypropylene centrifuge tubes. Following addition of the buffer with supplements (25 ml/tube) and rumen fluid (5 ml/ tube), tubes were flushed with CO_2 capped with a rubber stopper, and incubated at 39° C. Polyethylene tubing passed through the stoppers allowed gas produced during fermentation to be vented from the in vitro tube into a 125-ml Erlenmeyer flask where water was displaced by gas pressure through a second tube into a 10-ml graduated cylinder. Cumulative water displacement was recorded at 2 to 4 hour intervals over the 48 hour first stage fermentation period. Neutral detergent fiber analysis (Goering and Van Soest 1970) was conducted on grass samples and residues from the pepsin digestion to determine fiber disappearances.

Two separate analyses were conducted for this study. For the first analysis, effects of urea buffer addition on dry matter and neutral detergent fiber disappearances of the range grasses were analyzed as a two-way classification by least squares procedure using General Linear Models (GLM) of the Statistical Analysis System (SAS 1985). Supplement (Buffer alone or buffer with urea), range grasses, and their interaction were included in the model. Separation of the 6 subclass least squares means was accomplished by least significant difference. Gas production curves for incubations without added urea were linear and not included in analyses for determination of rate kinetics. Cumulative gas production curves for incubations with added urea were sigmoidal (Fig. 1). Nonlinear iterative least squares regression procedures (SAS 1981) were used to generate estimated rate kinetics (lag time, hour; rate of gas production, ml of H_2O displaced/hour; and time of maximum gas production, hour; Fig. 2) as explained by Dybing et al. (1988). In a second set of analy-

Table 2. Buffer supplements for in vitro fermentation of dormant range grasses.

Buffer supplement[a]	Treatment 1	2	3	4	5	6	7	8	9	10	11
Urea	106.4	106.4	100.0	100.0	100.0	100.0	100.0	106.4	106.4	106.4	106.4
L-arginine		155.6	—	—	—	—	—	—	—	—	—
L-histidine			138.4	—	—	—	—	—	—	—	—
L-isoleucine				117.2	—	—	—	—	—	—	—
L-leucine					117.2	—	—	—	—	—	—
L-methionine						133.2	—	—	—	—	—
Isobutyric							78.8	—	—	—	—
Isovaleric								91.2	—	—	—
2-methyl-butyric									91.2	—	—
Na_2SO_4										126.8	—
Starch											133.2

[a]mg/dl buffer.

Table 3. Effects of urea addition on in vitro dry matter and neutral detergent fiber disappearance of dormant range grasses

Item	Western wheatgrass	Japanese brome	Shortgrass mixture	SEM
Dry matter disappearance, %[1]				
Without urea	39.4^{a}	42.1^{b}	42.7^{b}	.84
With urea	49.6^{d}	59.5^{c}	43.1^{b}	.84
Neutral detergent fiber disappearance, %[1]				
Without urea	49.5^{a}	50.1^{a}	60.7^{b}	.83
With urea	62.3^{b}	69.9^{c}	61.6^{b}	.83

[1] Grass species x urea supplementation interaction ($P<0.05$)

^{a,b,c,d}Values within item lacking a common superscript letter differ ($P<0.05$).

ses, effects of buffer additions on dry matter and neutral detergent fiber disappearances and rate kinetics were analyzed separately for each range grass type by least squares procedures using GLM of SAS with supplement and run as independent variables. Treatment effects were tested using supplement x run as the error term. When a significant F value was indicated, supplement mean separation was accomplished by the Waller-Duncan test (SAS 1985).

Results and Discussion

Interactions occurred ($P<0.05$) between the effect of urea addition to the buffer and grass species for in vitro dry matter disappearance and in vitro neutral detergent fiber disappearance. The shortgrasses had higher ($P<0.05$) in vitro dry matter disappearance and in vitro neutral detergent fiber disappearance than western wheatgrass when no urea was added to the buffer (Table 3). Urea addition increased ($P<0.05$) in vitro dry matter disappearance of western wheatgrass and Japanese brome 10.2 and 17.4 percentage units over their respective counterparts with N free buffer. Values for in vitro neutral detergent fiber disappearance reflected those increases in in vitro dry matter disappearance when urea was added. Japanese brome had higher ($P<0.05$) in vitro dry matter disappearance and in vitro neutral detergent fiber disappearance than either western wheatgrass or shortgrasses when urea was added. Urea buffer addition did not improve shortgrass in vitro dry matter disappearance or in vitro neutral detergent fiber disappearance over buffer alone.

Composition differences between the cool and warm season grasses may explain the differing effects of urea addition on grass digestibility. The shortgrasses had higher crude protein content and lower fiber levels than either of the cool season grasses. Stern et al. (1978) suggested that carbohydrate availability was a major factor affecting NH_3-N utilization by rumen microbes. Assuming that a portion of the neutral detergent fiber content is available for cellulolytic digestion, then the ratio of crude protein to available carbohydrate would be higher and NH_3 would be less limiting for shortgrasses than for the warm season grasses. Lignin and ash content were higher in shortgrasses. The ash content, primarily silica, and lignin may have an additive effect in blocking further cell was digestion (Van Soest and Jones 1968) and limiting extent of final digestion (Mertens 1977) of the warm season grasses.

Cumulative gas production curves for incubations containing added urea were similar to typical cumulative cell wall digestion curves reported by Mertens (1977). Gas production was linear for incubations containing grass samples without urea addition and resulted in lower 48-hour total gas production. Gas production of nearly 0 was recorded for incubations containing buffers and rumen fluid without forage. In general, fermentation lag times were shorter than dry matter and neutral detergent fiber disappearance lag times determined by Clark and Petersen (1985). The mathematical model used to determine lag periods may influence calculated lag phases (Nocek and English 1986). Nonlinear iterative least squares regression tends to underestimate lag phase compared to logarithmic transformations when degradation of a single fraction (e.g., neutral detergent fiber) of the substrate is concerned (Mertens and Loften 1980; Nocek and English 1986). In vitro cumulative gas production incorporates disappearance of both soluble fractions and the less degradable components of the substrate and may result in shorter predicted lag phases.

In vitro dry matter disappearance of western wheatgrass was not increased by buffer additions over urea alone and was decreased ($P<0.05$) by arginine (Table 4). Methionine addition increased ($P<0.05$) in vitro detergent fiber disappearance of western wheatgrass over urea alone. Lag time and time to maximum fermentation for western wheatgrass were not changed over urea alone with the addition of amino acids, branched-chain volatile fatty acids, or Na_2SO_4. Starch addition did reduce lag time and time to maximum fermentation. Fermentation rate of western wheatgrass was increased ($P<0.05$) by methionine or starch and was decreased ($P<0.05$) by arginine compared to urea alone. Since starch addition did not affect in vitro dry matter disappearance or in vitro neutral detergent fiber disappearance, changes in rate and time of maximum fermentation are probably due only to starch fermentation.

Methionine increased ($P<0.05$) in vitro dry matter disappearance, and Na_2SO_4 or methionine increase ($P<0.05$) in vitro neutral detergent fiber disappearance of Japanese brome over urea alone (Table 5). Histidine or leucine decreased ($P<0.05$) in vitro dry matter disappearance and leucine decreased ($P<0.05$) in vitro neutral detergent fiber disappearance of Japanese brome over

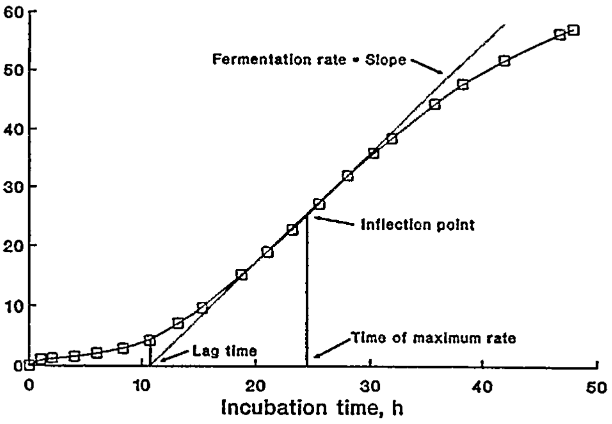

Fig. 2. Cumulative water displacement during 48 hour in vitro fermentation of WWG with methionine addition to the buffer solution. The slope of the iterative least squares regression line is equal to the rate of gas production during the growth phase. The value of x at the inflection point reflects time of maximum fermentation rate. The point at which the x axis is intersected by the least squares regression line is equal to duration of the lag phase.

Table 4. Effects of in vitro buffer supplements on digestibility of western wheatgrass

Addition	Dry matter disappearance	Neutral detergent fiber diasppearance	Lag time	Fermentation rate	Time of maximum rate
	(%)	(%)	(hour)	(ml $H^{2}0$/ hour)	(hour)
Urea	49.0^{a}	60.4^{ab}	16.9^{a}	1.70^{bcde}	30.6^{ab}
Amino acids					
Arginine	45.5^{b}	62.9^{bc}	16.6^{ab}	1.54^{def}	31.2^{a}
Histidine	48.0^{ab}	61.8^{abc}	14.9^{abc}	1.88^{abc}	28.9^{abc}
Isoleucine	48.6^{a}	61.6^{abc}	15.3^{abc}	1.77^{abcd}	28.7^{bc}
Leucine	47.9^{ab}	63.2^{bc}	16.2^{ab}	1.77^{abcd}	30.1^{abc}
Methionine	49.8^{a}	64.6^{c}	15.3^{abc}	1.92^{a}	29.8^{abc}
Branched-chain volatile fatty acids					
Isobutyric acid	49.4^{a}	61.2^{abc}	16.6^{ab}	1.68^{cde}	29.8^{abc}
Isovaleric acid	47.1^{ab}	62.7^{bc}	15.9^{ab}	1.43^{f}	29.3^{abc}
2-methylbutyric acid	48.3^{ab}	62.7^{bc}	15.9^{ab}	1.43^{f}	29.3^{abc}
Na_2SO_4	48.6^{a}	60.5^{a}	16.6^{ab}	1.50^{ef}	30.4^{abc}
Starch	47.6^{ab}	62.8^{bc}	13.4^{c}	1.94^{a}	28.1^{c}
SEM (n-2)	1.1	1.2	0.67	0.077	0.74

^{a,b,c,d,e}Values within a column lacking a comon superscript letter differ ($P<0.05$).

Table 5. Effects of in vitro buffer supplements on digestibility of Japanese brome

Addition	Dry matter disappearance	Neutral detergent fiber diasppearance	Lag time	Fermentation rate	Time of maximum rate
	(%)	(%)	(hour)	(ml $H^{2}0$/ hour)	(hour)
Urea	58.1^{bc}	68.8^{cde}	15.7^{ab}	1.81^{a}	31.4^{a}
Amino acids					
Arginine	56.4^{cd}	68.2^{def}	13.5^{abc}	1.82^{a}	31.0^{ab}
Histidine	54.4^{de}	67.2^{ef}	12.1^{c}	1.93^{ab}	29.3^{bc}
Isoleucine	59.0^{bc}	71.4^{abc}	13.3^{bc}	2.05^{b}	29.5^{bc}
Leucine	52.7^{e}	65.6^{f}	14.4^{abc}	1.71^{a}	32.1^{a}
Methionine	63.0^{a}	74.0^{a}	14.2^{abc}	2.81^{d}	26.9^{d}
Branched-chain volatile fatty acids					
Isobutyric acid	58.9^{bc}	69.8b^{cde}	15.7^{ab}	1.84^{ab}	30.9^{ab}
Isovaleric acid	55.8^{cde}	69.2^{cde}	13.5^{abc}	1.81^{a}	30.4^{abc}
2-methylbutyric acid	57.2^{bcd}	70.0^{bcde}	13.5^{abc}	1.77^{a}	29.7^{bc}
Na_2SO_4	60.4^{ab}	72.55^{ab}	16.1^{a}	1.90^{ab}	30.6^{abc}
Starch	57.5^{bcd}	70.6^{bcd}	12.1^{c}	2.29^{c}	29.0^{c}
SEM (n-2)	1.3	1.1	0.78	0.079	0.58

^{a,b,c,d,e}Values within a column lacking a comon superscript letter differ ($P<0.05$).

urea addition. Fermentation lag time for Japanese brome was decreased ($P<0.05$) by histidine, isoleucine, or starch. Time to maximum fermentation rate was decreased ($P<0.05$) by histidine, isoleucine, methionine, 2-methylbutyric acid, or starch compared to urea. Isoleucine, methionine, or starch increased fermentation rate of Japanese brome over urea.

Amino acid, branched-chain volatile fatty acid, Na_2SO_4, or starch additions did not affect in vitro dry matter disappearance or in vitro neutral detergent fiber disappearance of shortgrasses over urea (Table 6). methionine increased ($P<0.05$) shortgrass lag time. Arginine, leucine, or methionine increased ($P<0.05$) and starch decreased ($P<0.05$) time to maximum fermentation rate of shortgrasses. Fermentation rate of shortgrasses was increased ($P<0.05$) by histidine and starch over urea alone.

Fermentation rates and neutral detergent fiber disappearance of cool season grasses were increased with the addition methionine, These results were not observed with shortgrasses. As suggested previously, there appears to be very distinct digestible fiber and indigestible fiber/lignin/ash fractions in the shortgrasses. The higher lignin and silica content of shortgrasses has been associated with slower in vitro fermentation rates and extent of fiber digestibility (Smith et al. 1971; Van Soest and Jones 1968). The smaller digestible fiber fraction in combination with the relatively higher crude protein content of shortgrasses may have been the reason that no responses to urea, amino acid, or branched-chain volatile fatty acid buffer additions were observed with the warm season grasses. Clark and Petersen (1985) found that in vitro dry matter and neutral detergent fiber fermentation rates of dormant range forage were increased by methionine but saw no improvement in 48-hour forage disappearance. Methionine supplementation of cattle consuming mature cool season grasses has been shown to increase neutral detergent fiber and dry matter disappearance rates (Lodman et al. 1990; Wiley et al. 1991).

The addition of Na_2SO_4 with urea did not elicit the fermentation responses which were observed with methionine in this study. Clark and Petersen (1988) reported an increase in dry matter fermentation rate for heifers fed methionine compared to ammonium sulfate but found no differences in dry matter ruminal digestibility. The degree to which methionine is used as an intact amino acid versus being degraded and used as a sulfur source by cellulolytic microbes in the rumen remains unclear. Numerous researchers (Hunt et al. 1954; Gil et al. 1973 Spears et al. 1976) have demonstrated that methionine when used as a sulfur source increases cellulose digestion. Maeng et al. (1976) suggested that sulfur amino acids were utilized intact and improved in vitro microbial cell yields with cellobiose as the substrate. Gawthorne and Nader (1976) determined that only 50% of the sulfur amino acid content of microbial protein was derived from the sulfite pool with the remainder from direct amino acid incorporation into the microbes. Salter et al. (1979) found that microbial incorpora-

Table 6. Effects of in vitro buffer supplements on digestibility of shortgrass mixture

Addition	Dry matter disappearance	Neutral detergent fiber diasppearance	Lag time	Fermentation rate	Time of maximum rate
	(%)	(%)	(hour)	(ml $H^{2}0$/ hour)	(hour)
Urea	43.8^{a}	64.1^{a}	9.3^{abc}	1.13^{ab}	22.4^{b}
Amino acids					
Arginine	41.0^{bc}	63.6^{a}	9.6^{abc}	1.10^{a}	25.3^{cde}
Histidine	43.6^{abc}	63.9^{a}	8.9^{ab}	1.41^{cd}	22.4^{ab}
Isoleucine	44.0^{ab}	64.5^{a}	10.4^{abcd}	1.22^{abc}	24.0^{bcd}
Leucine	44.1^{a}	65.2^{a}	11.5^{cd}	1.33^{bcd}	25.2^{cde}
Methionine	42.8^{abc}	63.8^{a}	12.3^{d}	1.32^{bc}	26.5^{de}
Branched-chain volatile fatty acids					
Isobutyric acid	43.3^{abc}	64.7^{a}	10.6^{bcd}	1.26^{abc}	23.1^{abc}
Isovaleric acid	42.9^{abc}	64.5^{a}	10.2^{abcd}	1.16^{ab}	23.4^{abc}
2-methylbutyric acid	44.2^{a}	64.3^{a}	9.2^{abc}	1.11^{a}	22.3^{ab}
Na_2SO_4	41.7^{abc}	62.6^{a}	10.5^{abcd}	1.05^{a}	22.5^{ab}
Starch	42.7^{abc}	64.1^{a}	7.9^{a}	1.53^{d}	21.1^{a}
SEM (n=2)	1.1	1.0	0.82	0.072	0.83

^{a,b,c,d}Values within a column lacking a common superscript letter differ ($P<0.05$)

tion of methionine decreased when urea was the primary N source compared to a natural protein N source. While methionine is degraded more slowly than other amino acids in vivo, free amino acids exist in rumen fluid only in low concentrations (Scheifinger et al. 1976). In addition, during normal microbial turnover of a mixed rumen population, microbes that synthesize methionine from sulfite may provide methionine to microbes that utilize or degrade methionine. Scheifinger et al. (1976) determined that the group of cellulolytic bacteria *Butyrivibrio* cause a net degradation of methionine.

In vitro sulfur addition in combination with urea has long been known to increases microbial NH_3 fixation (Hunt et al. 1954) and enhance cellulose digestion (Barton et al. 1971). Sulfate is reduced to sulfite in rumen fluid and incorporated into microbial protein as sulfur containing amino acids (Mathers and Miller 1980). While Na_2SO_4 did increase in vitro neutral detergent fiber disappearance of Japanese brome in this study, improvements in extent or rate of forage digestibility for sulfur additions over urea alone were not observed. In this trial, sulfur was provided at 28.56 mg/deciliter buffer in order to be isosulfur to the methionine treatment. Kahlon et al. (1975) determined that 4.33 mg S/deciliter inoculum were near optimum for microbial protein synthesis, while levels above 10.0 mg S/ deciliter were inhibitory using a starch substrate. Although Fron et al. (1990) suggested that Na_2SO_4 had equal sulfur biological value as DL-methionine in cattle, Johnson et al. (1970) suggested that Na_2SO_4 was a more volatile sulfur source in the rumen than either methionine or elemental sulfur and would be less available for slowly degraded mature forages.

Branched-chain volatile fatty acids did not affect dry matter or fiber disappearance or improve fermentation kinetics of the dormant range grasses used in this study. Mir et al. (1986) found that these 3 branched-chain volatile fatty acids, when added alone or in combination, increased in vitro dry matter disappearance of barley straw. In agreement with out results, these same branched-chain volatile fatty acids had no effect on rate or extent of in vitro dry matter disappearance or in vitro neutral detergent fiber disappearance of dormant range forages collected via esophageal fistula in a study reported by Clark and Petersen (1985). Similarly, McCollum et al. (1987) determined that 4- and 5-carbon volatile fatty acids were not limiting in vivo cellulolytic activity in the rumen of cattle fed mature low protein prairie hay.

In vitro screening of amino acid and branched-chain volatile fatty acid buffer supplements with dormant range grasses showed that methionine offered the greatest potenial for improving digestibility and rate of fermentation of mature cool season grasses. Response of supplements appears to be forage specific. From this study, it can not be determined whether these improvements were due to intact methionine or highly available sulfur from methionine. Neither urea nor any of the amendments tested improved fermentation of the warm season grasses.

Conclusions

These in vitro results indicate a relative ranking of individual amino acid or branched-chain volatile fatty acid additions with regard to their potential for improving utilization of urea supplements for ruminants consuming mature low protein forages. While responses observed with in vitro ruminal fermentations may not always occur in vivo, screening a number of treatments for their effect on a given ruminal response is useful in deriving in vivo treatments. In this study, methionine would appear to offer some benefit for improving utilization of urea based supplements to dormant cool season forage.

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Water budget for south Texas rangelands

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Abstract

Understanding hydrologic processes is essential to determine if water yield augmentation is possible through vegetation manipulation. Nine large non-weighing lysimeters, each 35 m^2, were installed on the La Copita Research Area, 20 km south of Alice, in the eastern Rio Grande Plain of Texas. The non-weighing lysimeters were used to test the hypothesis that honey mesquite (*Prosopis glandulosa var glandulosa* Torr.) shrub clusters have greater evapotranspiration rates than grass interspaces. Annual evapotranspiration rates of shrub clusters and grass interspaces were found to be similar, and both were significantly greater than evaporative losses from bare soil. Surface runoff and deep drainage of water (> 2 m) from the bare soil were significantly greater than from the grass interspaces and shrub clusters. There was no drainage of water below 2 m from the shrub clusters. A total of 22 mm of water percolated below 2 m from the grass interspace during the 18 month study period. These results indicate that no net change in the water budget would occur if shrub clusters were replaced with grasses in years with below average or normal rainfall. Increasing water yield from converting shrub-dominated rangelands to grass-dominated rangelands in south Texas is marginal in this area and limited to years when winter and spring rainfall exceeds potential evapotranspiration. There is little evidence to suggest that the minimal (non-significant difference) increase in percolation and surface runoff from the grass interspaces could be reliably captured and dependably made available off-site.

Key Words: Evapotranspiration, runoff, soil water, drainage, lysimeter, water yield.

Controlling honey mesquite (*Prosopis glandulosa var glandulosa* Torr.) has traditionally been related to increased forage production (Scifres and Polk 1974, Brock et al. 1978, Bedunah and Sosebee 1984, Heitschmidt et al. 1986). Recently it has been suggested that an additional benefit of controlling honey mesquite would be increased water yield (Griffin and McCarl 1989). Investigations began several decades ago into the relationships among plants, soil water and land use on rangelands. A simple water balance model to express the total potential water yield that could be harvested from rangeland watersheds, ignoring, runon can be expressed as:

$$\text{Water yield} = \text{PPT} - \text{EY} \pm \text{S} \qquad (1)$$

where water yield includes surface and subsurface flow, and any percolation to groundwater; PPT is precipitation; ET is evapotranspiration; and S is the change in water stored in the soil profile or regolith (Hibbert 1979). If evapotranspiration can be reduced by altering vegetation, water yield will increase, the magnitude of which depends on the change in stored soil water.

Numerous studies have evaluated the water budget of forest and scrub woodlands, and excellent reviews of the literature are provided by Bosch and Hewlett (1982) and Hibbert (1983). Relatively few studies have evaluated components of the water budget for mesquite-dominated rangelands (Richardson et al. 1979, Carlson et al. 1990). Rechenthin and Smith (1964) estimated that a comprehensive vegetation manipulation program could save 12,000 million m^3 of water in the Rio Grande Plains of Texas. The estimate was based on research conducted primarily in Arizona and California. They assumed that removal of woody plants would reduce evapotranspiration, increase soil water content and forage production, and significantly increase water yield. There is little data available from south Texas rangelands to support or refute this estimate.

Walter (1971) proposed a 2-layer soil-water system to explain water use and the stability of savannahs. He proposed that herbaceous vegetation was a superior competitor for water in the topsoil and that woody plants had exclusive access to subsoil water. Knoop and Walker (1985) evaluated 2 savannah communities in South Africa to test this hypothesis. In an Acacia community with 7 fold more herbaceous biomass, mature woody-plant growth was reduced from competition with herbaceous vegetation. Their soil water and root distribution data indicated that herbaceous vegetation utilization of water in the topsoil was sufficient to reduce drainage into the subsoil. Herbaceous vegetation also withdrew water directly from the subsoil in direct competition with woody plants.

Heitschmidt and Dowhower (1991) and Carlson et al. (1990) evaluated the effect of removal of honey mesquite in Texas on herbage response and water balance. They reported that annual above-ground net primary productivity increased significantly following removal of honey mesquite. The increase was the result of increased production of the species present at the time of control rather than a shift in species composition. Evapotranspiration accounted for 95% of rainfall from both sites. They reported no

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net change in evapotranspiration, runoff, or drainage associated with removal of honey mesquite. Increased annual above-ground net primary productivity of the treated site offset any water yield benefit that accrued through removal of honey mesquite trees. Dugas and Mayeux (1991) reported that both percentage and absolute difference in evapotranspiration between treated and untreated mesquite dominated rangelands were greatest under dry conditions and were essentially zero immediately after rainfall. While mesquite used substantial amounts of water, evapotranspiration from rangelands with mesquite that was killed was essentially the same due to the increased annual above-ground net primary productivity of other species following mesquite control.

Two honey mesquite-dominated watersheds were evaluated in the Blackland Prairie region of Texas. Mesquite trees on 1 watershed were killed by hand application of 1 liter of diesel oil to the base of each tree. Removal of mesquite trees reduced evapotranspiration by 244 mm over a 3-year period and increased surface water runoff by 10% compared to an untreated watershed. Removal of honey mesquite had minimal effect on soil water in the surface soil profile during the growing season. The mesquite-dominated community used considerably more water from the subsurface than did the herbaceous vegetation (Richardson et al. 1979).

The effect of shrub communities on components of the water budget of western rangelands is not fully understood, and is poorly understood on mesquite-dominated rangelands in south Texas. The objectives of this study were to: (1) quantify the components of the water budget; and (2) evaluate the seasonal water use by mesquite-dominated shrub clusters, grass interspaces, and bare soil in south Texas.

Study Area and Climate

The research area is located in Jim Wells County approximately 20 km south of Alice, Tex., on the Texas Agricultural Experiment Station, La Copita Research Area. Mean elevation of the 1,093 ha research area is 76 m above sea level. Normal rainfall for the site is 704 mm, of which 493 mm (70%) usually falls from April through September. Average annual snowfall is less than 5 mm. Convection-type storms of high intensity occur about 30 days a year primarily during the summer months (Orton 1969, and Minzenmayer 1979). Mean annual temperature is 22.4° C and the mean frost free period is 289 days (Minzenmayer, 1979).

The research site is located on a Delfina fine sandy loam (1-3%)-Miguel fine sandy loam (1-3%) soil complex, and is classified as a sandy loam range site. The soil closely resembles a Miguel fine sandy loam soil. The Miguel soil series is classified as a fine, mixed, hyperthermic, Udic Paleustalf. The Miguel soil series is in hydrologic group D.

The Rio Grande Plains of southern Texas have been classified as a Prosopis-Acacia- Andropogon-Setaria savannah (Kuchler 1964). The potential plant community is an open grassland with 90% of the area's cover composed of grasses and 10% of forbs and woody shrubs (Minzenmayer 1979). Presently, the landscape is comprised of a matrix of shrub clusters and grass interspaces with 40% of the area occupied by shrub clusters. Shrub clusters range in size and complexity from a single mesquite tree with an average canopy area of 1.7 m^2 to dense shrub clusters with up to 15 woody species and an average canopy area of 56 m^2. Species that commonly occur within the shrub clusters are honey mesquite, brasil (*Condalia hookeri* Hook), spiny hackberry (*Celtis pallida* Torr.), lime prickly ash (*Zanthoxylum fagara* (L.) Sarg.), Agarito (*Berberis trifoliota* Moric.), Texas persimmon (*Diospyros texana* Scheele), Texas colubrina (*Colubrina texensis* (T. & G.) Gray), and wolfberry (*Lycium berlandieri* Dunal.). Many of the more productive grasses such as thin paspalum (*Paspalum setaceum* Michx.), root bristlegrass (*Setaria geniculata* (Lam.) Beauv.), and windmillgrass (*Chloris verticillata* Nutt.) have been replaced by red lovegrass (*Eragrostis secundifola* Presl.), red grama (*Bouteloua trifida* Thurb.), threeawn (*Aristida* spp. von Wolf), and common grassbur (*Cenchrus echinatus* L.). Taxonomic nomenclature for grasses follows Gould (1975) and for shrubs Scifres (1980).

Methods

Six dense shrub clusters and 3 grass interspace areas within a 5-ha enclosure were encircled within non-weighing lysimeters in the summer of 1984. The average canopy area of the shrub clusters was 30 m^2 and the shrub clusters were organized around a central mesquite tree (average basal diameter 0.2 m and 4.9 m tall). Mean species density was 60 shrubs per cluster. The non-weighing lysimeters were constructed by trenching around the perimeter of the treatment area to a depth of 2.5 m. The inside wall of the trench was double lined with plastic and the trenches were back-filled. Each lysimeter was approximately 5 m by 7 m long with the long axis parallel to the slope. Three shrub clusters were cleared by hand slashing and the debris was removed (hereafter referred to as bare soil). The area was sterilized with tebuthiuron[1] N-[5-(1,1-dimethylethyl)-1,3,4-thiadiazonal-2-yl)]-N,N'- dimethylurea (0.75 kg ai/ha) to prevent regrowth of herbaceous and woody vegetation. The remaining shrub clusters were left undisturbed.

Fiberglass sheets, 0.3 m tall, were used to form the sides and upper end of each lysimeter. Fiberglass sheets were glued to the plastic lining and inserted 0.1 m into the soil, creating a 0.2 m high border. A flume was constructed on the down-slope side to measure surface runoff. Four 2-m-long neutron access tubes were installed in each lysimeter in June of 1984. Soil water content was monitored with a calibrated neutron moisture depth gauge approximately once every 2 weeks. Volumetric water content (%) was measured at depths of 0.075, 0.15, 0.30, 0.60, 0.90, 1.20, 1.50, and 1.80 m.

A weather station was installed in a herbaceous vegetation clearing near the lysimeters. Weather variables measured were total rainfall and rainfall intensity with a standard rain gauge and tipping bucket, respectively, maximum and minimum temperature, and solar radiation. Normal rainfall based on the period of record from 1950-1980 was calculated from data collected in Alice, Tex.

Potential evapotranspiration (ET_p) was estimated with the

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[1] Product name provided for convenience of the reader and does not imply or constitute an endorsement by USDA.

Jensen-Haise equation (1963) as:

$$ET_p = T - (0.014\,T - 0.37)\,R_s / 580 \qquad (2)$$

where T is daily mean air temperature in degrees Fahrenheit and R_s is solar radiation in langleys. Evapotranspiration was calculated by the water budget method as the residual of precipitation minus runoff and drainage, and any change in water stored in the store profile.

Estimation of percolation required that several soil attributes such as particle size distribution (texture), organic carbon (%), bulk density (g cm^{-3}), gravimetric water content (g), porosity (E; %), soil moisture desorption curves, and saturated and unsaturated hydraulic conductivity (mm hr^{-1}) be determined for each horizon in the lysimeters. Approximately 3 kg of homogenized soil, integrated over the entire soil horizon, was collected from the outside wall of the lysimeter. The soil was air dried and passed through a 0.002 m sieve.

The mean of 2 subsamples of the soil was used to test for differences in organic matter and hydraulic conductivity within each horizon across treatments. Bulk density was determined from a 0.011 m^3 soil core removed from the center of each horizon along the outer wall of the lysimeters. A single subsample of homogenized soil was used to determine particle size distribution. Particle size distribution was measured by hydrometer method (Bouyoucos 1962). Organic carbon and bulk density were determined by the Walkley-Blake method (Broadbent 1965) and the core method (Blake 1965).

The mean of 2 gravimetric water content samples at each soil depth and tension were used to develop soil moisture desorption curves following methods outlined by Klute (1965a). Gravimetric water content was determined at 0.01, 0.03, 0.1, 0.3, 0.5, and 1.5 MPa. Changes in volumetric water content (O_V) over time at 1.5 and 1.8 m were estimated by taking the mean of 4 volumetric water content samples with a neutron probe at each sample date. The estimation of porosity and conversion of gravimetric to volumetric water contents followed methods outlined by Brady (1974). Unsaturated hydraulic conductivity was estimated for the soil at 1.5 and 1.8 m (Campbell 1974) as:

$$K = K_S\,(E/Ov)^{2b+2} \qquad (3)$$

where b is the slope of the line from a log-log transformation of the relationship between water potential (MPa) and O_V. Saturated hydraulic conductivity was determined as outlined by Klute (1965b).

The mean unsaturated hydraulic conductivity value between 1.5 and 1.8 m was then used in a one dimensional Darcy's law equation to estimate the potential percolation for each sample date.

$$D = K \; \frac{\partial H}{\partial Z} \qquad (4)$$

Where D is the total water movement (percolation) over the time period (hr), K is the unsaturated hydraulic conductivity of the soil, H is the difference in volumetric water content at 1.5 and 1.8 m, and Z is the difference in height at the 2 depths. To estimate the total percolation of water between sample dates, the mean percolation rate between 2 successive sample periods was utilized. Percolation was calculated as the period of time (hr) between sample dates multiplied by the mean percolation rate.

Ten 0.5 by 0.5 m plots were used to determine a monthly leaf area index of the herbaceous vegetation inside the lysimeters using the 10-point frame technique (Levy and Madden, 1933). Leaf area index was estimated as equal to the number of hits on live vegetation divided by the total number of pins lowered on the plot. Plots inside each lysimeter were permanently marked and were evaluated at monthly intervals. Leaf area index of the dominant shrubs within the shrub clusters were determined by using dimensional and regression analysis techniques (Kirmse and Norton, 1985; Ludwig et al., 1975). The dimensional analysis technique estimated total leaf biomass for a shrub at a point in time. Leaf biomass was estimated at 6 times during the study. Leaf area (cm^2) of the shrubs was determined by using a leaf area meter. A regression relationship was established to predict leaf area from leaf biomass. Leaf area index for the shrub clusters was then estimated by multiplying the estimated leaf weight times the appropriate leaf area equation, summing the total leaf area and dividing by the surface area of the lysimeter.

Root densities in the soil profiles were estimated by counting the number of roots in a single 0.1 by 0.1 m quadrat per soil horizon. The quadrat was located in the center of each horizon along the outside wall of the lysimeter. Roots were divided into 4 size classes based on diameter to facilitate counting: 1) < 1 mm; 2) > 1 < 2 mm; 3) > 2 < 5 mm; and 4) > 5 mm.

The soil profile was divided into 3 soil layers for analysis of soil water content. The soil layers were 0-0.6 m, 0.6-1.2 m, and 1.2-1.95 m and were chosen to evaluate the influence of evaporation (0-0.6 m), depth of root penetration of grass interspace (1.2 m) and depth of roots in the shrub clusters (1.95 m). Analysis of variance was used to test for differences in treatment means for soil water, evapotranspiration, runoff, and drainage ($P < 0.05$). Where appropriate, means were separated using Tukey's mean separation test ($P < 0.05$) (Steel and Torrie 1980).

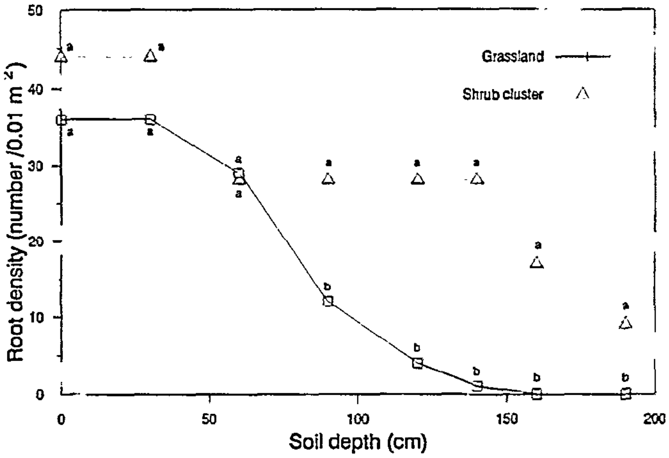

Fig. 1. Mean root density (number per 0.01 m^2) for grass interspaces and shrub clusters, La Copita Research Area, Alice, Tex. Mean root density with the same letter within depth are not significantly different ($P < 0.05$) based on Tukey's mean separation test.

Table 1. Physical soil characteristics of bare sandy clay loam soil, grass interspaces, and shrub clusters, La Copita Research Area, Alice, Tex.

Treatment	Horizon	Sand	Silt	Clay	Bulk density	Organic matter	Hydraulic conductivity
		(%)	(%)	(%)	($g\ m^{-3}$)	(%)	($cm\ hr^{-1}$)
Bare soil	1	73	3	14	1.22	0.90	3.5
Grass interspace	1	75	7	18	1.32	0.87	4.0
Shrub cluster	1	73	7	19	1.22	1.00	6.7
Bare soil	2	60	11	28	1.39	0.68	1.9
Grass interspace	2	60	7	33	1.38	0.84	2.1
Shrub cluster	2	69	7	24	1.25	0.67	3.0
Bare soil	3	59	6	35	1.36 b[1]	0.56	1.6
Grass interspace	3	60	9	31	1.54 a	0.50	1.7
Shrub cluster	3	64	8	28	1.34 b	0.59	2.5
Bare soil	4	56	11	33	1.40	0.37	1.2
Grass interspace	4	58	7	35	1.40	0.25	1.5
Shrub cluster	4	60	9	31	1.39	0.39	2.2
Bare soil	5	57	10	32	1.39	0.21	0.4
Grass interspace	5	57	9	34	1.41	0.18	0.7
Shrub cluster	5	57	10	32	1.43	0.29	1.3
Bare soil	6	58	11	31	1.34	0.09	0.4
Grass interspace	6	51	12	37	1.32	0.09	0.7
Shrub cluster	6	55	11	34	1.33	0.10	1.2

[1] Means for bulk density in the third horizon are significantly different ($P \le 0.05$) based on Tukey's mean separation test.

Results and Discussion

Soils

There were minimal differences in physical attributes of the soils from bared areas, grass interspaces, and shrub clusters. The only significant difference attributable to location occurred with bulk density (Table 1). Soils in the grass interspaces had significantly higher bulk density in the third soil horizon than did soil from either the shrub clusters or the bared areas. Greater soil bulk density in the grass interspaces supports field observations of a more highly developed argillic horizon in the grass interspaces.

Root Density

Use of soil water by vegetation is a function of root density and rooting depth. Shrubs developed both surface lateral roots and relatively deep tap roots. Roots of the woody plants penetrated to 2 m, although the majority (83%) of their roots were in the top 1.2 m of the soil profile (Fig. 1). Annual grass and forb roots extended to a depth of 1.2 m. The majority (95%) of the annual grasses' roots were in the upper 0.9 m of the soil profile, and no grass or forb roots were found below 1.4 m. There was no significant difference in root densities of the shrub cluster and grass interspaces from 0 to 0.65 m. From 0.9 to 2 m the density of woody plant roots beneath the shrub clusters was significantly greater than the density of grass roots in the grass interspaces.

Evapotranspiration

Between August and December, 1984, 310 mm of rainfall was recorded at the site (Fig. 2). There was no significant difference in soil water content among the 3 treatments at the beginning of the study (Fig. 3). Evapotranspiration from the bare soil was significantly lower than that from either the shrub clusters or the grass interspaces (Table 2 and Fig. 4). There was no significant difference in annual evapotranspiration between the shrub clusters and grass interspaces. Lower evapotranspiration rates of the bare soil resulted in a significant difference in stored soil water between the bare soil and the shrub clusters by the beginning of November (Fig. 3). Soil water contents of the grass interspaces were intermediate. No deep drainage was estimated to have occurred within any of the treatments in 1984.

Annual rainfall for 1985 was 125% of normal precipitation (last 30 years). The study area received 243% of normal rainfall in the first 6 months of the year. Rainfall exceeded potential evapotranspiration in December, 1984 and January, February, and May, 1985. In contrast to the wet spring, the summer was extremely dry (19% of normal rainfall). Rainfall in the fall was approximately half of normal rainfall. This distribution provided the opportunity to determine the effect of evapotranspiration during periods of above normal rainfall (January-June), drought (July and August), and a period of below normal rainfall (September-

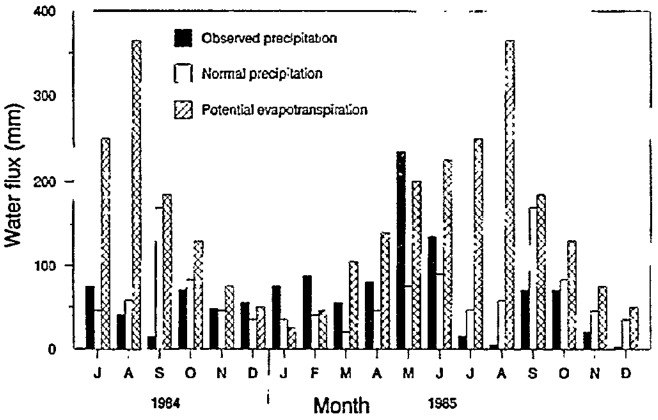

Fig. 2. Monthly rainfall (mm), long term normal monthly rainfall (mm), and potential monthly evapotranspiration (mm) for the La Copita Research Area, Alice, Tex.

Table 2. Water budget (mm) for bare sandy clay loam soil, grass interspaces, and shrub clusters, La Copita Research Area, Alice, Tex.

Year	Treatment	Rainfall	Evapo-transporation	Runoff	Drainage	Change in soil water
		(mm)	(mm)	(mm)	(mm)	(mm)
1984	Bare soil	310	208 b[1]	31 a	0 a	71 a
	Grass inter-space	310	298 a	3 b	0 a	9 b
	Shrub cluster	310	330 a	3 b	0 a	-23 c
1985	Bare soil	887	643 b	84 a	78 a	247 a
	Grass inter-space	887	833 a	28 b	22 b	5 b
	Shrub cluster	887	881 a	19 b	0 b	-13 b

[1] Means followed by the same letter are not significantly different ($P \leq 0.05$) based on Tukey's mean separation test.

Table 3. Annual and seasonal daily evapotranspiration (mm day^{-1}) for bare sandy clay loam soil, grass interspaces, and shrub clusters, La Copita Research Area, Alice, Tex.

		Precipitation regime		
Treatment	Annual	Above normal (1/85-6/85)	Drought (7/85-8/85)	Below normal (9/85-12/85)
	(mm day^{-1})	(mm day^{-1})	(mm day^{-1})	(mm day^{-1})
Bare soil	1.8 a[1]	2.4 b	1.1 c	1.3 a
Grass inter-space	2.3 a	2.9 ab	2.9 a	1.2 a
Shrub cluster	2.4 a	3.4 a	1.8 b	1.5 a

[1] Means followed by the same letter are not significantly different ($P \leq 0.05$) based on Tukey's mean separation test.

December).

Evapotranspiration accounted for 73%, 94%, and 99% of rainfall for 1985 received by the bare soils, grass interspaces, and shrub clusters, respectively (Table 2). This corresponds with annual evapotranspiration rates as a percentage of rainfall for other semiarid grass and woodland plant communities (90-147%) (Rowe and Reimann 1961, Gifford 1975, and Carlson et al. 1990). Average annual daily evapotranspiration values were 2.4, 2.3, and 1.8 mm/day for the shrub clusters, grass interspaces, and bare soil, respectively. Average daily evapotranspiration for the grass interspaces and shrub clusters compares favorably with daily evapotranspiration rates from grasslands (1.4-4.2 mm/day) in Colorado and Texas (Lauenroth and Sims 1976, and Carlson et al. 1990) and mesquite dominated rangelands in Arizona (1.6-2.5 mm/day) and Texas (0.5-5 mm/day) (Gatewood et al. 1950, Trombel 1977, and Dugas and Mayeux 1991).

Potential evapotranspiration is usually twice actual evapotranspiration in south Texas and potential evapotranspiration may be greater than 3 times evapotranspiration during dry years (Dugas and Ainsworth 1983). Annual evapotranspiration did not differ significantly between the shrub clusters and the grass interspaces (Table 2). There was a significant difference in the pattern of soil water use and seasonal evapotranspiration (Fig. 3 and 4). Average daily evapotranspiration rate from the shrub clusters was significantly greater than that from the bare soil during the spring (Table 3). Average daily evapotranspiration rates from the grass interspaces was similar to the shrub clusters and the bare soil. Dugas and Mayeux (1991), also working in Texas, reported that evapotranspiration was similar between grass and mesquite dominated landscapes when soil water availability was high.

Average daily evapotranspiration from the grass interspaces during the drought was significantly greater than that from the shrub clusters or bare soils (Table 3). Wan and Sosebee (1991) also reported substantial variability in transpiration rates for honey mesquite between wet and dry periods. Average daily evapotranspiration of shrub clusters was significantly greater than the daily evapotranspiration of the bare soils. The lower evapo-

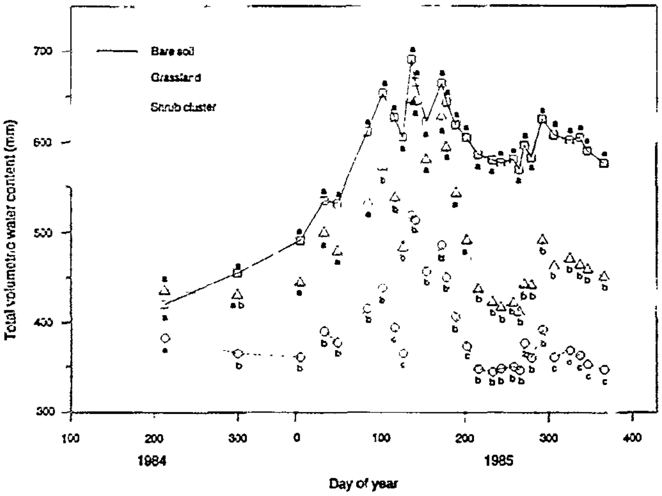

Fig. 3. Mean volumetric soil water content (mm) for bare sandy clay loam soil, grass interspaces, and shrub clusters, La Copita Research Area, Alice, Tex. Means followed by the same letter by date are not significantly different ($P < 0.05$) based on Tukey's mean separation test.

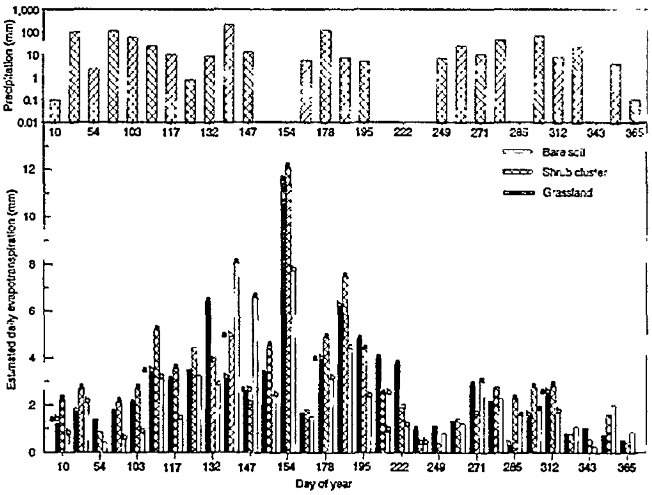

Fig. 4. Mean estimated daily evapotranspiration rate (mm) between sample dates and cumulative precipitation between sample dates for sandy clay loam soil, grass interspaces, and shrub clusters, La Copita Research Area, Alice, Tex. Means followed by the same letter by date are not significantly different ($P < 0.05$) based on Tukey's mean separation test.

transpiration rate of the grass interspaces during the spring resulted in a significant difference in total soil water content between the shrub clusters and grass interspaces from January through the middle of August (Fig. 3). Soil water content of the grass interspaces at the initiation of the drought was 150% higher than the previous year. Annual grasses and forbs in the grass interspaces utilized this stored soil water to compensate for the reduction in rainfall to sustain higher evapotranspiration rates and leaf area than the shrub clusters. Shrub cluster's leaf area decreased by 50% with a corresponding decrease in evapotranspiration rates (47%) in response to the reduced water availability during the drought. By September the grasses had utilized the available soil water and leaf area had decreased 90% in the grass interspaces.

A similar study using non-weighing lysimeters to contrast evapotranspiration from mesquite, herbaceous, and bare soil was initiated in northern Texas in 1986 (Carlson et al. 1990). They found that evapotranspiration was greater from bare soil than from the vegetated sites during an extended dry period. They attributed the increased evapotranspiration from the bare soil to 2 factors. The bare soil had more available water within the soil profile at the initiation of the drought than the vegetative treatments and to differential soil cracking between treatments. The vegetated sites had more canopy and litter cover than the bare soil treatment which reduced the depth of soil cracking during the extended dry period. In contrast, deep cracking was observed within the bare soil which allowed evaporation to occur from deeper within the soil profile (up to 0.8 m).

Daily evapotranspiration rates of all 3 vegetation treatments were similar from September through the end of the year. Stored soil water was similar between the grass interspaces and shrub clusters in September. With the onset of fall rains the shrub clusters responded with an immediate increase in evapotranspiration rate and significantly reduced the stored soil water. There was a 3-week lag in evapotranspiration rates from the senescent grass interspaces as new leaf area was produced in the fall. Lower evapotranspiration rates of the bare soil and grass interspaces during the fall resulted in a significant increase in stored soil water content over the shrub clusters. This study and the data reported by others indicate that mesquite and mesquite-dominated shrub clusters are facultative phreatophytes.

The higher evapotranspiration rate and the reduction of stored soil water beneath the shrub clusters can be attributed in part to higher interception losses. Although there was no direct measurement of canopy and litter interception during the study, the interception rate of the shrub clusters is estimated to be approximately 15% of annual rainfall based on work in other shrub dominated plant communities. Annual interception losses for chaparral communities in California range from 8 to 20% of annual rainfall (Rowe 1948, Hamilton and Rowe 1949, and Corbett and Crouse 1968). Thurow et al. (1987), working in central Texas, estimated that for oak mottes, midgrass, and shortgrass dominated areas, canopy interception of annual rainfall was 25%, 18%, and 11%, respectively.

Soil Water

Although annual evapotranspiration was not significantly different between the shrub clusters and the grass interspaces, there was a significant difference in the pattern of soil water use. Total soil water content was similar for all 3 treatments at the beginning of the study in August of 1984 (Fig. 3). By January of 1985 soil water content was significantly greater in the grass interspaces and bare soil areas than the shrub clusters. Soil water content of the bare areas was significantly greater than that of the shrub clusters for the remainder of the study. Soil water content of the grass interspace was significantly greater than that of the shrub clusters from January through the middle of July. Soil water content of the grass interspaces was similar to that of the shrub clusters during the drought. In the fall, the reduced evapotranspiration rate of the grass interspaces resulted in significantly more water being stored in the soil profile beneath the grass interspaces than the shrub clusters.

Sturges (1983) found that grass in areas where sagebrush had been controlled used more water from the 0 to 0.9 m soil layer that did vegetation on the untreated sagebrush site. However, the sagebrush used more water than did the grass from the total soil profile (0-1.8 m). Johnson (1970) reported that aspen extracted water to a depth of 3 m, while herbaceous-covered areas extracted water to a depth of only 1.2 m. In the bare soil control area evaporation was limited to the surface 0.6 m of the soil profile.

Grass interspace had significantly more water in the surface soil profile (0-0.6 m) than the shrub clusters for the first 6 months of 1985 (Table 4). Soil water contents in the surface soil profile beneath grass interspaces and shrub clusters were similar during the drought and both were significantly less than the bare soil. Bare soil contained significantly more water in the subsoil (0.6-1.2 m) than the shrub clusters for the entire year (1985) but was similar to the grass interspace during the first 6 months of the year. Soil water contents in the grass interspaces were significantly greater than the shrub clusters at the beginning of the year. By the end of the drought the soil water contents in the subsoil beneath the grass interspaces and the shrub clusters were similar. Water content of the lower soil profile (1.2-1.95 m) did not differ significantly among vegetative treatments throughout the year. Bare soil accumulated significantly more water by January than the shrub clusters did, and this difference was maintained for the remainder of the study.

Runoff

Runoff is often assumed to be zero on arid and semiarid range-

Table 4. Mean seasonal (1985) soil water content (mm) for bare sandy clay loam soil, grass interspaces, and shrub clusters, La Copita Research Area, Alice, Tex.

		Treatment		
Soil depth	Season	Bare soil	Grass interspace	Shrub cluster
(mm)		(mm)	(mm)	(mm)
0-0.6	Jan.-July	150 a[1]	153 a	121 b
	Aug.-Sep.	132 a	94 b	79 b
	Oct.-Dec.	145 a	118 b	87 c
0.6-1.2	Jan.-July	234 a	221 a	167 b
	Aug. Sep.	229 a	191 b	145 c
	Oct.-Dec.	224 a	165 b	137 b
1.2-1.95	Jan.-July	235 a	193 ab	150 b
	Aug.-Sep.	237 a	189 b	144 b
	Oct.-Dec.	222 a	165 b	137 b

[1] Means followed by the same letter are not significantly different ($P \leq 0.05$) based on Tukey's mean separation test.

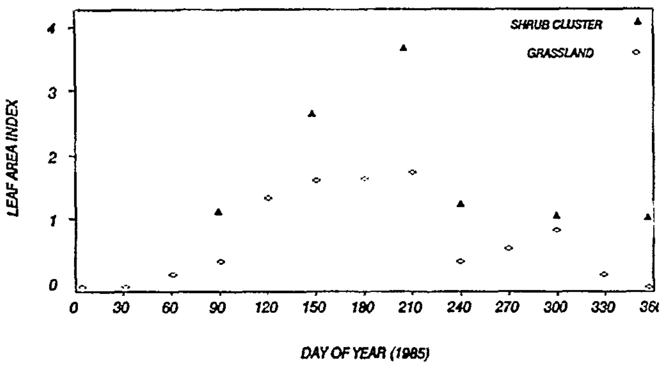

Fig. 5. Mean estimated leaf area index for grass interspaces and shrub clusters, La Copital Research Area, Alice, Tex.

lands (Lauenroth and Sims 1976, Wight et al. 1986, and Gee and Kirkham 1984). Measured annual surface runoff accounted for 1 to 10% of rainfall in 1984. Runoff from the bare soil was significantly greater than from either the shrub clusters or grass interspaces. There was no difference in runoff between the shrub clusters and grass interspaces in 1984. Annual surface runoff from the shrub clusters, grass interspaces, and bare soil was 1, 3, and 10%, respectively, of rainfall in 1985. Surface runoff was significantly greater from bare soil than from either the grass interspaces or the shrub clusters in 1985. Annual surface runoff from the grass interspaces was 32% greater than that from the shrub clusters although there was no statistical difference. The 2 largest rainfall events (> 100 mm) occurred within a 5-day period in May, 1985. The average rainfall intensity of these 2 storms was 48 mm/hr. The surface runoff from the grass interspace areas from these 2 storms was significantly greater (60%) than that from the shrub clusters. More than 50% of the surface runoff, regardless of vegetation cover, was the result of these two large rainfall events.

Grass and shrubs intercept a significant portion of incident rainfall (Rao 1987, Thurow et al. 1987, Calheiros De Miranda and Butler 1986, Tromble 1983, Young et al. 1984, Burgy and Pomerory 1958, Corbett and Crouse 1968, and Hamiltion and Rowe 1949) and thus reduce the impact of falling raindrops. Raindrops impinging directly on a bare soil surface dislodge soil particles which clog soil pores and increase surface runoff (Osborn 1954). Depending on the plants' morphological characteristics and growth form, much of the intercepted rainfall is channeled to the base as stemflow (Young et al. 1984, Glover et al. 1962, and Gwynne 1966). Litter accumulation at the base of the shrubs alters the microclimate resulting in increased root density and macroporosity, and prevents crusting of the soil surface. Initially, there were micro-depressions throughout all three vegetation treatments and the soil surface was granule. After the first several rainfall events a surface crust (2-3 mm thick) formed on the bare soil. Micro-depressions were filled with sediment after the first large rainfall event (> 20 mm), creating a uniform gradient to the flume on the bare soil.

In the grass interspaces and shrub clusters the plants aided microrelief development and stability and prevented crusting of the soil surface. Numerous debris dams were noted in both the grass interspace and shrub clusters. Micro-depressions and debris dams increased retention time of water on the soil surface and decreased surface runoff. The increase in surface runoff from the bare soil was attributed to a reduction in infiltration rate, detention storage and surface roughness caused by soil crusting, and the erosion and leveling of the coppice dunes associated with the shrubs.

Drainage

Deep drainage from the bared soils was significantly greater than that from soils with vegetative cover and is attributed to a wetter profile from reduced total evaporation and not due to differences in macropores. The quantity of water lost through deep percolation was similar for the grass interspaces and the shrub clusters from January through April 1985. Deep drainage began in the grass interspaces in late May and continued through July. The hypothesis that water reaches depths below active root uptake in the grass interspaces is supported by the presence of soil mottling in the lower portions of the soil profile. No soil mottling was present beneath the shrub clusters or the bare soil. No deep drainage occurred beneath the shrub clusters during the study. Deep drainage beneath the bared soil areas began in late February and continued throughout the remainder of the year. When the soil water content was above 35% (by volume) in the lower soil profile, deep percolation occurred. Conditions favorable for initiation of percolation were prolonged periods of above normal rainfall during the dormant and early growing season. Only 20 mm of water was added to the lower soil profile of the shrub clusters. More than 80 mm of water was added to the lower soil profile within the grass interspaces, including 22 mm of water lost through deep percolation.

Summary and Conclusions

Shrub clusters responded more quickly to available soil water in both the spring and fall than did the grass interspaces. Shrub clusters transpired water whenever soil water was available. Shrub cluster transpiration rate was greater than the unsaturated flow rate, thus precluding any substantial downward movement of water into the lower soil profile. Winter and early spring rainfall was more effective than either summer or fall rainfall in recharging the soil profile. Maximum recharge of the soil profile occurred when rainfall exceeded potential evapotranspiration. High potential evapotranspiration demand during the summer and fall prevented recharge of the lower soil profile, regardless of vegetative cover. Evapotranspiration rates were greatest following rainfall events and higher from the grass interspaces than from the shrub clusters through the first 2 months of drought. Higher evapotranspiration rates of the grass interspaces during the summer was a function of the greater quantity of available soil water at the beginning of the drought. Evaporation from the bare soil was limited to the surface 0.6 m of the soil profile.

Soil water was extracted first from the upper horizons of the soil profile regardless of vegetative cover. As the surface horizon dried out, the water was extracted from progressively lower horizons. Once the water was beyond the active root zone in the grass interspaces, it continued to percolate as unsaturated flow and was not available for evapotranspiration. Evapotranspiration and runoff were essentially the same for the grass interspaces and shrub clusters. Elimination of the shrub clusters and all the associated vegetation significantly increased water yield by 16% and decreased evapotranspiration by 28% compared to the shrub clusters.

These results imply that no net change in evapotranspiration, runoff or drainage would occur if shrubs are replaced by deep rooted perennial grasses in south Texas. Increasing water yields in south Texas through vegetation manipulation is marginal and limited to those years when rainfall exceeds potential evapotranspiration.

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Predicting buffelgrass survival across a geographical and environmental gradient

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Abstract

This research was designed to identify relationships between T-4464 buffelgrass (*Cenchrus ciliaris* L.) survival and climatic and soil characteristics. At 167 buffelgrass seeding sites in North America we collected climatic and soils data where the grass: 1) persisted over time and increased in area covered (spreads), 2) persisted over time but does not increase in area covered (persists), and 3) declined over time and all plants eventually died (dies). At 30 sites in Kenya we collected climatic and soils data in the area where T-4464 seed was originally collected. Only total soil nitrogen and organic carbon differed among survival regimes. Total soil nitrogen and organic carbon concentrations were least where buffelgrass spreads, intermediate where the grass persists and greatest where the grass dies. To predict buffelgrass survival among the 3 survival regimes, and between areas where the grass spreads or dies, we used discriminant function analyses. A model including organic carbon, total soil nitrogen, sand, clay, potassium and cation exchange capacity correctly classified 78% (r^2=0.8) of the seeding sites in the 3 survival regimes. A model including sand, total soil nitrogen, calcium, mean minimum temperature in the coldest month, annual precipitation and winter precpitation correctly classified 88% (r^2=0.8) of the seeding sites between spreads and dies. Survival regime selection prior to brush control, seedbed preparation and sowing will reduce planting failure probabilities, soil erosion and economic losses, and enhance long-term beef production.

Key Words: *Cenchrus Ciliaris* L., range seeding, climate, soil nutrients, Mexico, Texas, Kenya

Buffelgrass (*Cenchrus ciliaris* L.), a perennial warm-season bunchgrass is native to Africa, Asia, and the Middle East (Bogdan 1961, Khan and Zarif 1982, Holt 1985, Mannetje and Jones 1990). The species predominates where surface soils are sandy and annual precipitation ranges from 200 to 1,200 mm (Cox et al. 1988).

Buffelgrass seed collected in the Turkana Desert, northcentral Kenya, was sown in Texas during the 1940's and resulting stands were evaluated for seedling establishment, forage production and persistence (Holt 1985). Seedlings from seed sown in summer were easily established and mature plants survived winter in south Texas.

In 1949, the USDA-Soil Conservation Service informally released T-4464 buffelgrass (Holt 1985). T-4464 plants were established at most planting sites in south Texas, and between 1949 and 1985, the grass was established on over 4 million ha (Cox et al. 1988). Seed was transported to Mexico and successfully established along the eastern and western coasts (Cota and Johnson 1975, Molina et al. 1976, Agostini et al. 1981, Hanselka 1985). Land managers assumed that plant populations would persist under a variety of climatic and soil conditions. However, spread of stands occurred only at a few locations. At other seeded sites, plant stands have persisted but have not spread or have disappeared. Similar observations have been reported in Africa (Brzostowski 1962, Brzostowski and Owen 1964, DuToit et al. 1976), Australia (Wilson 1964, Coaldrake and Russell 1969, Ebersohn 1970, Anderson 1974, Hacker 1989, Silcock and Smith 1990, Walker and Weston 1990) and the United States (Ball

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1964, Gonzales and Dodd 1979, Gonzales and Latigo 1981).

Because T-4464 was originally collected in northcentral Kenya, and spreads most frequently in south Texas and northwest Mexico, we hypothesized that climate and soils around the original collection site and where the plant spreads in North America were more similar than where the plant fails to spread or dies. If the hypothesis is true, then climatic and soil information from south Texas, northwestern Mexico and northcentral Kenya can be used worldwide to select seeding sites where buffelgrass has a high probability for establishment and persistence.

If range reseeding continues to be an economical alternative in reclamation of degraded rangeland, then information which increases success in species establishment and persistence is needed. The objectives of this study were i) to identify climatic and soil properties which determine where the species either 1) persists over time, and increases in area coverage (spreads), 2) persists over time but does not increase in area coverage (persists) or 3) declines over time and all plants eventually die (dies); and ii) to develop predictive models that can be used by land managers and ranchers to select seeding sites where buffelgrass has a high probability for establishment and persistence.

Methods and Materials

Study Site Selection

Historical records and journals were examined to determine where T-4464 seed was collected in Africa and where the plant had been established in North America (Fig. 1). Rangeland conservationists in Kenya, Texas and Mexico identified the original seed collection area or located and aged sites where the grass survived for 10 or more years. Together we selected 167 buffelgrass seeding sites in North America, and 30 sites around the area where T-4464 seed was collected in northcentral Kenya. Seeding site sizes varied from 50 to 500 ha, and approximately 95% of the annual biomass production was harvested by domestic livestock and wildlife. Forty-seven stands were located in northwest Mexico, 59 in northeast Mexico, 27 in south Texas, and 34 in southeast Mexico. Northwest Mexico sites were between the settlements of Hermosillo and Mazatlan; southeast sites were within the Yucatan Peninsula; and northeast Mexico and south Texas sites were between Ciudad Victoria, Tamaulipas and Monterrey, Nuevo Leon, Mexico, and San Antonio and Laredo, Tex. (Fig. 1).

Planting sites in northwest Mexico were at low elevations between the Sierra Madre Occidental and the Gulf of California Plain (22° 30' and 31° 00' N lat.; and 105° 30' and 111° 20' W long.). Climate varies from tropical dry, semitropical subdesertic, subtropical very dry, to semitropical desertic (FAO-UNESCO 1975a). Dominant soils are Yermosols and Regosols with lithic Yermosols, lithic Xerosols, lithic Kastanozems, Lithosols, lithic orthic Luvisols, Fluvisols and Gleysols.

Sites in northeast Mexico and south Texas were between the Gulf of Mexico Coastal Plain, the Rio Grande Plain, and the Sierra Oriental foothills (23° 00' and 28° 30' N lat.; and 97° 50' and 100° 00' W long.). Climate within this area varies from humid to very dry subtropical, and rather humid to very dry warm temperate to semitropical subdesertic (FAO-UNESCO 1975a, 1975b). Dominant soils are luvic and calcic Kastanozems, Rendzinas, luvic Phaeozems, pellic Vertisols, eutric Cambisols, eutric Fluvisols, eutric Gleysols and Regosols.

Sites in southeast Mexico were within the Yucatan Peninsula (20° 21' and 21° 25' N lat.; and 88° 45' and 90° 25' W long.). Climate within this area varies from dry tropical to very dry tropical (FAO-UNESCO 1975a). Dominant soils are Rendzinas, pellic Vertisols, Lithosols, eutric Nitosols, lithic chromic Luvisols, lithic chromic Cambisols and shallow Miocene Histosols.

Sites in northcentral Kenya were west of Lake Turkana; between the Ethiopian Highlands and the East African Plateaus (0° 30' and 4° 30' N lat.; and 35° 45' and 36° 20' W long.). Climate in this area varies from semiarid tropical to hot tropical desert (FAO-UNESCO 1977). Dominant soils are eutric and calcaric Regosols, Xerisols, Fluvisols, Vertisols and Solonchaks.

Site elevations vary from 20 to 700 m in North America, and from 15 to 580 m in Kenya. Slopes range from 2 to 10%. Precipitation ranges from 200 to 1,200 mm in North America, and is bimodally distributed in either spring and summer or winter and summer. In Kenya, precipitation ranges from 200 to 400 mm, and is bimodally distributed in early and late summer.

Study Site Classification

At North American seeding sites the plant stabilized at one of the following end points: 1) plants survived in the seeded area and new plants established naturally from seed outside the planting area (spreads), 2) plants survived in the seeded area but did not spread outside the seeded area (persists), and 3) plants persisted in the seeded area for 10 or more years, and over time all plants eventually died (dies). Where T-4464 spreads, densities inside and outside the seeded area exceed 1 plant m^{-2}. Where the

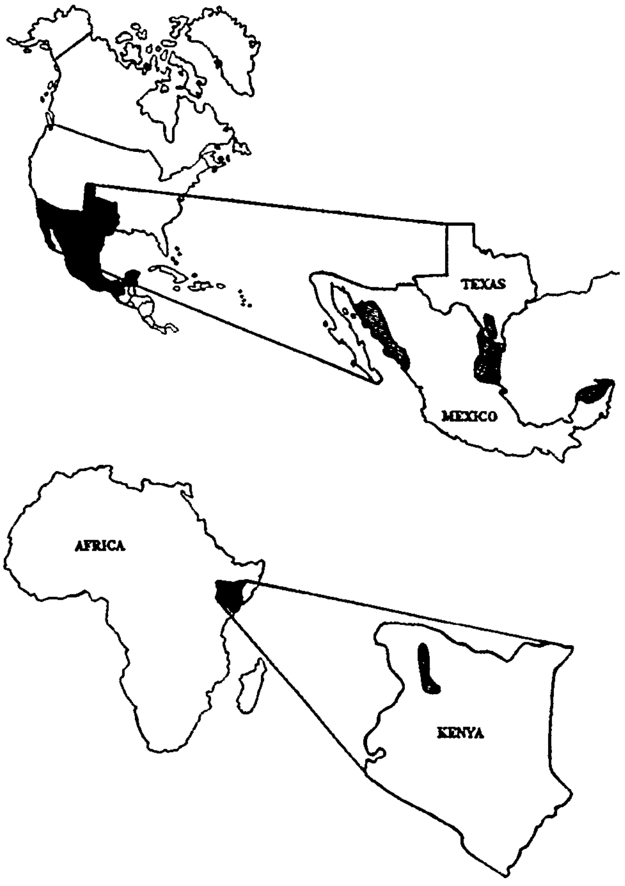

Fig. 1. Location of buffelgrass (*Cenchrus ciliaris*) sampling sites.

Table 1. Soil textural classes at buffelgrass seeding sties where the plant either spreads (82 sites), persists (50 sites), or dies (35 sites) in Mexico and south Texas.

	Survival Regime		
Textural Class	Spreads	Persists	Dies
Sand	6	1	-
Loamy sand	12	5	-
Sandy loam	21	4	2
Sandy clay loam	21	7	-
Loam	7	4	8
Clay loam	7	13	15
Clay	8	13	6
Silty clay loam	-	3	1
Silty clay	-	-	3
TOTAL	82	50	35

plant persists, densities inside the seeded area exceed 1 plant m^{-2}, and densities outside the seeded area were <1 plant in 4 m^{-2}. Where the plant dies no plants were observed inside or outside the seeded area. Based on these criteria, seeding sites in Mexico and Texas were divided among 3 survival regimes: 1) 82 sites were classified in survival regime 1 (spreads), 2) 50 sites were classified in survival regime 2 (persists) and 3) 35 sites were classified in survival regime 3 (dies).

Soil Sampling

Soils were collected at 0-10, 10-20, and 20-30 cm depths near the crown of 3 buffelgrass plants or in open areas where buffelgrass plants died. Three soils samples were collected at each soil depth. Composited samples were air dried, passed through a 2-mm sieve and thoroughly mixed. Duplicate subsamples from each composite were analyzed for particle-size distribution (Day 1950), pH (saturated paste), electrical conductivity of the saturated extract and cation exchange capacity (U.S. Salinity Laboratory Staff 1954), ammonium acetate soluble cations including calcium, potassium, sodium and magnesium, total nitrogen, organic carbon, (Jackson 1958) and available phosphorus was extracted with NAHC0$_3$ (Olsen and Sommers 1982).

Climatic Parameters

Climatic data were collected at or from nearby areas where seed was orginially collected, and where plants either spread, persisted or died. Climatic reporting stations were selected based upon 1) topographic similarities between reporting stations and the 3 survival regimes plus areas where seed were collected, and 2) having 20 or more years of continuous records which corresponded with actual planting and subsequent growing years. Climatic data are summarized in the following categories: 1) winter 2) summer and 3) total precipitation, and mean monthly 4) maximum and 5) minimum temperatures. We selected 17 stations in northwest Mexico, 25 stations in northeast Mexico and south Texas, 10 stations in southeast Mexico, and 7 stations in north-central Kenya (Agroclimatological Data for Africa 1984, Climatography of Mexico 1982, Climatography of the United States 1985).

Data Analysis

Because site selection was not random and site numbers within survival regimes were unequal, the treatment variances were compared. A Hartley test (Zar 1984) was used to determine differences ($P \leq 0.05$) among survival regimes for each weather parameter and soil component. When significant differences existed, a log (X+1) transformation was performed. All measured parameters were compared across survival regimes using a multiple-analysis-variance (MANOVA) test. Univariate comparisons were adjusted according to the Bon Ferroni correction (Winer 1971).

A mean and coefficient of variation were generated for each soil component using data from the 3 depths at each sampling

Table 2. Surface soil (0-10 cm) means and standard deviations for particle-size distribution and selected chemical properties at sites where buffelgrass either spreads, persists or dies at planting sites in south Texas and Mexico, and where the seed was originally collected in northcentral Kenya. An asterisk (*) indicates a significant difference ($P \leq 0.05$) among variances in the 3 survival regimes.

Soil Properties	Survival Regime			Hartley test	Kenya
	Spreads	Persists	Dies		
Sand (%)	61.0 ± 20.2	44.9 ± 24.6	35.3 ± 15.4	NS	82.0 ± 14.8
Silt (%)	17.5 ± 10.8	24.1 ± 13.2	32.3 ± 7.2	NS	11.9 ± 9.2
Clay (%)	21.5 ± 11.6	31.0 ± 15.3	32.4 ± 11.2	NS	6.1 ± 6.1
Silt + clay (%)	39.0 ± 18.7	55.1 ± 24.3	64.7 ± 16.2	NS	18.0 ± 14.8
pH	7.8 ± 0.5	7.6 ± 0.6	7.5 ± 0.4	NS	8.1 ± 0.5
Electrical conductivity (ds m^{-1})	0.3 ± 0.2	0.3 ± 0.1	0.3 ± 0.1	NS	0.2 ± 0.1
Total nitrogen (%)	0.1 ± 0.1	0.3 ± 0.2	0.5 ± 0.3	*	0.1 ± 0.1
Organic carbon (%)	0.9 ± 0.7	2.6 ± 2.9	4.4 ± 3.6	*	0.6 ± 0.2
Phosphorus (mg kg^{-1})	10.6 ± 11.9	12.9 ± 12.7	10.0 ± 22.3	NS	17.2 ± 9.2
Cation exchange capacity (cmol kg^{-1})	22.5 ± 13.4	38.1 ± 24.4	61.8 ± 24.9	NS	15.6 ± 13.7
Sodium (cmol kg^{-1})	0.4 ± 0.6	0.4 ± 0.4	0.4 ± 0.2	NS	0.2 ± 0.2
Potassium (cmol kg^{-1})	1.1 ± 0.7	1.9 ± 1.3	1.8 ± 0.9	NS	1.0 ± 0.9
Calcium (cmol kg^{-1})	35.9 ± 26.5	42.0 ± 23.0	47.8 ± 16.6	NS	12.4 ± 13.5
Magnesium (cmol kg^{-1})	1.9 ± 1.5	3.2 ± 2.2	3.7 ± 2.5	NS	2.1 ± 1.6

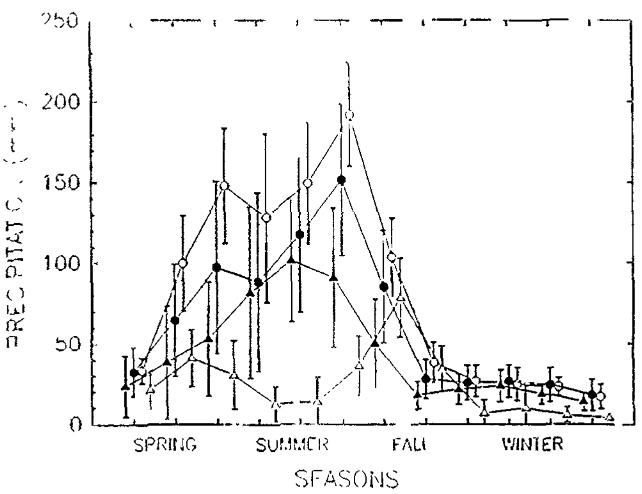

Fig 2. The variation in mean monthly precipitation distribution at buffelgrass seeding sites in North America and where seed was originally collected in Africa. Lines represent sites where the plant persists and spreads from a seeding (▲), persists but does not spread from a seeding (•), dies (o), and where seed were originally collected in northcentral Kenya (Δ).

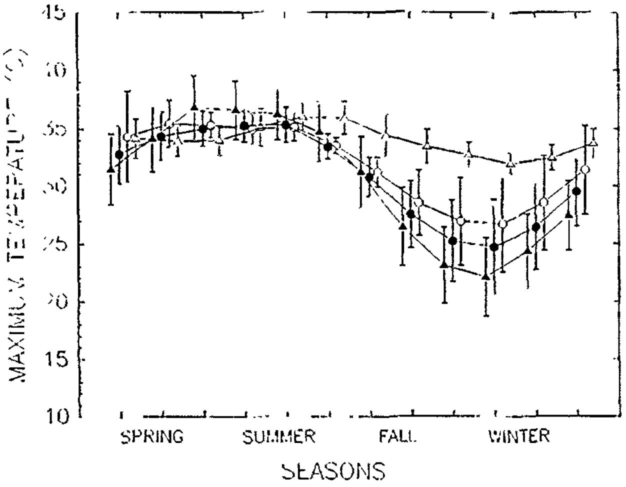

Fig. 3. The variation in mean monthly maximum temperatures at buffelgrass seeding sites in North American and where seed were originally collected in northcentral Kenya. Lines represent sites where the plant persists and spreads from a seeding (▲), persists but does not spread from a seeding (•), dies (o), and where seed were originally collected in northcentral Kenya (Δ).

site. Individual depth means, an overall depth mean, and the coefficient of variation were included in the analyses to generate predictive equations for the different buffelgrass survival regimes. Because climatic and soil variables are correlated, discriminant function analyses was used to select the best predictors of buffelgrass survival. In initial discriminate function analyses runs we included the 3 survival regimes. Because variable values in regime 2 frequently overlapped those in regimes 1 and 3, we excluded regime 2 in the second model. Data from Kenya were not included in discriminate function analyses because different survival regimes were not assigned to sampling sites. Climatic and soil data from Kenya were included in order to compare conditions where the plant evolved with those of the 3 survival regimes in Mexico and Texas. Analyses were performed using the SAS statistical package for personal computers (SAS 1988).

Results and Discussion

Soil Physical and Chemical Properties

Where buffelgrass spreads in North America, soils are generally coarse-textured (Table 1). At 73% of the sampling sites where the species spreads, textural classes are predominantly sandy. Where the species persists, 34% of the textural classes are sandy and 66% are silty or clayey. Where the species dies, 94% of the textural classes are either silty or clayey. On sandy and loamy soils in southeast Mexico, T-4464 dies because a shallow hardpan limits downward water movement and seasonal flooding saturates the soil profile. In Australia, poor soil aeration limits buffelgrass growth and survival (Humphreys 1967, Anderson 1972).

Of the measured soil chemical properties, only total nitrogen and organic carbon variances differed ($P \leq 0.05$) among T-4464 survival regimes (Table 2). Total nitrogen and organic carbon quantities are least where the species spreads, intermediate where the species persists and greatest where the species dies. In northcentral Kenya, soils are coarser and less fertile than where the species has been planted in North America. However, chemical and physical soil properties where the species evolved in Africa are similar to where the species spreads in North America; with the exception of available phosphorus, which is consistently higher in Kenya than North America. This verifies the hypothesis that soils in Kenya where T-4464 mother plants evolved are more similar to soils in North America where the plant spreads, than soils where plants either persist or die.

In Queensland, Australia the growth of buffelgrass plants on sandy red soils was delayed when available phosphorus (0.01N H_2SO_4 extractable) was less than 25 mg kg^{-1}, and when available phosphorus was limiting few plants survived drought (Christie 1975) Where buffelgrass spreads in North America and evolved in Kenya, available soil phosphorus varied from 0.1 to 26.4 mg kg^{-1}, averaged 13.1 mg kg^{-1}, and seldom exceeded 16.5 mg kg^{-1}. Low available soil phosphorus in North American soils may limit buffelgrass productivity (Molina et al. 1976, Gonzales and Dodd 1979, Gonzales and Latigo 1981) but concentrations below 0.1 mg kg^{-1} do not appear to impact the plant's ability to either establish from seed or survive.

Climatic Parameters

In North America, buffelgrass spreads where annual precipitation amounts range from 330 to 550 mm, and the species persists and dies when amounts range from 600 to 1,200 mm (Fig. 2). Buffelgrass seed from plants established on planted sites actively colonize adjacent nonplanted sites between Crystal City and Larado, Tex. and Carbo and Hermosillo, Mexico. At these locations, summer rainfall varies from 170 to 400 mm and winter rainfall varies from 10 to 285 mm. Dry periods totaling 150 to 210 days occur in either winter or fall and spring, and mean maximum and minimum temperatures in the coldest month range between 24 and 32° C (Fig. 3), and 5 and 15°C (Fig. 4), respectively.

Annual precipitation in northcentral Kenya varies from 200 to 400 mm, and is bimodally distributed in 2 summer growing seasons (Fig. 2). Mean minimum and maximum temperatures annu-

Table 3. Disciminant function analyses statistics. Model I differentiates among sites where buffelgrass either spreads, persists or dies, and Model II differentiates between sites where the grass either spreads or dies.

Parameter	F	P	Partial R^2	Total R^2
		MODEL I		
Sand (%) at 0-10 cm	25.3	0.0001	0.6479	0.267
Total nitrogen (%) at 0-10 cm	13.9	0.0001	0.80	0.434
Clay (%) at 20-30 cm	8.2	0.0004	0.6146	0.539
Organic carbon (%) at 0-10 cm	6.3	0.0025	0.7934	0.622
Potassium (cmol kg^{-1}) at 0-30 cm	5.1	0.0072	0.4476	0.691
CEC-CV (cmol kg^{-1}) at 0-30 cm[1]	3.0	0.0222	0.0994	0.744
		MODEL II		
Total nitrogen (%) at 0-10 cm	30.7	0.0001	0.9488	0.242
Mean min. temperature (°C)	21.1	0.0001	0.7348	0.422
Sand (%) at 0-10 cm	18.9	0.0001	0.6517	0.586
Winter precipitation (mm)	15.5	0.0002	0.5144	0.725
Total precipitation (mm)	9.4	0.0028	0.8225	0.814
Sand (%) at 10-20 cm	8.0	0.0056	0.9447	0.891
Calcium (cmol kg^{-1}) at 10-20 cm	6.4	0.0129	0.4059	0.954

[1] CEC = Cation exchange capacity; CV = Coefficient of variation

ally vary from 21 to 24 C and 31 to 36 C (Figs. 3 and 4), respectively, and buffelgrass growth occurs whenever soil moisture is available (Cox et al. 1988). Temperature extremes in Texas and Mexico differ from those in northcentral Kenya but rainfall amount and distribution where the plant evolved in Africa are more similar to where the plant spreads, than where the plant persists or dies in North America.

Model Development

Comparisons of log-transformed means among soil depths within the 3 survival regimes indicate the importance of cation exchange capacity, organic carbon, total nitrogen, potassium, sand, silt, clay, silt plus clay, and magnesium when selecting buffelgrass seeding sites. Climatic parameters influencing seedling persistence and spread were mean minimum temperature in the coldest month, summer precipitation, and total annual precipitation.

In Model I, plant survival among the 3 survival regimes was influenced by sand (%) at 0-10 cm, total nitrogen (%) at 0-10 cm, clay (%) at 20-30 cm, organic carbon (%) at 0-10 cm, potassium (cmol kg^{-1}) at 0-30 cm, and the cation exchange capacity (cmol kg-1) coefficient of variation at 0-30 cm (Tables 3 and 4). The combined parameter group classified 78% of the seeding sites in the correct survival regime (overall Wilk's lambda = 0.39, composite r^2 = 0.80). Predictive equations for the 3 survival regimes were:

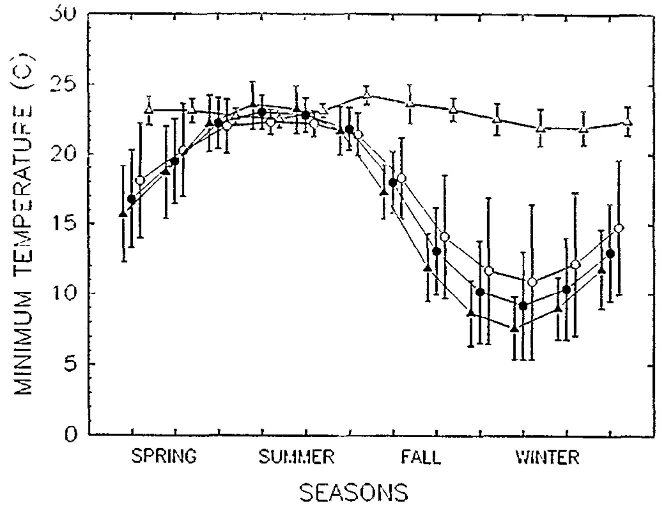

Fig. 4. The variation in mean monthly minimum temperatures at buffelgrass seeding sites in North America and where seed were originally collected in northcentral Africa. Lines represent sites where the plant persists and spreads from a seeding (▲), persists but does not spread from a seeding (•), dies (o), and where seed were originally collected in northcentral Kenya (Δ).

spreads =- 3.01 + 1.61 (sand) + 1.0 (total nitrogen) + 0.84 (clay) - 1.0 (organic carbon) - 0.16 (potassium) - 0.05 (cation exchange capacity - coefficient of variation);

persists =+ 2.90 - 1.09 (sand) - 4.77 (total nitrogen) - 0.59 (clay) + 1.03 (organic carbon) + 0.82 (potassium) - 0.16 (cation exchange capacity - coefficient of variation);

dies = + 1.11 - 0.52 (sand) + 3.77 (total nitrogen) - 0.25 (clay) - 0.02 (organic carbon) - 0.66 (potassium) + 0.21 (cation exchange capacity - coefficient of variation).

Due to data variability and overlapping values between survival regimes 1 and 2, and between survival regimes 2 and 3 we developed Model II to differentiate between the spreads and dies regimes (Table 5). Plant survival between the 2 regimes was influenced by total nitrogen at 0-10 cm, mean minimum temperature in the coldest month (C), sand (%) at 0-10 cm, winter precipitation (mm), total annual precipitation (mm), sand (%) at 10-20 cm, and calcium (cmol kg^{-1}) at 10-20 cm. The combined parameter group classified 88% of the seeding sites in the correct survival regime (overall Wilk's lambda = 0.34, composite r^2 = 0.82). Predictive equations for the 2 survival regimes were:

spreads =- 0.82 - 3.22 (total nitrogen) + 1.37 (mean minimum temperature in the coldest month) + 2.41 (sand at 0-10

Table 4. Means and standard deviations for parameters in Model I that discriminate among seeding sites where buffelgrass either spreads, persists or dies.

	Survival Regime		
Parameter	Spreads	Persists	Dies
Sand (%) at 0-10 cm	63.09 ± 18.7	41.61 ± 24.4	37.28 ± 16.4
Total nitrogen (%) at 0-10 cm	0.12 ± 0.11	0.25 ± 0.23	0.52 ± 0.34
Clay (%) at 20-30 cm	26.90 ± 12.8	35.78 ± 17.6	34.59 ± 16.9
Organic carbon (%) at 0-10 cm	0.84 ± 0.55	2.19 ± 2.32	4.10 ± 3.25
Potassium (cmol kg^{-1}) at 0-30 cm	0.76 ± 0.51	1.39 ± 0.83	1.38 ± 0.93
CEC-CV (cmol kg^{-1}) at 0-30 cm[1]	14.54 ± 14.5	9.71 ± 7.45	10.49 ± 8.29

[1] CEC = Cation exchange capacity; CV = Coefficient of variation

Table 5 Means and standard deviations for parameters in Model II that discriminate between seeding sites where buffelgrass either spreads or dies.

Parameter	Survival Regime	
	Spreads	Dies
Total nitrogen (%) at 0-10 cm	0.12 ± 0.11	0.52 ± 0.34
Mean Min. Temperature (°C)	7.89 ± 2.44	13.37 ± 4.88
Sand (%) at 0-10 cm	63.09 ± 18.7	37.28 ± 16.4
Winter precipitation (mm)	165.15 ± 60.1	158.92 ± 69.2
Total Precipitation (mm)	535.80 ± 130	928.64 ± 260
Sand (%) at 10-20 cm	59.50 ± 20.1	38.09 ± 17.9
Calcium (cmol kg^{-1}) at 10-20 cm	38.24 ± 27.1	45.80 ± 20.2

cm) + 0.88 (winter precipitation) - 1.21 (total precipitation) - 1.38 (sand at 10-20 cm) + 0.20 (calcium)

dies =+ 1.82 + 3.22 (total nitrogen) - 1.37 (mean minimum temperature in the coldest month) - 2.41 (sand at 0-10 cm) - 0.80 (winter precipitation) + 1.21 (total precipitation) + 1.38 (sand at 10-20 cm) - 0.20 (calcium).

Our inability to measure freezing temperature impact on exposed T-4464 crowns may account for predictive differences (10%) between the 2 models. To illustrate freezing temperature importance, we will describe the fate of 4 T-4464 seeding sites in southern Arizona (unpublished data, USDA-Agricultural Research Service, Tucson, Ariz.). Soils at the 4 sites were similar in depth and classified as sandy loam, elevations varied from 1,100 to 1,125 m, and 3.0 kg ha^{-1} of T-4464 seed (PLS) was sown on disk plowed fields in July 1980. In summer 1981, plant densities varied from 3 to 4 plants m^{-2}, and all sites were heavily grazed in summer-fall 1981 through 1985. Following a rapid drop in temperatures during mid-January 1986, plants at 2 sites died, and plants at 2 sites persisted. Where T-4464 died, temperatures at the crown base varied from 3 to 5 C for 4 hours. Where plants persisted, temperatures at the crown base varied form 3 to 5° C for 1.5 hours.

To generate predictions from discriminant function analyses models, all equations are solved using data from the potential seeding site. The prediction for a potential seeding site is from the equation where the solution is closest to 1.0. For example, if we solve for the 3 equations in **Model I** and generate values of 0.21, 0.87 and 0.01 for spreads, persists and dies, respectively, the model prediction is that T-4464 would persist.

Management Implications

Many range seeding failures occurred because land managers did not appreciate the importance of climate and soil to species adaptation. To emphasize this point, Cox et al. (1988) summarized rangeland revegetation techniques most frequently used in the past 100 years. The most widely used procedure has been to: 1) chemically or mechanically reduce competition, 2) prepare a seedbed, 3) plant seed of as many species, accessions or cultivars as possible, and 4) hope for rain. In about 1 of every 10 attempts, plants were successfully established but it was not possible to predict planting success at another site or estimate plant adaptability because climate and soils were not compared among sites.

To determine the importance of climate and soil on T-4464 buffelgrass survival, we classified 167 seeding sites into 3 survival regimes. We conclude that planting success or failure can be predicted with selected climatic and soil parameters, and climatic and soil parameters where T-4464 seed was collected in northcentral Kenya are more similar to where the species spreads than where it persists or dies in North America. Our results are practical and easily used by land managers who wish to maximize plant survival, and minimize soil erosion and economic loss.

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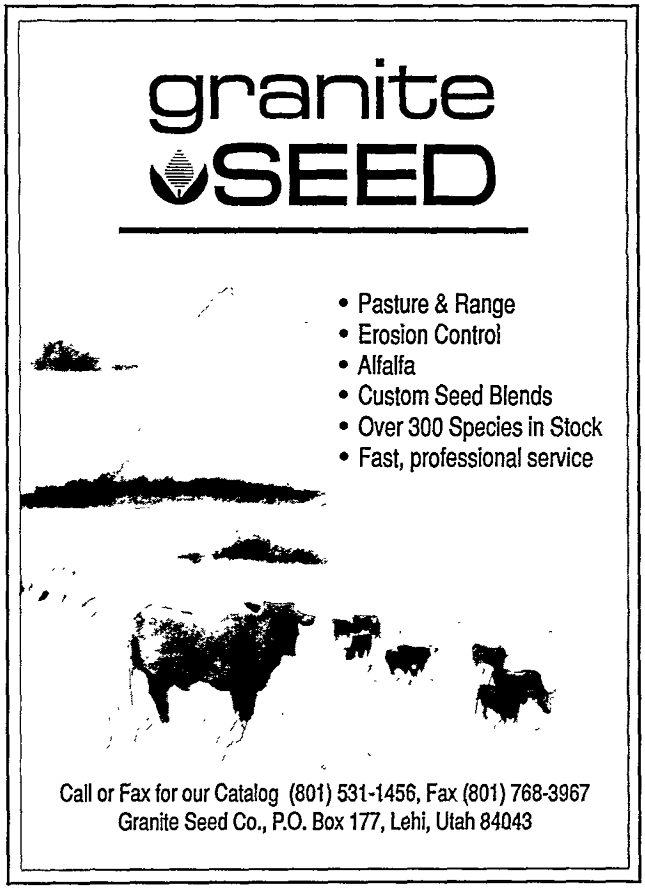

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Climatic effects on buffelgrass productivity in the Sonoran Desert

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Abstract

Buffelgrass (*Cenchrus cilaris* L.), a perennial bunchgrass from northcentral Kenya has been successfully seeded on 400,000 ha in northwest Mexico. To determine if carrying capacity increased after buffelgrass introduction we measured live, recent-dead standing, old-dead standing and litter at 2-week intervals for three years. Live biomass was produced throughout the year but peak production, over the 3 years was in August. Peak live biomass production varied from 465 kg/ha in a summer of below-average precipitation to 3,045 kg/ha in a summer of above-average precipitation. Recent- and old-dead standing quantities were highly variable among years and transfers among components were dependent on temperature and precipitation. Buffelgrass annually produces about 3 times more green forage than native grasses.

Key Words: *Cenchurs ciliaris* L., above-ground biomass components, perennial introduced grass, northwest Mexico, hot desert, North America

In the late 1600's cattle were introduced in the Sonoran Desert of northwest Mexico, but numbers remained low until Indian raids declined in the 1800's (Hasting and Turner 1972). Since 1890, wet periods with abundant forage have been followed by overstocking, droughts and livestock reductions (Waggoner 1952). With each successive cycle, perennial grass productivity declined and northwest Mexico rangeland supported fewer livestock (Bryan 1925). Excessive and continuous grazing has been associated with the conversion of semidesert Sonoran grasslands into shrublands (Cooke and Reeves 1976).

Attempts to restore grassland productivity with native perennial grasses began in the 1950's (Cota and Johnson 1975), but plantings failed because native grass seedlings could not compete with shrubs and introduced annuals for moisture and nutrients (Cox et al. 1982). In the mid 1950's seed from African perennial grasses were introduced into northwest Mexico. One of these grasses, T-4464 buffelgrass (*Cenchrus ciliaris* L.) has been successfully seeded throughout the Sonoran Desert (Ibarra-F. et al. 1987).

It appears that the carrying capacity of rangelands in northwest Mexico increased after the introduction of T-4464 (Hanselka and Johnson 1991), but production potential needs to be measured to determine if this hypothesis is true. One of the steps in a program to evaluate carrying capacity should be to quantify the annual accumulation and decomposition characteristics of live biomass, dead standing biomass and litter in years with different weather-patterns (Weaver 1954).

Several studies have evaluated buffelgrass production (Paull and Lee 1978, Gonzales and Dodd 1979, Anning 1982, Ibarra-F. et al. 1987), but none have attempted to evaluate productivity as influenced by climate. The objective of this study was to determine how precipitation amount and distribution affected plant above-ground biomass accumulation and decomposition.

Materials and Methods

Study Site

The study site is located 82 km north of Hermosillo in northwest Sonora, Mexico (29° 41' N lat.; 115° 57' W long.) at the Carbo Livestock Research Station. Elevation is 470 m, slope is 1-2%, and soil is a Anthony fine loam (thermic Typic Torrifluvent). Soils are recent alluvium, weathered from granitic rocks, moderately basic (pH= 8.5-8.9), and depth ranges from 2 to 6 m (Hendricks 1985).

Average annual precipitation is 320 mm (Centro de Investigaciones Pecuarias del Estato de Sonora 1989). Precipitation is bimodally distributed: approximately 60% comes between July and September, and about 40% comes between October and April. May, June, and September are usually dry but exceptions do occur (Fig. 1). Summer rainfall comes as thunder-

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storms which are frequently localized and of high intensity. Daytime temperatures average 34° C, but frequently exceed 40° C in June through August. Nighttime temperatures average 8° C in winter, and may approach 0° C in either December, January, or February.

A 2.5 ha stand of dense, shrub-free buffelgrass was fenced to exclude livestock. Nine 20 by 70-m plots were established with 3 plots in each of 3 blocks. One plot in each block was randomly selected for sampling at 2-week intervals between 15 July 1985 and 1 July 1986. Three additional plots were sampled between 15 July 1986 and 1 July 1987. The remaining plots were sampled between 15 July and 1 July 1988. The Experimental design was randomized complete block with 3 replications each year.

Field Measurements

On each sampling date, 5 previously unsampled 1 by 1-m quadrats were randomly selected in each plot. Buffelgrass plants were harvested at the soil surface and litter collected from the soil surface.

Forage from 3 of the 5 quadrats in a plot was separated into live (green), recent-dead standing (yellow), and old-dead standing (gray) components. Separated and unseparated forage samples and litter were dried in a forced-draft oven at 40° C for 72 hours and weighed. Forage component dry weights from the 3 quadrats were pooled and the contribution of each to the total forage dry weight expressed as a percentage. Average component percentages were multiplied by the total forage dry weight of the unseparated quadrats. The derived dry weight component value for the 2 unseparated and the 3 separated quadrats were averaged to provide an estimate of the plot dry biomass for each forage component at each sampling date.

Precipitation was measured daily at the Carbo Livestock Research Station. Daily precipitation was summed for all dates between harvest (Fig. 1).

Statistical Analyses

The year effect was evaluated for each forage component on each sampling date using analysis of variance. When F-values were significant ($P \leq 0.05$) Least Significant Difference Tests (Steel and Torrie 1960) were used to separate means. Regression and correlation analysis were used to determine the relationship between precipitation and forage production in summer and winter.

Results and Discussion

Live Biomass

The distribution of warm- and cool-season precipitation (Fig. 1) directly influences the bimodal peaks in live biomass production

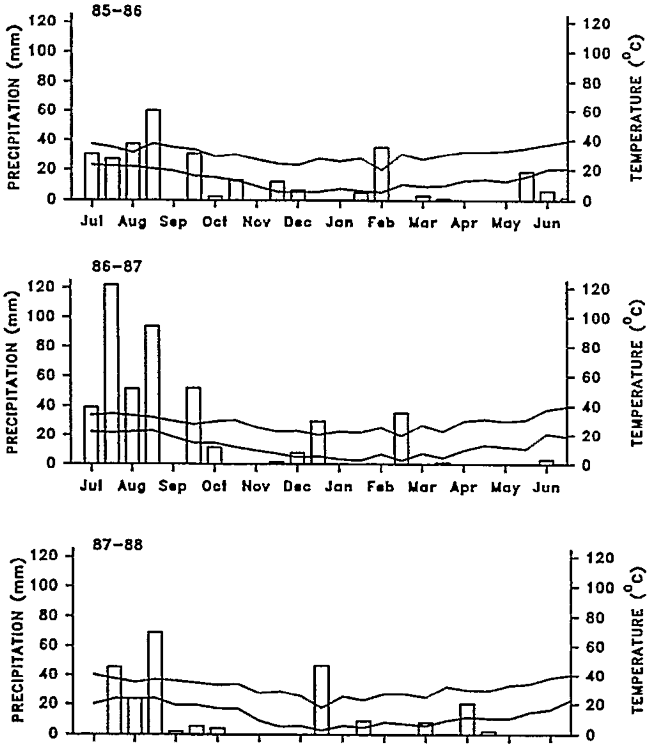

Fig. 1. Monthly precipitation (bars), mean daily maximum temperatures (upper solid line) and mean nighttime minimums (lower solid line) during 3 years at Carbo Livestock Research Station in Northwestern Mexico.

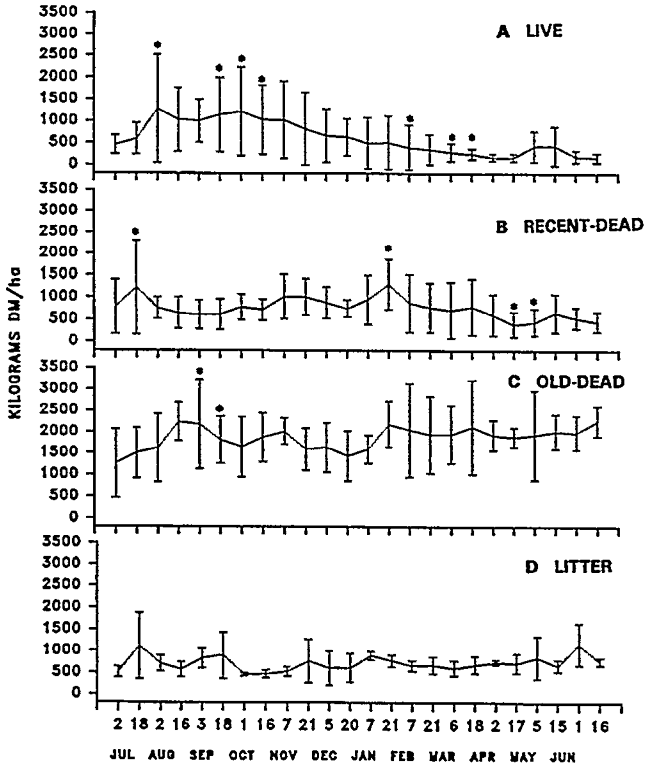

Fig. 2. Three year means and standard errors for live biomass (A), recent-dead standing biomass (B), old-dead standing biomass (C), and litter (D) of buffelgrass sampled over 3 years in Sonora, Mexico. An asterisk (*) indicates a significant difference ($P \leq 0.05$) among years at the same sampling dates. Sampling years were from 15 July 1985-1 July 1986, 15 July 1986-1 July 1987, and 15 July 1987-1 July 1988.

Table 1. Total accumulative summer or winter precipitation (mm) between 1985-88, on buffelgrass biomass (kg/ha) components.

Season	Biomass component	Regression equation	r^2
Summer	Live	$Y = -1527.9 + 19.8X$	0.85*
	Reecent-dead	$Y = -979.0 + 5.5X$	0.22 NS
	Old-dead	$Y = -3299.1 + 5.1X$	0.03 NS
	Litter	$Y = -716.9 + -0.1X$	0.01NS
Winter	Live	$Y = 1431.2 + -1.7X$	0.04 NS
	Recent-dead	$Y = 197.9 + 39.1X$	0.30 NS
	Old-dead	$Y = -1666.5 + 69.9X$	0.25 NS
	Litter	$Y = 1060.8 + 14.3X$	0.10 NS

*Significant at $P \le 0.05$.
NS = Not significant.

(Fig. 2-A). Live biomass was different ($P \le 0.05$) among years on 2 summer, 2 fall and 3 winter sampling dates, and similar at remaining dates over the 3 years.

Summer (July-September) accumulative precipitation was above the long-term average (192 mm) in 1986 (358 mm), and below average in both 1985 (186 mm) and 1987 (146 mm). Peak live biomass production was greatest in 1986 (3,025 kg/ha), intermediate in 1985 (1,040 kg/ha) and least in 1987 (465 kg/ha).

Plants began to actively grow 15 days after 20 mm storms on 14 July 1985, 10 July 1986, and 28 July 1987. After initial 20 mm storms, culms elongated in 20 days, leaves elongated in 25 to 27 days and seedheads were present in 30 days. Green leaves produced at the plant base grew horizontally and were protected by recent-and old-dead standing biomass. Most summer leaves became dormant in fall and winter but a few leaves remain green throughout the year. Following fall, winter, and spring moisture, green leaves emerge at the crown base but leaves elongate only when minimum temperatures approach 15° C (Cox et al. 1988).

Observations made during this 3 year study suggest that buffelgrass initiates leaf production whenever soil moisture is available and minimum temperatures exceed 15° C. When more than 150 mm of precipitation was recorded in summer (Fig. 1), live biomass exceeded 1,000 kg/ha (Fig. 2-A). When summer precipitation was less than 150 mm live biomass approached 500 kg/ha.

In northwest Mexico precipitation is bimodally distributed, and summer precipitation has the greatest effect on plant growth (Table 1). The coefficient of determination between accumulative summer precipitation and summer buffelgrass growth ($r^2 = 0.85$) is 20% greater than that reported for other warm-season African grasses (Cox et al. 1990) and native grasses (Cable 1975) in Arizona. Hence about 80% of the summer growth of buffelgrass can be accounted for by accumulating the July to September precipitation. The lack of correlation between winter precipitation and winter growth is because winter temperatures of 5°C or less limit leaf growth (Cox et al. 1988).

Recent-Dead Standing

Recent-dead biomass was different ($P \le 0.05$) among years on 1 summer, 1 winter and 2 spring sampling dates, and similar on remaining dates over the 3 years (Fig. 2-B). Recent-dead generally increased in summer, decreased in fall, increased in winter and decreased in spring.

Recent-dead accumulations in summer and winter were highly variable and the rate of transfer to old-dead standing was dependent on the presence or absence of precipitation. With each successive July and August storm, recent-dead weathered and transferred to old-dead. In summer, the recent-to old-dead transfer may occur in as few as 20 days (1986) on as many as 35 days (1987). Immediately following precipitation in February 1986 and 1987, and December 1987, we observed a rapid recent-dead to old-dead transfer and a winter greenup (Fig. 2). The recent- to old-dead transfer occurred in 15 days during the mild spring of 1986, and in 30 days during the cool spring of 1987.

Old-Dead Standing

Old-dead biomass was different ($P \le 0.05$) at 2 summer sampling dates, and similar at all remaining dates over the 3 years (Fig. 2-C). Unusually low quantities in summer and fall 1985 were related to livestock activities prior to fencing, and rapid transfer from old-dead to litter occurred during the atypically wet summer of 1987. During the atypically wet summer, we observed termites (*Gnathamitermes perplexus*) harvesting old-dead standing in native grass stands, we did not observe termite activity in buffelgrass stands. Buffelgrass seed stalks may contain more lignin than native grass seed stalks.

Litter

Litter quantities were similar ($P \le 0.05$) at all sampling dates over the 3 years (Fig. 2-D). Litter amounts in summer of 1985 exceeded those in other years because old culms dislodged by cattle prior to fencing accumulated on the soil surface after summer thunderstorm activity.

Litter quantities generally peaked in spring and summer, and disappeared in fall and winter. Observations suggest that spring winds dislodge dead leaves and culms, and summer rains move leaf and culm fragments from open areas between plants to areas beneath buffelgrass canopies. Litter accumulations beneath plant canopies may serve as a nitrogen reserve which becomes available to forbs in late winter and to perennial grasses in summer (Cox et al. 1984).

Management Implications

Above-ground net primary production (ANP) of buffelgrass was 7,025 kg/ha in south Texas (Gonzales and Dodd 1979, Hanselka and Johnson 1991), ranged from 3,000 to 7,000 kg/ha in Queensland, Australia (Paull and Lee 1978), and averaged 6,950 kg/ha during the 3 years of this study. ANP of 10 North America ungrazed temperate grasslands averaged 2,350 kg/ha, and ranged from 540 to 5,230 kg/ha (Sims and Singh 1978). At selected sites in northwest Mexico and south Texas, buffelgrass production is about 25% greater than the most productive grasslands in North America.

In the Sonoran Desert, livestock carrying capacity varies from 27 to 40 ha/AUY (animal unit year) on native range, from 9 to 15 ha/AUY on planted buffelgrass pasture, and from 3 to 4 ha/AUY on combinations of native range and buffelgrass pasture (Ibarra-F. and Cox 1988, Martin-R. 1989). In pastures where buffelgrass occurs with native forbs, grasses and shrubs we observed livestock grazing shrubs in winter and spring, forbs and buffelgrass leaves in spring, buffelgrass in summer, and buffelgrass and shrubs in fall. This seasonal pattern of animal selectivity may explain why livestock productivity increased when buffelgrass plantings were strategically located in native rangeland pastures.

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Response of a mixed native warm-season grass planting to nitrogen fertilization

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Abstract

Plant available nitrogen limits production of native warm-season grasses on marginal farmland in the Southern Plains. In this western Oklahoma study, N was applied at 0, 35, 70, or 105 kg N ha^{-1} yr^{-1} to a mixed stand of blue grama (*Bouteloua gracilis* (H.B.K.) Lag. ex Griffiths), sideoats grama (*B. curtipendula* (Michx.) Torr.), little bluestem (*Schizachyrium scoparium* (Michx.) Nash), sand bluestem (*Andropogon hallii* Hack.), switchgrass (*Panicum virgatum* L.) and indian grass (*Sorghastrum nutans* (L.) Nash). The grass was established on sandy loam soil farmed an estimated 90 years. With near-normal precipitation the first year, production of perennial grasses increased linearly with 26 kg herbage produced kg^{-1} N applied. In drouth conditions, the second and third years, production averaged 10 kg herbage kg^{-1} N applied. The fourth and fifth year the stand was not fertilized and residual effects measured. Herbage production increased 10 kg for each kg N applied over the previous 3 years. Blue Grama made up much of this increased herbage production along with warm-season annuals (*Panicum capillare* L. and *Amaranthus retroflexus* L.). With increasing N rates the residual N effect increased the proportion of blue grama and decreased the proportion of taller perennial grasses. Thus, N fertilization of mixed native warm-season grass stands established on marginal farmland, typical of stands established on sandier soils under the USDA Conservation Reserve Program, can result in substantial herbage yield increases, however, some of the increased yield may be from weedy species.

Key Words: Southern Plains, marginal farmland, nitrogen use efficiency, blue grama, sideoats grama, warm-season annuals

Native warm-season grass mixtures have been established in USDA Conservation Reserve Program (CRP) plantings on several million hectares of highly erodible marginal farmland in the Southern Great Plains. Upon termination of CRP contracts, the major options will be to graze the grass or return the land to wheat (*Triticum aestivum* L.) or sorghum (*Sorghum bicolor* (L.) Moench) production. In some cases, this land use decision will depend upon the productivity of the grass. The grass mixtures often include blue grama (*Bouteloua gracilis* (H.B.K.) Lag. ex Griffiths), sideoats grama (*B. curtipendula* (Michx.) Torr.), little bluestem (*Schizachyrium scoparium* (Michx.) Nash), sand bluestem (*Andropogon hallii* Hack.), switchgrass (*Panicum virgatum* L.) and indian grass (*Sorghastrum nutans* (L.) Nash).

Grass production on marginal farmland in the Southern Plains has been shown to be limited by N availability (Herndon 1974, Salih and Burzlaff 1975, Berg 1990) following years of cultivation and erosion that reduced organic C and N in these soils (Haas et al. 1957). Nitrogen fertilization of introduced warm-season grasses is a common practice in the region (Dahl and Cotter 1984, Berg 1990). However, native warm-season grasses are seldom N fertilized. This may be for a number of reasons including:

1) research showing increased cattle gain with N fertilization of native rangeland dominated by warm-season grasses is not economically attractive (Huffine and Elder 1960, Donart et al. 1978);
2) weedy species increase with N fertilization (Huffine and Elder 1960, Launchbaugh 1962, Petit and Deering 1974); and
3) the taller native grasses will not persist under intensive grazing commonly used on N-fertilized introduced grasses (Bidwell 1992).

This study was designed to determine the response of a native mixed grass planting on marginal farmland to 3 rates of N applied at April greenup or 3 and 6 weeks later. Time of N application was included as a variable to investigate the effect on herbage production and species composition, particularly weedy annuals. Nitrogen was applied at rates estimated to represent minimum, moderate, and maximum practical applications. A record drouth during the second and third years of the study provided an opportunity to observe the response of the planting to the combination of N fertilization and drouth.

Materials and Methods

This field study was conducted from 1989 through 1993 at the USDA-ARS Southern Plains Range Research Station near Woodward in northwestern Oklahoma. The land had been cultivated an estimated 90 years since the native mixed-grass prairie was plowed. Plots were on Enterprise fine sandy loam (coarse-silty, mixed thermic Typic Ustochrepts) which contained an average of 4.8 g organic C kg^{-1} (Mebius method, Nelson and Sommers 1982), 0.57g N kg^{-1} (Kjeldahl procedure, Bremner and Mulvaney 1982), and pH of 7.0 (1:1, wt:wt) in the surface 15 cm. Nitrate tested low at 2 mg N kg^{-1} (calcium sulfate extraction, Hanlon and Johnson 1983) as did ammonium at 5 mg N kg^{-1}

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(steam distillation, Kenney and Nelson 1982). Phosphorus tested adequate at 50 mg P kg^{-1} (Bray #1, Hanlon and Johnson 1983) as did potassium at 430 mg K kg^{-1} (ammonium acetate extraction, Hanlon and Johnson 1983).

A seed mixture of the following species and rates was drilled in April 1987: 'Hachita' blue grama 30 pls m^{-2}, 'El Reno' sideoats grama 30 pls m^{-2}, 'Cimarron' little bluestem 30 pls m^{-2}, 'Woodward' sand bluestem 12 pls m^{-2}, 'Blackwell' switchgrass 20 pls m^{-2}, and 'Cheyenne' indian grass 20 pls m^{-2}. Grass establishment was good with sideoats grama and blue grama the dominant grasses established. The stand was not grazed or hayed in 1987 or 1988, in April 1989 the aftermath was mowed and left in place.

In April 1989 an 18 x 60-m study area was selected and treatments randomly assigned to 3 x 9-m plots within each of 4 blocks and repeated on the same plot for 3 years (1989, 1990, 1991). Treatments were a check (0 N) and factorial combination of 3 N application dates (early April, late April, and mid May) and 3 N application rates (35, 70, and 105 kg ha^{-1}). The N was broadcast as ammonium nitrate.

In this area, these warm-season native grasses commonly start to greenup in early April and have 5 to 10 cm of new growth by mid-May. Herbage production was determined by using a sicklebar mower to cut a 1.25 x 7.75-m area within each plot, weighing, subsampling, and drying at 57°C. Harvests at a cutting height of 5 cm were made on 18 July 1989, 5 July 1990, and 27 June 1991. A 0.2 x 5-m area was hand clipped in each plot on 20 July 1989 and the harvest separated into annuals and perennials. Dormant season aftermath harvests were made in early winter 1989 and 1990. A dormant season harvest was not made in 1991 since there was no regrowth in this drouth year. After each sampling the entire plot area was harvested and herbage discarded off the plot area.

Precipitation in the October through September period was 645 mm in 1988-89, 340 mm in 1989-90, 355 mm in 1990-91, 585 mm in 1991-92, and 640 mm in 1992-93. The 1914-1993 average annual precipitation was 593 mm; precipitation for 1990 and 1991 was the least for any 2 consecutive years within this period. Precipitation for 3 years the study was N fertilized is shown in Fig. 1.

Because of the drouth, the study was not fertilized in 1992 and the following sampling done in mid July 1992 and 1993. Herbage production by species or groupings of species was measured by hand clipping at 2 cm, two 0.5 x 2-m quadrats in each plot and drying at 57°C. The remaining herbage in each plot was not cut after the 1992 sampling so as to allow seed production by weedy annuals. The aftermath was mowed in March 1993 and left in place.

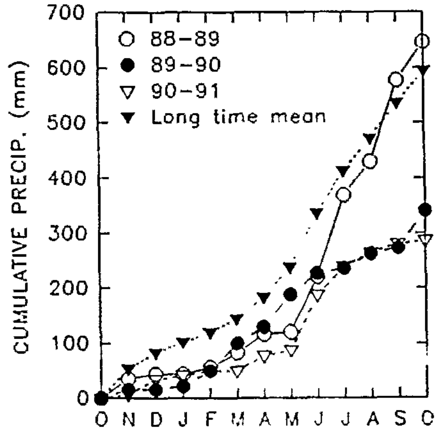

Fig. 1. Precipitation at Woodward, Okla. was below normal in October through March the first 3 years of the study and much below normal for the second and third growing seasons.

Frequency by species rooted within each quadrat was determined in 1992 within fifty 0.1 m^2 quadrats within each plot, quadrat placement was at 0.25-m intervals along two 6-m poles randomly placed length wise in the plots. Frequency sampling was also extended to four 3 x 9-m plots each adjacent to 1 of the 4 blocks but outside of the original plot area. These additional plots received no N treatments and were not harvested during the 1989, 1990, or 1991 growing seasons, these plots were mowed in the early spring of each year and the cuttings left in place.

Analysis of variance was used to determine effect of N application dates on herbage production. Herbage yields from the earliest 1989, 1990, and 1991 N application dates were partitioned into linear, quadratic, cubic, and residual components by year, only regressions significant at the 0.05 level are reported. Mean herbage yield from all 3 times of N application treatments were used to calculate residual N effects in 1992 and 1993 as there was no significant difference among N application dates these years.

Results

Herbage yield in 1989 increased linearly with N applied (Fig. 2.). The slope of the regression line (Fig. 2) is the efficiency of fertilizer N to increase herbage yield. Thus for 1989, slope = 26 kg herbage yield kg^{-1} N applied. In 1989, precipitation was below normal until June rain of 150 mm brought accumulative precipitation to near normal (Fig. 1) and enhanced growth of the warm-season grasses. Annuals comprised an average of 1.9% of the herbage yield in July 1989 with nonsignificant differences among N treatments.

Drouth in 1990 and 1991 (Fig. 1) drastically reduced herbage yields on all treatments and resulted in an average of 10 kg herbage yield kg^{-1} N applied (Fig. 2). Or if a probability of <0.10 is accepted, the relationship in 1991 is curvilinear (quadratic) with smaller yield increases per kg N applied as N rates increased. Grass in N treatments wilted and leaf tips burned during summer drouths, whereas unfertilized grass was only slightly affected. Herbage production by annuals was not determined in 1990 and 1991 since by inspection annuals made up less than 2% of the mass of herbage harvested.

Nitrogen application in April 1989 or early April 1990 produced greater July herbage yields than mid May application in 2 of the 3 years N was applied (Table 1). However, total yearly herbage yield was not affected by time of N application. Perennial grasses comprised most of the herbage yield in 1989, 1990, and 1991 following considerably below normal October through March precipitation prior to these 3 growing seasons (Fig. 1).

Regrowth after the 27 July 1991 harvest was negligible and by April 1992 it was obvious that many sideoats grama plants were dead. As a consequence, the plots were not fertilized in 1992 and the residual effect of the previous 3 years of N fertilization was measured on herbage production in 1992 and 1993. The residual effect over 2 years was directly proportional to the amount of N

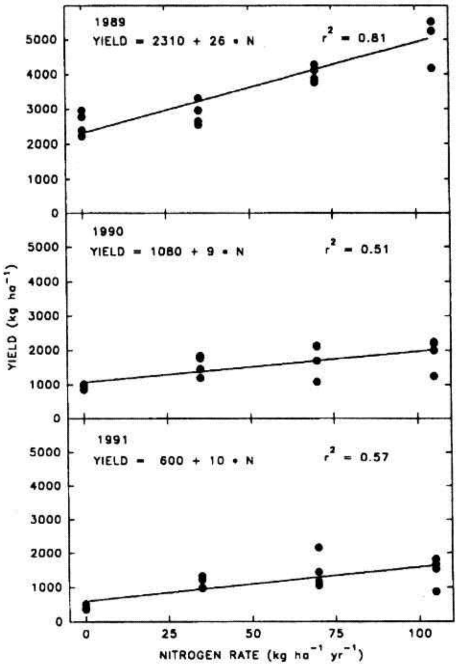

Fig. 2. Herbage yields from a mixed native grass planting in western Oklahoma as related to the rate of N applied each of 3 years.

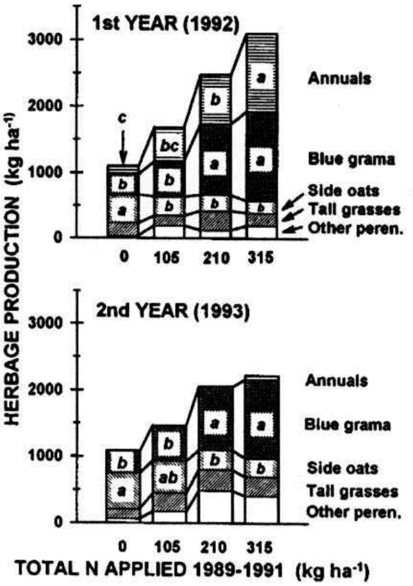

Fig. 3. First and second year residual effects on herbage production by species following N application the previous 3 years to a mixed warm-season grass planting. Herbage production across N rates within a species and year indicated by a common letter or no letter are not significantly (P>0.05) different.

applied, with herbage production increasing 10 kg for each kg N applied over the previous 3 years. Herbage production (kg ha^{-1}) in 1992 = 1,070 + 6.8 • total N applied 1989-91, r^2 = 0.78**. Blue grama made up about one-half of the increased production in 1992, the remainder was largely warm-season annuals, predominately annual panicum (*Panicum capillare* L.) and pigweed (*Amaranthus retroflexus* L.) (Fig. 3).

The residual N response in 1993 was less, with herbage yield = 1,150 + 3.6 • total N applied 1989-91 r^2 = 0.76**. Blue grama made up nearly all this increased herbage production (Fig. 3). Annuals were unimportant, and production by sideoats grama decreased at the higher residual N rates (Fig. 3). Western ragweed (*Ambrosia psilostachya* DC.) was the major herbage producer among the other perennials on the higher residual N rate treatments.

The residual effects were also shown in species frequency determined in 1992 when blue grama and annuals increased and sideoats grama decreased as N rates increased (Fig. 4). Frequency of tall grasses (sand bluestem, little bluestem, switchgrass, indian grass) decreased and frequency of blue grama and annuals increased on unfertilized plots harvested annually in mid-summer as compared with unfertilized plots that were not harvested in mid summer (Fig. 4).

Discussion

Grazing is the major use of native grass seedings in the Southern Plains. Clipping studies, such as reported here, may provide information, but must be used with caution when extrapolating to grazing. This is because N is recycled with grazing (Russelle 1992), herbage production may not be closely correlated with cattle gains (Rogler and Lorenz 1974), and plant physiological responses may be different to clipping than grazing.

Herbage production on the unfertilized native grass planting in this study averaged 1,230 kg ha^{-1} yr^{-1}. Most of this production was by perennial grasses. This production is about half of that suggested by SCS (Cole et al. 1966) standards for the loamy prairie site on the Enterprise soil series, but is near the 1,200 kg ha^{-1} yr^{-1} forage production measured over 8 years on moderately stocked native range in the area (McIlvain and Shoop 1961). Thus, forage production on the unfertilized native grass planting on marginal farmland may be similar to production on native rangeland that has a history of heavy grazing by domestic livestock.

Table 1. Herbage yields of a native grass planting in western Oklahoma as affected by time of N application. Herbage yields are averaged over 3 N rates.

Time of application	Year of N application and 1st harvest date					Residual	
	1989		1990		1991	1992	1993
	18 Jul.	Total	5 Jul.	Total	27 Jun.	21 Jul.	21 Jul.
	-kg ha^{-1}-						
early Apr.	2,820 a*	4,040 a	1,300 a	1,750 a	1,350 a	2,260 a	1.900 a
late Apr.	2,900 a	4,130 a	970 b	1,410 a	1,390 a	2,770 a	1,910 a
mid May	2,230 b	3,710 a	990 b	1,400 a	1,430 a	2,370 a	1,890 a
	-cv,%-						
	8	7	12	12	11	19	7

*Yields within a column designated with a common letter are not significantly (P>0.05) different.

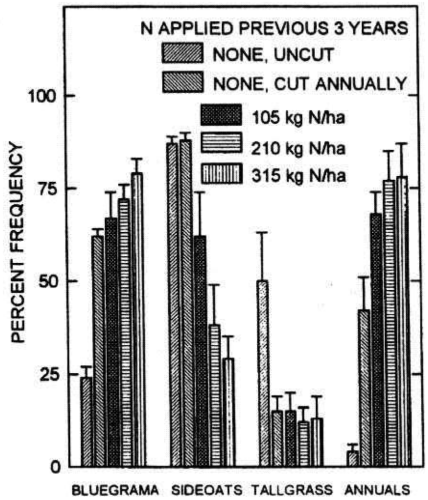

Fig. 4. Plant frequency within 0.1 m^2 quadrats the year 1992 following 3 years of N treatments on a mixed warm-season grass planting. Vertical, capped lines equal + SE.

Nitrogen fertilization over 3 years increased herbage yield by an average of 15 kg herbage kg^{-1} N applied (Fig. 2). Adding the residual effect (Fig. 3) gives an overall N use efficiency of 25 kg herbage production kg^{-1} N applied. This N fertilizer use efficiency is within the range of 10 to 34 kg herbage produced kg^{-1} N applied for cool-season- grasses (Wedin 1974), and 15 to 40 for warm-season grasses (Wilkinson and Langdale 1974, Tucker and Murdock 1984). However, comparisons should be made with caution since the maturity of grass when harvested can greatly influence herbage production, and residual effects were not accounted for in the cited studies. The substantial herbage production response to residual N in this study is apparently a reflection of limited herbage production on N-fertilized treatments in drouth conditions in 1990 and 1991.

Herbage production by weedy annuals was negligible on all N treatments in 1989, 1990, and 1991 following much below normal October through March precipitation. This finding is in contrast to research in New Mexico where annuals increased with N fertilization with drouth conditions (Fulgham et al. 1977).

Weedy annual production in 1992 (Fig. 3) was greatly enhanced by the previous 3 years of N fertilization. This finding is in agreement with studies showing an increase in production of annuals with N fertilization of native warm-season grasses (Huffine and Elder 1960, Launchbaugh 1962). In 1993, weedy annual production was small or negligible regardless of the previous N treatments. Overall, enhanced production of weedy annuals following N fertilization appears to be dependent upon both the timing and amount of precipitation. Annual bromes (*Bromus* spp.) were not important herbage producers in our study, but would be expected to be important with N fertilization and normal precipitation patterns (Lauchbaugh 1962). In the longer term, western ragweed, a perennial may be more of a problem in N-fertilized native grass plantings than annuals. Blue grama increased and taller warm-season grasses decreased with the combination of N fertilization and growing season defoliation in this study.

Overall, this study indicates that herbage production is limited by N availability to native warm-season grasses established on marginal farmland typical of much of the sandier land now in the Conservation Reserve Program in the Southern Plains. Nitrogen fertilization increased herbage production with a fertilizer N use efficiency equal to or somewhat less than that on introduced grasses in the area (Berg 1990) and other warm-season grasses in the southeastern U.S. (Wilkinson and Langdale 1974).

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Optimization of rangeland management strategies under rainfall and price risks

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Abstract

Dynamic programming was used to obtain optimal management and marketing policies for stocker operations in Southeastern Colorado under different stocking rates, rainfall, and price scenarios. Simulated steer liveweights at low, moderate, and high stocking rates were incorporated with simulated steer prices to maximize the present value of net returns from the sale of 0, 50, and 100% of the steer inventory in July, August, September, or October. Two low-risk, 1 moderate-risk, and 2 high-risk scenarios were considered. The 2 low-risk scenarios were *favorable rainfall-optimistic price* and *favorable rainfall-pessimistic price*. The moderate-risk scenario was *average rainfall-average price*. The 2 high-risk scenarios were *unfavorable rainfall-optimistic price* and *unfavorable rainfall-pessimistic price*. The highest net returns from the low-risk and moderate-risk scenarios were obtained at the high stocking rate with sales in September and October. The highest net returns from the high-risk scenarios were obtained at the moderate stocking rate with sales in September and October. Risk-averse operators who are not prepared to handle sales before October will be better off using a low stocking rate. Risk-taker operators will obtain higher net returns than risk-averse operators using a high stocking rate providing they are prepared to sell half of the herd in July if cumulative rainfall up to June is below 149 mm. If this high stocking rate is maintained beyond July, operators should sell in September independently of the amount of rainfall or the level of prices in August.

Key Words: rangeland resource economics, risk analysis, dynamic programming.

Rangeland livestock producers face the challenge of managing in the present and planning for the future under ever-changing production, marketing, and financial conditions. Surveys conducted by Walker and Mapp (1984) and Patrick et al. (1985) showed that livestock price fluctuations, erratic weather, and uncertain input costs were ranked by ranchers and farmers as the leading sources of net-return variability. Early proceedings from the Committee on Economics of Range Use and Development of the Western Agricultural Economic Research Council (1966) indicated high expectations from potential applications of risk management research. However, a survey conducted by Walker and Nelson (1980) among teaching and extension faculty across the nation reflected only modest levels of instruction on risk and decision theory.

A renewed interest in risk analysis has developed in the last 10 years. Most of the models developed in this period have treated risk within a static, risk-averse framework. A static approach may not be consistent with the way decision-makers behave under risk. Rangeland production is a dynamic process in which rainfall and price uncertainty compromise biological efficiency and expected income throughout. Management flexibility is extremely important to counteract negative rainfall and price influences. Moreover, risk influences farmers and ranchers' decisions, whether they are risk-neutral or risk-averse. Consequently, dynamic, risk-neutral optimization models may be more useful than static, risk-averse optimization models in obtaining management and marketing policies for rangeland livestock operations.

Dynamic optimization models have a recursive structure and can incorporate non-linear production functions. In these type of models, the optimal solution depends on the level of control applied to the system level of production, input costs, and price variability. Fisher (1985), Rodríguez and Taylor (1988), Lambert (1989), Garoian et al. (1990), and Schroeder and Featherstone (1990) incorporated production and price variability into dynamic optimization models. Most of these previous efforts concentrated in obtaining optimal marketing policies for cow-calf and cow-calf/yearling operations. With the exception of Rodríguez and Taylor (1988), no research efforts have looked into the development of intra-seasonal optimal marketing policies for stocker operations in the presence of rainfall and price risks at different stocking rates.

This paper addresses:

a) The need to model marketing and management decisions in rangeland stocker operations in a dynamic rather than static setting. A dynamic approach is more reflective of how decision-makers operate.

b) The demand for a spectrum of optimal alternatives for stocker operations instead of an unique solution. The alternative cho-

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sen by the operator depends on his/her own degree of risk aversion relative to the degree of rainfall and price risks present in each situation.

In a stocker operation, the producer either buys 160-kg calves in October/November expecting to sell them at 340 kg in October/November of the next year, or buys 227-kg steers in May and expects to sell them at 340 kg in October/November of the same year. The study presented here incorporated the means of simulated steer live weight for low (5.6 ha/steer), moderate (3.8 ha/steer), and high (2.5 ha/steer) stocking rates with the means of simulated steer prices to maximize the present value of net returns (NPV) from the total or partial sale of the steer inventory in July, August, September, or October.

Two low-risk, 1 moderate-risk, and 2 high-risk scenarios were considered. The 2 low-risk scenarios were *favorable rainfall-optimistic price* and *favorable rainfall-pessimistic price.* The moderate-risk scenario was *average rainfall-average price.* The 2 high-risk scenarios were *unfavorable rainfall-optimistic price* and *unfavorable rainfall-pessimistic price.*

A Dynamic Programming Model for Stocker Operations

Dynamic programming was used to maximize the present value of net returns in July, August, September, and October. Net return was a function of the state variable *inventory of stocker steers on hand* (IN) and 2 dependent variables, *steer liveweight* (LWT) and *steer price* (PR). The state variable *inventory of stocker steers on hand* was represented by initial values of 34, 50, and 75 steers in a 190-ha pasture for low (5.6 ha/steer), moderate (3.8 ha/steer), and high (2.5 ha/steer) stocking rates (SR), respectively. The optimal value function was obtained with the following recurrence relationship:

$$f_t(IN_t) = \max[\{(PR_t^k*LWT_{t,l}*CS(u))-(COM*CS(u))-(VCH_t*IN_t)\} + ß_t * f_{t+1}(IN_{t+1})] - f_0 \qquad (1)$$

where:

$f_t(IN_t)$ = the present value of net returns from following an optimal policy with t stages remaining in the planning horizon, given a specific inventory at hand IN_t.

LWT_t = the mean of steer live weight in time t.

PR_t^k = the mean of steer price of the k weight-class in time t. The weight-class is determined by LWT_t.

$CS_t(u)$ = number of steers sold in time t according to the control applied *u*.

u = applied control represented by the sale of 0, 50, or 100 percent of the steer inventory (IN) in July, August, September, or October.

COM = the value of sales commission estimated at $8/steer.

VCH_t = the variable costs comprising labor, minerals, and veterinary expenses in stage t. These costs were estimated at $0.40 /head/day.

$ß_t$ = discount factor based on the annual nominal inflation.

$f_{t+1}(IN_{t+1})$ = the maximum net present value from allocating IN steers from stage t+1 to the end of the process.

f_0 = initial outlay of buying steers in May which is a function of $IN_1 * PR_1^k$. Initial outlay also included the interest paid for borrowing the initial amount of money to purchase the steers. Interest on borrowed capital was estimated at 11.5% annually.

Equation (1) was numerically solved by backward enumeration subject to the following transition equation for the state variable:

$$IN_t = IN_{t-1} - CS_t \qquad (2)$$

where the *inventory of steers on hand (IN)* at stage t was a function of the *inventory of steers on hand* (IN_{t-1}) in the previous stage minus the *number of steers sold* (CS) in stage t. The value for the *number of steers sold* depended on the control *u* applied. Changes in the *inventory of steers on hand* affected the stocking rate. This in turn made *steer liveweight* fall into a different weight-class and consequently into a different *steer price* value.

The model algorithm was built into subroutines of the dynamic programming software CSUDP (Labadie 1990). The subroutines were enumerated in Carande (1992). The simulation model RANGES (Carande 1992) was used to obtain the values of steer liveweight under the 5 different scenarios. The model was calibrated for Southeastern Colorado conditions using historical rainfall and production data. Afterwards, RANGES was customized with a Gamma-distributed rainfall generator (Carande 1992). The model was set for 300-year iterations obtaining a frequency distribution of steer liveweight under stochastic rainfall.

For the *average rainfall* scenario, the means of *steer liveweight* for each grazing period were obtained from a complete frequency distribution generated with the 300-year simulation run. For the *unfavorable rainfall* scenario, the means of *steer liveweight* were selected from those years with rainfall values falling in the lower quartile of the frequency distribution. The lower quartile contained cumulative values of rainfall below 107 mm in the first, 149 mm in the second, 196 mm in the third, 241 mm in the fourth, 268 mm in the fifth, and 287 mm in the sixth grazing period. For the *favorable rainfall* scenario, the means of *steer liveweight* were selected from those years with rainfall values falling in the upper quartile of the frequency distribution. The upper quartile contained cumulative values of rainfall above 175 mm in the first, 229 mm in the second, 285 mm in the third, 339 mm in the fourth, 373 mm in the fifth, and 398 mm in the sixth grazing period.

Table 1. End-of-season steer liveweight as influenced by stocking rate and rainfall.

Stocking Rate	Rainfall Scenarios		
	Favorable	Average	Unfavorable
(ha/steer)		(kg)	
2.5	350	334	304
3.8	352	346	333
5.0	353	347	338
5.6	353	348	339
7.6	353	349	341
10.0	354	349	342
11.2	354	350	343
14.6	354	351	343
19.0	354	350	344
21.1	354	350	344
37.1	354	350	344
38.0	354	350	344

The model was run for 12 different stocking rates. These stocking rates were the result of differences in initial stocking rates and changes in steer inventory due to partial sales in July, August, September, or October. Table 1 lists the end-of-season means of steer liveweight at each stocking rate from the average, favorable, and unfavorable rainfall scenarios. As previously reported in

Table. 2 Average simulated real prices of stocker steers for different weitht classes from July to October for each scenario considered.

Weight Class	Price Scenario	July	August	Sept.	Oct.
		($/100 kg)			
	optimistic	181.72	182.60	183.26	184.14
363-Kg	average	164.34	165.66	167.20	168.74
	pessimistic	147.62	148.72	151.36	152.90
	optimistic	185.46	186.78	187.88	189.20
317-Kg	average	167.86	169.62	171.38	173.36
	pessimistic	150.26	152.02	155.10	156.86
	optimistic	192.28	193.38	194.48	195.36
272-Kg	average	174.02	175.34	176.88	178.64
	pessimistic	154.66	156.20	159.06	160.82
	optimistic	205.26	204.82	204.16	203.50
227-Kg	average	185.24	185.02	184.80	185.02
	pessimistic	163.24	163.24	164.56	164.78

Carande (1984), the effect of stocking rate on steer liveweight increases as rainfall decreases.

The means of *steer price* were obtained from monthly distributions of cross-correlated prices generated with the simulation model PRIGEN (Carande 1992). The model generates cross-correlated steer prices with seasonal and cyclical components for 6 weight classes. It uses coefficients from a harmonic regression model combined with a set of serially independent residuals obtained with a Markov-chain procedure using a set of random deviates. This set of random deviates was drawn from a Weibull distribution and multiplied by a variance-covariance upper-right triangular matrix. For the *average price* scenario, means of steer price were obtained from a frequency distribution including all values generated with a 200-year simulation run. For the *pessimistic price* scenario, means were obtained from the lower quartile of the frequency distribution. For the *optimistic price* scenario, means were obtained from the upper quartile of the frequency distribution. Table 2 lists the means of *steer price* for all weight-classes from July to October for the pessimistic, average, and optimistic price scenarios.

Optimal Intraseasonal Marketing Decision for Stocker Operations

Table 3 presents a summary of the optimal policies chosen and present values of net returns obtained from following the optimal marketing strategy. Cases were listed by increasing level of risk and stocking rate. Steers were kept on the range until October in the *favorable rainfall-optimistic price* and *favorable rainfall-pes-*

Table. 3. Optimal policies and net present values (NVP) from stocker operations at 3 initial stocking rates and 5 rainfall-prices scenarios.

Stocking Rate	Rainfall and Price Scenario	Optimal Marketing Policy	NPV
(ha/steer)			($)
	Favorable Rainfall - Optimistic Price	Sell in October	$2,052
	Favorable Rainfall - Pessimistic Price	Sell in October	$1,630
Low (5.6)	Average Rainfall - Average Prices	Sell 1/2 in September - 1/2 September - 1/2 in October	$1,579
	Unfavorable Rainfall - Optimistic Price	Sell 1/2 in September - 1/2 in $1,398 October	
	UnFavorable Rainfall - Pessimistic Price	Sell in October	$1,125
	Favorable Rainfall - Optimistic Price	Sell in October	$2,974
	Favorable Rainfall - Pessimistic Price	Sell in October $2,361	
Moderate (3.8)	Average Rainfall - Average Price	Sell 1/2 in September - 1/2 in $2,221 October	
	Unfavorable Rainfall - Optimistic Price	Sell 1/2 in September - 1/2 in October	$1,776
	Unfavorable Rainfall - Pessimistic Price	Sell 1/2 in September - 1/2 in $1,412 October	
	Favorable Rainfall - Optimistic Price	Sell in September - 1/2 in October	$4.419
	Favorable Rainfall - Pessimistic Price	Sell 1/2 in September - 1/2 in October	$3.546
High (2.5)	Average Rainfall - Average Price	Sell 1/2 in September. - 1/2 in October	$2,817
	Unfavorable Rainfall - Optimistic Price	Sell 1/2 in July - 1/4 in September - 1/4 in October	$1,510
	Unfavorable Rainfall - Pessimistic Price	Sell 1/2 in July - 1/2 in September	$931

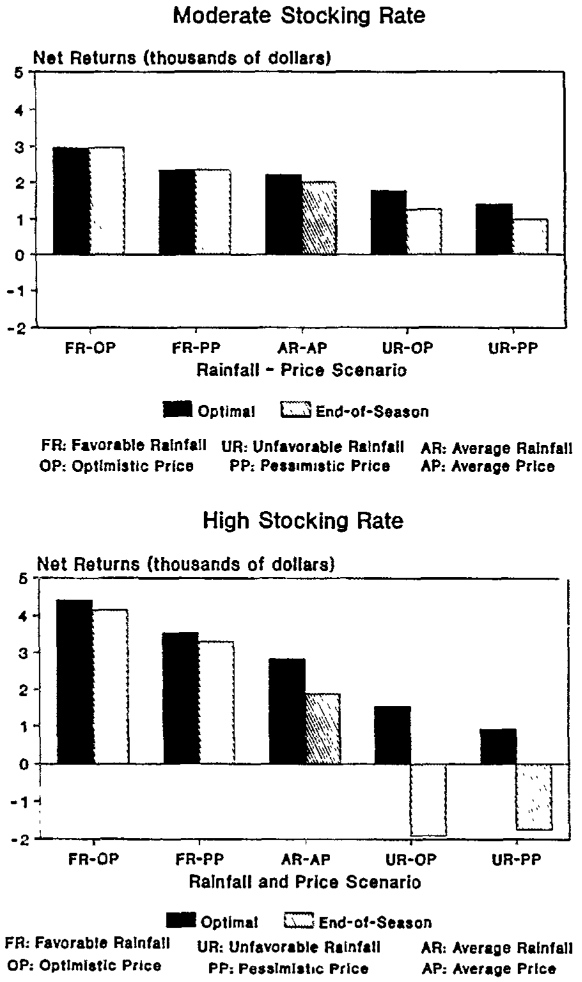

Fig 1. Net returns obtained under the optimal marketing policy vs. net returns from the traditional end-of-season marketing policy for 2 stocking rates.

simistic price scenarios at low and moderate stocking rates. Steers were also kept on the range until October in the unfavorable rainfall-pessimistic price scenario at the low stocking rate. Steers were sold half in September and half in October in the *unfavorable rainfall-optimistic* price scenario at the low and moderate stocking rate, in the *average rainfall-average price* scenario at the low, moderate, and high stocking rates, in the *unfavorable rainfall-pessimistic price* scenario at the moderate stocking rate, and in the *favorable rainfall-optimistic price* and *favorable rainfall-pessimistic* price scenarios at the high stocking rate. Steers were sold half in July, 1 quarter in September, and the remaining quarter in October in the case of the *unfavorable rainfall-optimistic price* scenario at the high stocking rate. Steers were sold half in July and half in September in the *unfavorable rainfall-pessimistic* price scenario at the high stocking rate.

The highest net returns in the low-risk and moderate-risk scenarios were obtained at the high stocking rate with sales in September and October. The highest net returns from the high-risk scenarios were obtained at the moderate stocking rate with also sales in September and October. The difference between the net returns from the low and high-risk scenarios was $927 at low stocking rate. This difference climbed to $1,562 at the moderate stocking rate, and $3,488 at the high stocking rate. These differences in net returns, according the level of stocking rate level and the degree of risk, reaffirm the *higher return-higher risk* rule of financial analysis. The relativity of optimizing under "average conditions" was evidenced by the difference of $1,886 between the net returns from the *average rainfall-average price* scenario and the net returns from the *unfavorable rainfall-pessimistic price* scenario at the high stocking rate.

The differences in net returns obtained from optimizing intervals (dynamic approach) rather than an end-of-season point (static approach) proved the importance of early sales when applying a high or moderate stocking rate under below-average rainfall conditions (Figure 1). Moreover, early sales when applying a high stocking rate saved the operation from losses of $1,907 in the *unfavorable rainfall-optimistic price* scenario and $1,725 in the *unfavorable rainfall-pessimistic price* scenario.

Conclusions

In making optimal decisions under rainfall and price variability, early sales was an important factor in whether the stocker operation was to avoid negative returns. These findings agreed with those of other authors such as Garoian et al. (1990), Schroeder and Featherstone (1990), and Rodriguez and Taylor (1988). When all 15 optimal policies were compared, rainfall had more effect on the timing of sales than price. Under favorable rainfall conditions, price level did not change the timing of sales at any of the stocking rates. Under unfavorable rainfall conditions, price level did change the timing of sales at the low and high stocking rates.

When using high stocking rates, flexible marketing strategies decreased the risk of obtaining negative net returns. This was specially true when rainfall and/or prices realized at lower levels than the long-term average. Conversely, inflexible marketing strategies called for lower stocking rates independently of the level of rainfall and/or prices. The resulting spectrum of policies according to the stocking rate applied and the rainfall and price levels reaffirmed the relevance of dynamic optimization as a procedure to obtain management and marketing policies under risk. Under price variability, alternatives that manipulate the purchase and/or selling price, such as future contracts or hedging, could be more important than the overall price level. Under rainfall variability, flexible rules of management will have a positive effect on the economic sustainability of the enterprise and the biological sustainability of rangelands.

Management Implications

When making decisions under rainfall and/or price variability, the strategy chosen by the operator will depend on his/her own degree of risk aversion and the flexibility allowed by the enterprise. A risk-averse stocker operator who is not prepared to handle early sales in September will be better off using a low stocking rate. If the same operator is prepared to handle early sales, higher profits will be obtained using a moderate stocking rate. He /she should sell in September unless the cumulative rainfall in August is above 339 mm.

A risk-taker operator will obtain higher profits than a risk-averse operator by using a high stocking rate, providing the cumulative rainfall up to the month of May is above 107 mm. The operator can apply a high stocking rate only if the range is in good or excellent condition, and be prepared to sell half of the herd in July if the cumulative rainfall through May is below 149 mm. The remaining steers should be sold in September regardless of the level of price or rainfall in this month. Stocker operators should avoid the temptation of running a higher than 3.8 ha/steer stocking rate in the presence of high seasonal prices under an inflexible marketing scheme. If below-average rainfall occurs while stocking at this stocking rate, the operation will register end-of-season losses of $10.50/ha.

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How much sagebrush is too much: An economic threshold analysis

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Abstract

Much research concerning sagebrush control methods and forage response after control has been conducted due to the importance of sagebrush-grass dominated rangelands for livestock and wildlife in the western United States. Very little research has addressed the economic feasibility of sagebrush control at various levels of abundance. This study estimates the economic threshold abundance of sagebrush based on forage response data from a sagebrush control experiment in Carbon County, Wyo. Forage response data are based on the difference in herbage between treated and untreated experimental units from sites ranging in initial sagebrush canopy cover from 4 to 40%. Breakeven returns per AUM were estimated for each sagebrush canopy cover level assuming 2,4-D (2,4-dichlorophenoxyacetic acid) or burning (for 28 to 40% canopy cover) as a control method with lives of control at 15, 20, and 25 years. These breakeven returns were compared to a net lease rate of $6.13/AUM. Results indicate the economic threshold abundance of sagebrush is 12% assuming, 2,4-D as the control method and a control longevity of 25 years, but the feasible sagebrush abundance increases as longevity of control decreases. If the longevity of the control only lasts 20 years, the sagebrush abundance must be at least 20% before treating sagebrush becomes economically feasible. If the longevity of control is only 15 years, sagebrush abundance must be at least 24% canopy cover before treatment is economically viable. Given estimates of the cost of burning are almost half that of spraying with 2,4-D, all the scenarios which had enough biomass to sustain a burn (28% to 40%) indicated sagebrush control by fire was economically viable.

Key Words: *Artemisia tridentata* ssp. wyomingensis, breakeven return per AUM, life of control, 2,4-D, and burning.

The sagebrush-grass ecosystem occupies a substantial portion of rangelands in the western United States. Acreage estimates of sagebrush-grass rangeland vary from 30 million ha to 109 million ha (Blaisdell et al. 1982). Estimates indicate that big sagebrush (*Artemisia tridentata* Nutt.) is the dominant range cover on approximately 39 million ha in the West (Alley 1965). Since sagebrush-grass rangelands are used predominantly to produce forage for livestock and wildlife, sagebrush control methods, degree of control and forage response have been the subject of much research.

Research has primarily focused on control methods and forage response after control. The literature indicates burning and spraying with 2-4,D are the most successful and cost effective methods for controlling sagebrush (Kearl and Brannan 1967, Kearl 1965, Krenz 1962, Mueggler and Blaisdell 1958, Smith et al. 1985). Forage response after control varies greatly, from 0 to 400% of production on comparable uncontrolled sites, depending on such factors as precipitation, composition of understory vegetation, sagebrush mortality, method of control, grazing management after control, and density of sagebrush population before control (Alley and Bohmont 1958, Bartolome and Heady 1978, EPA 1972, Kearl and Brannan 1967, Kearl 1965, Mueggler and Blaisdell 1958, Pechanec et al. 1954, Smith and Busby 1981, Sturges 1986, Tabler 1959, Tanaka and Workman 1988, Wambolt and Payne 1986).

Information concerning control methods and forage response is important to the range manager when making sagebrush control decisions. A major problem for managers is identifying a site where (1) the infestation of sagebrush is dense enough to cause a significant reduction in forage yield and (2) the potential increase in forage production would be sufficient to economically justify the control of sagebrush (Jacobs 1987).

Early research focused on the question of proper chemical mixture and recommended percent sagebrush mortality rather than identifying economic threshold sagebrush densities. Hull et al. (1952) treated plots of sagebrush averaging 25 to 30 plants per 30.5 m^{-2}. They used a total of 57 different herbicide and carrier mixtures in 1949 and 59 different mixtures in 1950. They concluded grass production could be increased 2 to 3 times in 2 years after chemical control of sagebrush as long as there was fair grass understory before treatment. They also concluded the increases were to some degree proportional to the percent of sagebrush plants killed. Native grass production was increased approximately 2 to 3 times by killing 60 to 97% of the sagebrush.

Alley (1956) used different rates and esters of 2,4-D and 2,4,5-T to better understand chemical control of sagebrush and the corresponding forage response after control in the Bighorn Mountains of Wyoming. Sagebrush clumps "averaged 26.9 inches in height by 30.0 inches in diameter and 32 clumps per square rod" (Alley, 1956). By sampling vegetation within the treated and untreated strips Alley (1956) determined the influence of various

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degrees of sagebrush control upon the grass-like species, forbs and shrubs. Data was summarized on the basis of 0, 50 to 75, 76 to 95, and 96 to 100% of sagebrush control. Alley (1956) concluded native grass production was increased as control of sagebrush increased. The most grass production was observed in the 96 to 100% sagebrush controlled areas.

Miller et al. (1980) tried to document changes in forage production and plant species abundance following application of 2,4-D in three mountain big sagebrush (*Artemisia tridentata* ssp. *vaseyana* (Rydb.) Beetle) habitat types. Shrub cover varied between 21 and 33% canopy cover on the 3 habitat types. Percent mortality of sagebrush ranged between 81 and 97%. Across the three habitat types bluebunch wheatgrass (*Agropyron spicatum* (Pursh) Scribn. and Sm.) was more responsive on the sprayed sites than Idaho fescue (*Festuca idahoensis* Elmer). Total forb production was lower on sprayed sites.

Whitson and Alley (1982) established experimental plots near Ten Sleep, Wyoming on sagebrush infested land to evaluate the potential of tebuthiuron {N-[5-(1,1-demethylethyl)-1,3,4-thiadiazol-2-yl] -N,N'-demethylurea} as a potential chemical control method on sagebrush. Three rates of 20% granular material, 0.29, 0.62, 0.86 kg/ha a.i. (active ingredient), were applied. Oven dry yields gathered 3 years after control from the 0, 0.29, 0.62, and 0.86 kg/ha rates were 283, 351, 658, and 508 kg/ha, respectively. Sagebrush defoliation for the 0.29, 0.62, and 0.86 rates of tebuthiuron were 69, 96, and 99.5%, respectively.

Clary et al. (1985) studied the effectiveness of tebuthiuron in controlling woody plants on Utah juniper (*Juniperus osteosperma* (Torr.) Little) and mountain big sagebrush dominated sites and evaluated responses of herbaceous species. Application rates of 0, 0.6, 1.0, and 1.3 kg/ha a.i. of 10% pellets was applied on the mountain big sagebrush strips. The authors found a high proportion of control at the 0.6 (approx. 80%) rate and nearly complete control of the original sagebrush plants at the 1.3 kg/ha rate (approx. 93%). Total production of herbage (including leaf and twig growth on shrubs) ($P>0.05$) was not significantly different from the control in the third growing season after sagebrush treatment. Fairway wheatgrass (*Agropyron cristatum* (L.) Gaertn.) was initially depressed, but recovered by the third year.

Hull and Klomp (1974) tried to evaluate 3 different control methods at different big sagebrush densities and how that affected, (1) yields of crested wheatgrass (*Agropyron desertorum* (Fisch. ex Link) Schult) growing under sagebrush, (2) amount of rain and snow reaching the soil and (3) soil moisture content. In 1950 and 1954 several sites in Idaho were cleared of sagebrush and seeded to crested wheatgrass. Big sagebrush reinvaded seeded ranges to a density of 20 plants per 30.5 meters^2. In 1965 big sagebrush was reduced to 10, 5, and 0 plants per 30.5 meters^2 (50, 75, and 100% kills) by grubbing, burning, and spraying with 2,4-D. The authors concluded that the 3 methods of control did not differ in the amount of grass produced following brush control, and where wildlife or livestock do not need sagebrush, all the brush should be killed. Any remaining sagebrush suppresses grass and produces seed for reinvasion.

Tanaka and Workman (1988) extended Hull and Klomp's (1974) work into an economic framework developed for estimating the optimum rate of initial overstory kill for increasing seasonal forage availability. The model was formulated using, (1) biological data from Hull and Klomp (1974) to estimate a production function relating understory production to initial kill percentage, (2) a derived demand function for seasonal forage value by using linear programming to estimate shadow prices for additional production of crested wheatgrass, and (3) a cost of overstory kill function for each control method. Tanaka and Workman (1988) used the big sagebrush- crested wheatgrass vegetation type on a "typical case ranch" (cow-calf-yearling operation) in Utah. For the case ranch analyzed, a big sagebrush kill rate between 92 and 100% was optimal.

While these pieces of research tried to ascertain forage responses using different chemical mixtures, in different habitat types and different percentages of sagebrush mortality, they do not provide much information in terms of what initial sagebrush abundance level will be economically feasible to consider control. Additionally, today's managers must consider the possible environmental effects sagebrush control might have on ecosystems managed for multiple uses. These economic and environmental factors preclude a manager from indiscriminately controlling sagebrush. Managers need additional information to aid them in assessing whether sagebrush control is an economically viable alternative.

The focus of this study is to determine the economic threshold abundance level for big sagebrush control. The economic analysis in this study is based on forage response data from a study of sagebrush control in Carbon County, Wyo.

Materials and Methods

Study Area

The forage response data comes from an area in southcentral Wyoming, approximately 19 km northeast of Saratoga, Carbon County, Wyo. The area is on the west slope of the Medicine Bow mountain range at an elevation of 2,245 m and receives about 33 cm of precipitation annually. Vegetation in the area is dominated by an overstory of Wyoming big sagebrush (*Artemisia tridentata ssp. wyomingensis* Beetle and Young) with an herbaceous layer featuring western wheatgrass (*Agropyron smithii* Rydb.) and needle-and-thread grass (*Stipa comata* Trin. & Rupr.). Forbs are not abundant in the study site.

Within this area, 20 study sites were selected across a range of big sagebrush abundances as measured by canopy cover, but on similar sandy soils and topographic positioning. On each study site 2 experimental units (approximately 30 m by 30 m each) with the same big sagebrush abundances were selected and randomly designated, one with sagebrush controlled and the other not treated. Two replicate pairs of each sagebrush abundance level were included in the design. Sites had big sagebrush canopy cover (cover was determined using 6-100 point transects) ranging from 4 to 40% in approximately equal increments.

Big sagebrush was treated by spraying with 2,4-D in early June of 1987[1]. For each study site, peak standing biomass of all herbaceous vegetation has been measured in late July each year of the study by harvesting vegetation on quadrats protected by movable cages (6 per experimental unit). The herbaceous biomass consisted primarily (approx. 90%) of western wheatgrass and needle-and-thread grass. A small portion of the clipped herbage sometimes included annuals and forbs (approx. 10%). All of the herbage was usable by cattle and sheep at least during part of the

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[1] It is important to note that ground application of 2,4-D occurred in June 1987 on the study sites in Carbon County, Wyo. for the experiment used in this analysis. Sagebrush control was in excess of 95% mortality on all treated sites.

grazing season. The difference in herbaceous biomass between the treated and untreated experimental units was assumed to be the forage response due to controlling sagebrush.

These data were adjusted for precipitation and soil moisture differences among study sites using regression analysis. While these models are linear in nature, it is important to remember that they are used to normalize the data, and they are not a simulation or production function model used to estimate production over the life of the sagebrush control. Assumptions concerning the pattern of utilization over the life of control will be discussed later in the economic analysis section of the text.

Linear regression models used to normalize the data should be fairly accurate across the sites. Sala et al. (1988) found production at the site level was largely accounted for by annual precipitation, soil water-holding capacity, and an interaction term. This simple linear model accounted for 90% of the variation in production from site to site. Sala et al. (1988) found the addition of other climatic variables such as potential evapotranspiration, temperature, or the precipitation:potential evapotranspiration ratio for the growing season or the entire year did not significantly improve the model. The more sophisticated models including such variables did not account for more than 90% of the variation in production.

The variables used to estimate the regression parameters for calculating the adjusted production data across experimental sagebrush sites for this study were percent sagebrush (sage), precipitation for April, May, and June (precip), percent May soil moisture for check plots (mayc), percent soil moisture for treated plots (mayt) and year (yr). The regression models were as follows:

MODEL FOR UNTREATED CHECK PLOTS

$$\text{Yield} = \beta_0 + \beta_1\,\text{sage} + \beta_2\,\text{precip} + \beta_3\,\text{Mayc} + \beta_4\,\text{yr} + \varepsilon$$

MODEL FOR TREATED PLOTS

$$\text{Yield} = \beta_0 + \beta_1\,\text{sage} + \beta_2\,\text{precip} + \beta_3\,\text{Mayt} + \beta_4\,\text{yr} + \varepsilon$$

where:

β's = estimated regression parameters
Yield = Yield based on clip data for that year and corresponding plot
sage = percent sagebrush (4 to 40)
precip = sum of precipitation collected from site gauges April, May and June for each year of study period
Mayc = soil moisture for each year of study period in May on check plots
Mayt = soil moisture for each year of study period in May on treated plots
yr = Year (1987= -2, 1988= -1, 1989= 0, 1990= 1, 1991= 2)
ε = Error

The normalized yields were estimated by calculating the predicted yields for each year and percent sagebrush using the estimated regression parameters, mean soil moisture for the study period for both the check plots and the treated plots and mean precipitation for the months of April, May, and June during the study period. These normalized yields were designed to take out variability associated with differences in annual precipitation from year to year and differences in soil moisture across study sites, so that yield differences for each year were associated with percent of sagebrush. The differences in these normalized yields between treated and untreated plots for each level of sagebrush abundance was then estimated and the increased forage production was assumed to be a function of treating the sagebrush. These regression adjusted differences are reported in Table 1.

Table 1. Forage Response (difference between controlled and uncontrolled sites) adjusted for differences between sites in seasonal precipitation and soil moisture (DM basis).

	% Sagebrush Canopy Cover									
Year	4%	8%	12%	16%	20%	24%	28%	32%	36%	40%
1987[1]	Kg/ha									
1988	17	50	83	116	150	183	216	249	282	315
1989	124	157	190	223	256	289	322	356	389	422
1990	230	263	297	330	363	396	529	462	495	528
1991	337	370	403	436	469	502	536	569	602	635

[1] Year of treatment. Grazing considered to be deferred and forage not utilized.

Economic Analysis

Information needed to identify the economic threshold abundance level of big sagebrush includes the control methods to be analyzed and their associated costs, quantification of herbage responses and utilization associated with treatment, and valuation of the forage over the life of control.

Control Methods and Associated Costs

Several techniques are available for sagebrush control. Much of the earlier research looked at chemical control with 2,4-D. However, other methods of chemical control, as well as, burning and mechanical control are available to the land manager. Each one of these alternatives needs to be evaluated by the individual manager in terms of characteristics of the land, managerial objectives for the operation and economic feasibility.

Tebuthiuron has been found to control big sagebrush at the application rate of 0.6 to 1.1 kg a.i./ha by Whitson and Alley (1984). However, several drawbacks may exist with the use of tebuthiuron. Steinret and Stritzke (1977) found that phytotoxicity decreased forage production the first year after tebuthiuron application. Britton and Sneva (1983) found that mean herbaceous yields decreased with each increased rate of tebuthiuron. Bjerregaard et al. (1977) found forage yields were depressed for two years after application, but production increased later and the residual tebuthiuron showed potential for effective control against sagebrush seedlings for several years. Whitson and Alley (1984) observed that in the first year following application of tebuthiuron cool season grasses were chlorotic in appearance. However, reduced symptoms were noted in subsequent years.

Burning is an effective method for controlling sagebrush (Smith and Busby 1981). Mueggler and Blaisdell (1958) conclude that burning is by far the least expensive sagebrush control method despite the 1 year grazing deferment. Wambolt and Payne (1986) concluded that of 4 control methods, burning, spraying with 2,4-D, rotocutting and plowing with seeding, burning was most effective in reducing sagebrush canopy. Plowing with seeding was found to be least effective. After 18 years burning provided the most production from dominant forage species and important vegetal classes, but burning and spraying were equally successful when production was totaled for all years sampled.

Shariff (1988) studied vegetation, soil moisture, and nitrogen responses with respect to 3 different methods used in controlling big sagebrush. This study compared 2,4-D, burning and tebuthiuron. Shariff concluded that the burn treatment exhibited the best response in the control of big sagebrush and total production. The 2,4-D treatment was found to be as effective as the burn treatment when the proper timing and application techniques were used. These conclusions concerning burning and spraying with 2,4-D are consistent with Hull and Klomp (1974). The tebuthiuron treatment appeared to be effective only on loamy soils.

In this study, spraying with 2,4-D was the method of control used on the experimental units. For this analysis $26.54/ha[2] is used as the chemical and application cost for 2,4-D. Given the findings of previous studies, this analysis also explores burning as a control method. According to data from the Soil Conservation Service average cost of burning in several Wyoming counties was estimated and adjusted for inflation to represent 1987 dollars. The estimated cost of burning used in this analysis was $13.73/ha[3].

The burning scenario is only estimated for those experimental units which had enough biomass to sustain a burn. Smith et al. (1985) found when brush cover is below 30%, fine fuel amounts must exceed approximately 333 kg/ha (for continuous sod forming species) to near 667 kg/ha (for discontinuous bunchgrass or rhizomatous wheatgrass species) for good fire spread to occur. If brush cover exceeds 30-35%, fire spread will usually occur with lesser amounts of fine fuels. Given these criteria, those plots exhibiting 28 to 40% sagebrush cover were considered feasible for the burn scenario in this analysis.

One year of grazing deferment after treatment is assumed in this analysis. This is an additional cost associated with treatment which must be recaptured over the life of the control. An opportunity cost of not grazing that first year after treatment is calculated and added to the cost of treatment. The normalized yield data on the untreated plots for 1987 is multiplied by a 50% utilization rate and a conversion factor of 360 kg DM/AUM (Society for Range Management 1974, Scarnecchia and Kothmann 1982) to estimate animal unit months (AUM) of grazing forgone for each level of sagebrush abundance. The AUM's of grazing forgone is then multiplied by a net forage value of $6.13/AUM to estimate the opportunity cost of deferment in the first year of treatment. The net lease rate of $6.13/AUM is an average of common lease rates for Wyoming during the years of 1981 to 1991 minus an estimate of 30% of the lease rate associated with services provided by lessors and adjusted to 1987 dollars (Wyoming Agricultural Statistics Service 1993, Torrell et al. 1988).

Quantification of Herbage Response and Utilization

Increased forage production resulting from sagebrush control lasts for varying periods. The longevity of control and amount of increased forage production varies from site to site and is influenced by degree of control. Johnson and Payne (1968) found that unkilled sagebrush was the major cause of reinvasion. Hull and Klomp (1974) found that killing the last 25% of a big sagebrush stand resulted in 98 to 135% more crested wheatgrass than killing the first 75% at southern Idaho sites.

In order to evaluate the feasibility of sagebrush control, the quantification of increased forage production must be estimated throughout the life of control for relevant planning horizons. Kearl and Brannan (1967) used different figures for effective life of control depending on observed results for different methods. Chemical spraying with 2,4-D had a projected life of 15 years. Kearl and Freeburn (1983) found sites sprayed on National Forest land to be highly productive after 20 years. Tanaka and Workman (1988) used a planning horizon of 25 years for sagebrush control. Based on the literature and the sagebrush mortality on the experimental sites, 15 to 25 years is used as a reasonable planning horizon for the economic threshold analysis.

It is also important to understand long term trends in forage response, as well as utilization of forage to quantify the value of herbage response after sagebrush control. Blaisdell et al. (1982) discussed trends in sagebrush reinvasion and grass production after a controlled burn near Dubois, Ida. from 1936 to 1966. Much of the discussion was based on Harniss and Murray (1973). Over the 30 year period, mountain big sagebrush demonstrated a very dominant role in the plant community. During the first 12 years following burning, nearly all species of grasses, forbs and other shrubs increased in yield. In the subsequent 18 years following the burn, yields of the grasses, forbs and other shrubs decreased as sagebrush regained control. Forage production returned close to the preburn levels by the end of the 30 year period.

The economic analysis by Kearl and Freeburn (1983) assumed the usable forage production doubling in 2 years, forage production being sustained for years 3 through 10 and then forage production declining to the pretreatment levels in years 11 through 15. Jacobs (1987) used forage utilization by livestock to depict an increase in physical response due to sagebrush control. Jacobs assumed forage utilization to increase by 50% in year 2, 100% in year 3, sustained levels of utilization equal to year 3 in years 4 through 10 and forage utilization declining to pretreatment levels in years 11 through 15.

Tanaka and Workman (1988) however, based the production function on the assumption that any increase in forage from an overstory treatment remained constant from the first year of grazing until the end of the project life. The production function values were adjusted for both desired utilization rate and availability of forage to livestock. The availability function was based on observations by Hull and Klomp (1974) and assumed to be linear between 40 and 90% as big sagebrush canopy varied from 34 to 0%.

Workman and Tanaka (1991) illustrate several cases which suggest as utilization of forage increases and or sagebrush mortality decreases, reinvasion of sagebrush increases. In the first dynamic case illustrated by Workman and Tanaka (1991) a 50% utilization rate and 95% initial overstory removal is assumed. This case resulted in a 20 year project life due to big sagebrush encroachment, while a 75% utilization rate and 95% mortality on sagebrush resulted in a 15 year project life. In the case where only 50% of the sagebrush were removed and 50% of the forage was utilized the projected life was 10 years.

Unfortunately, for this analysis only 4 years of forage response data is available for analysis (Table 1). Based on Blaisdell et al. (1982) and Harniss and Murray (1973) it seems reasonable to expect the forage response after sagebrush control to increase over a period of years and then decrease as sagebrush reinvades the treated area. It also seems reasonable based on the previous discussion to expect sagebrush control to last between 15 and 25 years. For this analysis, assumptions concerning the utilization of the forage are used to take into account a forage response curve.

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[2] This based on commercial rates from Sky Aviation in Worland, Wyo. for 1987.

[3] This is based on personal phone interviews with personnel in the Cheyenne and Buffalo offices.

Increased forage utilization is based on the adjusted production data in Table 1. One year of grazing deferment is assumed. It is also assumed that only 50% of the increased forage production is utilized annually and that 360 kg DM provides 1 AUM. Maximum forage utilization increase is assumed to occur in year 4. It is further assumed that this level of utilization is maintained until year 10. The increased forage utilization is assumed to decrease in equal increments after year 10 as sagebrush reinvades until the infestation reaches the pre-treatment level at the end of the specified planning horizon. Figure 1 illustrates the expected forage response versus the estimated forage utilization over the life of the control.

Valuation of the Forage and Estimate of Breakeven Price Over the Life of Control

Range managers may have different objectives for controlling sagebrush, and thus, different values may be placed on the increased forage production associated with treatment. Due to the unique characteristics of each individual situation, different values may need to be considered by a range manager. Workman (1986) discusses several possible approaches. One approach is to use a private lease rate. This "market value" approach is deemed reasonable because a manager would have an opportunity to lease these AUMs to stockmen if returns to the operation from the additional forage were less than the lease rate. Nielsen and Hinckley (1975) and Stevens and Godfrey (1976) used lease rate approaches to value additional forage from range improvements. Workman and Tanaka (1991) state that in many cases valuing revegetation benefits as privately leased forage is simple, straightforward and often yields accurate estimates of the value of additional forage particularly when the operation currently leases and or can avoid leasing forage in the future due to the improvement.

Private range lease rates, however, do have some caveats associated with valuing forage for an improvement. Jacobs (1987) states that while some economists feel that grazing lease rates are a defendable value, they may tend to overestimate the value of forage for several reasons. One problem is lease rates may include a number of services as a premium (for example lessor may provide salt, fence repair, and herding). Workman and Tanaka (1991) report that published private lease rates include a premium for landlord services of about 30% (Torell et al. 1988) and that the value of additional forage, itself, is only about 70% of published lease rates. A second problem according to Jacobs (1987) is that most grazing fees are based on short term leases. In many instances a producer would only consider variable costs when determining the maximum lease rate that would be feasible. Due to the short run nature of a lease "market value" of the forage could be higher than a long term arrangement where the fixed and variable costs are both considered. Workman and Tanaka (1991) note that pricing at the private lease rate often yields a higher revegetation benefit than does valuation as increased livestock production (Workman 1986).

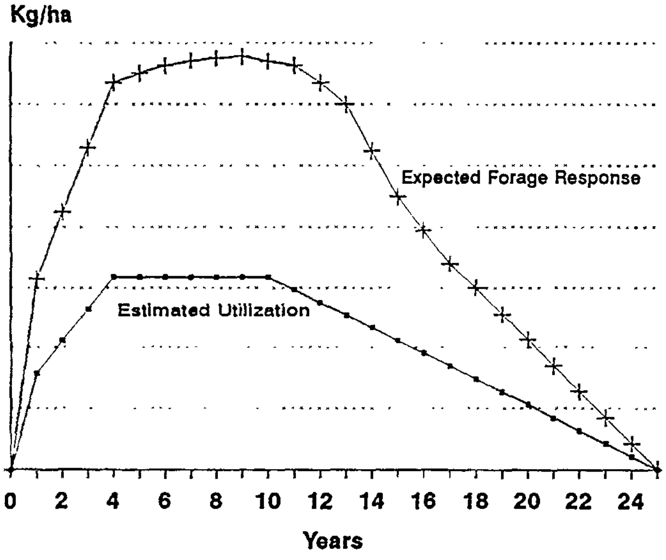

Fig. 1. Illustration of expected forage response curve versus estimated utilization based on assumptions used in the analysis.

Due to the possible shortcomings of grazing fees some economists prefer a total ranch budgeting approach when valuing additional forage from a range improvement. Nielsen (1967), Kearl and Freeburn (1983), and Tanaka and Workman (1988) all took a ranch budgeting approach. The general technique was to estimate additional ranch income due to the improvement. These additional income flows were then discounted back to present value and compared to the cost of the improvement. For a producer, a budgeting approach based on the specific requirements of the individual operation could offer more accurate information concerning the added profitability from a proposed improvement.

According to Workman (1986) ranch budgeting might also be used to calculate the average value of an added AUM. All non-forage costs can be subtracted from annual gross ranch income. The result of that calculation could then be divided by the total number of AUMs of forage used by the operation annually. This average value might then be used to do the analysis.

Perhaps the biggest advantage to a total ranch budget approach is this approach requires the manager to inventory all the resources available to the operation and decide whether the improvement can be done without creating a shortage elsewhere (Nielsen 1967). The producer may not want to increase spring grazing if the operation cannot meet the increased hay requirements brought on by increased stocking due to the improvement for example.

Unfortunately, the ranch budgeting approach is more complicated in terms of accounting for all resource inventories, valuing and planning the timing of resource usage and accurately reflecting all the effects of the improvement. Workman (1986) suggests the complexity of this approach is the biggest drawback. The ranch budgeting approach has some shortcomings for a researcher trying to make general recommendations concerning various improvements. The "typical case ranch" budget may be less representative of the intended audience of the research than a market value or lease rate approach. For this study, a large number of scenarios are investigated concerning initial sagebrush canopy cover levels, control methods and associated costs and different planning horizons for longevity of control, and the results are intended for a relatively broad audience of managers who might consider sagebrush control as an alternative. Thus, the ranch budgeting approach seems less desirable.

This economic analysis estimates the breakeven price the increased forage production must receive per AUM for each planning horizon, method of treatment and sagebrush abundance level to cover the initial cost of control and opportunity cost of deferment. The higher the breakeven price the less likely the range improvement will be feasible given the manager's objectives.

Since the investment in sagebrush treatment is not recaptured immediately, the returns associated with control must be discounted over the life of the control. Nearly all individuals display a positive time preference for money (Barry et al. 1983). A dollar received today is preferred to a dollar received a year from now. Thus, for an investment to be economically feasible, the sum of the future returns from the investment discounted to a present value must be greater than or equal to the initial cost of the investment.

The net present value (NPV) method uses discounting formulas to obtain the value of the projected cash flows associated with an investment alternative. In this fashion, the net present-value criterion directly accounts for the timing and magnitude of the projected cash flows for alternative investments having different planning horizons and cash flows. Given the concepts used in the net present value method, the following formula was derived and used to estimate the breakeven prices (PF in formula) for this analysis. The PF (price of forage) value was solved for in an iterative fashion until NPV was equal to zero or as close to zero as possible without being negative.

$$\mathrm{TRTCST} = \sum_{n=0}^{N} \frac{((UF)*(PF))_n}{(1+i)^n}$$

Where:

TRTCST = Cost of treatment (including deferment).

UF = Increase in utilizable forage due to treatment (converted to AUMs).

i = Discount rate.

N = Number of years in planning horizon.

PF = Price of forage per AUM.

$((UF)*(PF))_n$ = The return received for each conversion period (n) due to controlling sagebrush.

To express the value of the income flows in present terms they must be discounted at a relevant rate (i in the above equation). Barry et al. (1983) state that for capital budgeting procedures the discount rate is a firm's required rate of return on its equity capital. The discount rate is generally considered to contain 3 components. There is a risk free rate for time preference, a rate reflecting the riskiness of the expected net cash flows and an inflation premium. The authors go on to state that the discount rate is much like an opportunity cost and should reflect a rate the firm's equity capital could earn in the most favorable alternative use.

Workman (1986) discusses criteria for picking a discount rate which are consistent with Barry et al. (1983). He states that ideally a discount rate should be the higher of either the interest rate on borrowed capital for the improvement or the opportunity cost rate. Given the best alternative use of range improvement capital is not always known, Workman (1986) suggests a representative borrowing rate is often used for discounting or comparison purposes. Generally since returns are measured in real terms, the appropriate discount rate should be in real terms as well.

For this analysis a discount rate of 6% was chosen. This was based on a long term (1950 to 1992) average real prime interest rate of 3% (U.S. Government Printing Office 1993) plus a 3% risk premium. Tanaka and Workman (1988) used a 7% discount rate, using a 4% rate plus a 3% risk premium. The higher the discount rate the larger breakeven price of the forage would have to be over the life of control to cover the initial cost of control plus the opportunity cost of deferment. For example, if the maximum increase in forage utilization was based on an increase of 232 kg/ha in year 4 using 2,4-D and with a 20 year expected longevity, the average value of the increased forage or breakeven price would have to be $11.08/AUM to cover the cost of treatment at a 6% discount rate. At a 7% discount rate, assuming everything else remained the same, the price of the forage would have to be $11.92/AUM, and if a 10% discount rate were used, the breakeven return for the forage would increase to $14.82/AUM.

These estimated breakeven forage prices (PF) must be compared to estimates of what that forage is actually worth before conclusions can be drawn about which initial sagebrush abundance level could be considered as economically feasible to control. As mentioned earlier, one problem with private grazing leases is the lease rate may include a number of services (for example, salting, fence repair, and herding). Thus, a net lease rate which has these types of services subtracted out may more accurately reflect the value of forage. A net lease rate of $6.13/AUM is used as an estimate for comparison in this analysis. Conclusions concerning the economic threshold level of big sagebrush are drawn by comparing this inflation adjusted value less services to the estimated breakeven prices for each scenario.

Results

A breakeven return per AUM has been calculated for each sagebrush abundance level, life of control and treatment method scenario (2,4-D, burn) with only half of the increased forage production assumed to be available for grazing after 1 year of deferment (Fig. 2). The return per AUM represents what the increased forage production must receive annually over the life of control in order to equal the sum of the cost of the treatment and opportunity cost of deferment.

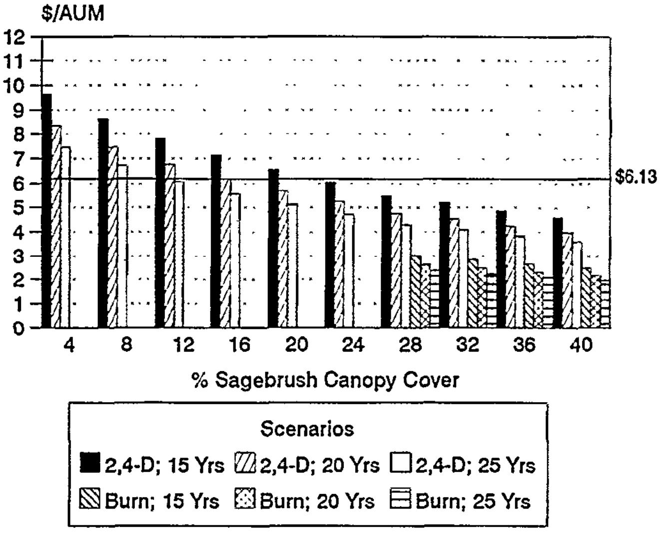

Fig. 2. Breakeven return per AUM needed to cover treatment cost and deferment under various scenarios of control method and expected life of control.

The breakeven return per AUM for increased forage production from various scenarios of sagebrush control ranges from a high of \$9.66/AUM to a low of \$1.95/AUM. The high occurs at the 4% sagebrush abundance level, assuming a 15 year life of control and spraying with 2,4-D as the control method. The low of \$1.95/AUM occurs at the 40% sagebrush abundance level, assuming a 25 year life of control and burning as the control method. The breakeven return per AUM needed to cover the treatment cost decreases as the life of control increases (Fig. 2). This is expected since more total forage can be utilized the longer the treatment lasts. Given the cost of burning is assumed to be about half that of 2,4-D, it is no surprise that the breakeven returns required per AUM in the burn scenarios for the 28 to 40% sagebrush abundance levels are almost half that of spraying with 2,4-D. The other general conclusion which can be drawn from Figure 2 is the relationship of the initial sagebrush abundance level and the breakeven return per AUM. The lower the sagebrush infestation level, the less increase in forage production (Table 1) and the higher the return per AUM of forage must be to cover the investment in control.

If \$6.13/AUM is a reasonable value to place on forage, the 12% sagebrush scenario becomes feasible if the control lasts 25 years, 2-4,D is the control method, forage response is at least the amount reported in Table 1 and utilization assumptions used in this analysis are met (Fig. 2). At the 24% sagebrush level all 3 longevity of control scenarios become feasible. Since burning is assumed to cost almost half of the 2,4-D treatment all of the burn scenarios are economically feasible if \$6.13/AUM is the value placed on forage (Fig. 2).

Discussion and Conclusions

Given \$6.13/AUM is a representative value for forage, the economic threshold level for control occurs within a broad range of sagebrush abundance levels (12 to 24% cover) depending on life of the control and forage response. As the cost of control increases, the initial abundance level and corresponding production response must be higher before control becomes economically feasible. As the longevity of control increases relatively less production response is needed to make sagebrush control feasible.

Although the results of this analysis are meant to be generally applicable to a wide readership, it is important to keep in mind the limitations of this study. This analysis involved data from an experiment in Carbon County, Wyo. The results of this experiment could be site specific. No other studies in native vegetation report forage responses associated with different initial sagebrush abundance levels. Thus, the production responses used in the analysis may not be representative of other areas which might benefit from big sagebrush control.

Another limitation of this analysis stems from the projections used to estimate increased forage utilization over the life of control given response data for a limited number of years. Results from Blaisdell et. al (1982) and others indicate forage response would tend to peak later than year 4. This might suggest the analysis is conservative in estimating total possible forage utilization over the life of the control.

An additional consideration is that the economic analysis in this study assesses only the added benefits and costs associated with controlling big sagebrush. A manager may want to do a more complete budget that takes into account all the characteristics of this type of improvement which are unique to the operation and manager's objectives before controlling sagebrush. However, we do identify some of the major considerations and outline a framework for the economic analysis, as well as provide a general indication of the sagebrush abundance and forage responses needed before big sagebrush control enters the realm of economical feasibility.

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Effects of grazing management on standing crop dynamics in tallgrass prairie

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Abstract

Grazing system and stocking rate effects on forage standing crop of tallgrass prairies in north-central Oklahoma were evaluated from 1989 to 1993. Twelve experimental units, consisting of pastures dominated by big bluestem [*Andropogon gerardii* Vitman], little bluestem [*Schizachyrium scoparium* (Michx.) Nash], indiangrass [*Sorghastrum nutans* (L.) Nash], and switchgrass [*Panicum virgatum* L.], were arranged in a completely randomized design with either a short duration rotation or continuous grazing system and stocking rates ranging from 127 kg animal live-weight/ha to 222 kg live-weight/ha. Yearling steers grazed the units from late April to late September. Herbage standing crop was sampled in July and September. Total, live, and dead standing crops did not differ significantly between the 2 grazing systems in July. Total standing crop was significantly higher in the rotation units in September (3,600 versus 3,020 kg/ha, $P<0.05$). Dead standing crop was also higher in the rotation units in September (1,950 versus 1,570 kg/ha, $P<0.05$). Evidence suggests the difference in standing crop between systems is due, in part, to reduced forage intake by the livestock. Grazing system did not interact with either stocking rate or year. Stocking rate had significant effects on total, live and dead standing crops at both sample dates. The slope of the total standing crop-stocking rate relationship varied over years and ranged from -12 to -36 kg/ha per kg live-weight/ha in July and from -12 to -27 kg/ha per kg live-weight/ha in September. Higher standing crop at the end of the grazing season in the rotation units would mean greater soil protection and higher fuel loading for prescribed burning, and would suggest a lower impact on plant vigor. However, if the higher standing crop is a result of lower forage intake, we would expect livestock weight gains to decline.

Keywords: continuous grazing, rotation grazing, tallgrass prairie, forage production

Short duration rotational grazing has been suggested as a method for increasing livestock numbers while maintaining range condition (Booysen and Tainton 1978, Savory 1978). However, research results comparing rotational grazing to continuous grazing at equal stocking rates have not shown dramatic increases in herbage standing crop with rotation grazing. Gammon and Roberts (1978), Hart et al. (1988), and White et al. (1991) found no differences in caged standing crop on continuous and rotational systems.

Observation and a large body of research indicate that standing crop decreases with increasing stocking rate (Herbel and Anderson 1959, Van Poollen and Lacey 1979, Brummer et al. 1988, Heitschmidt et al. 1989). Some authors have suggested that stocking rate affects standing crop more than grazing system (Van Poollen and Lacey 1979, Wilson 1986). Possible interactions between grazing system and stocking rate have been hypothesized but seldom completely studied. Most research has compared continuous grazing at a moderate stocking rate with rotation grazing at stocking rates 50 to 100% higher. Results from such studies confound grazing system with stocking rate and make interpretation open to question.

Tallgrass prairie response to less intensive grazing systems is well documented (Owensby et al. 1973, Owensby and Smith 1978, Owensby et al. 1988) but less research is available concerning short duration rotation grazing (Gillen et al. 1991, Brummer et al. 1988). Studies of stocking rate effects on tallgrass prairie are limited (Herbel and Anderson 1959, Owensby et al. 1988). The purpose of this study was to evaluate the effects of continuous and rotational grazing systems at several stocking rates on standing crop dynamics of tallgrass prairie.

Study Area

The study was conducted from 1989 to 1993 at the Oklahoma State University Research Range, located approximately 21 km southwest of Stillwater, Okla. (36°04' N, 99°13' W). The climate is continental with an average frost-free growing period of 204 days, extending from April to October. Average annual precipitation for the area is 831 mm with 65% falling as rain from May to October. The mean annual temperature is 15°C, and ranges from an average daily minimum of -4.3°C in January to an average daily maximum of 34°C in August (Myers 1982).

Major range sites found on the area are shallow prairie (33%), loamy prairie (25%), and eroded prairie (22%). Sandy savannah dominates the remaining area. The shallow prairie sites have

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Grainola series soils (fine, mixed, thermic Vertic Haplustalf), which have a loam surface with silty clay subsoil. Coyle series soils (fine-loamy, siliceous, thermic Udic Argiustoll) comprise the loamy prairie sites. These soils have fine sandy loam surfaces with sandy clay loam subsoils. The eroded prairie sites are on old fields and have Renfrow (fine, mixed, thermic Udertic Paleustoll), Mulhall (fine-loamy, siliceous, thermic Udic Paleustoll), and Coyle series soils.

Vegetation on the experimental units was in a high seral state during the course of the study. Vegetation composition on a dry weight basis, determined by the dry weight rank method in August 1991, consisted of 28% little bluestem [*Schizachyrium scoparium* (Michx.) Nash], 25% combined big bluestem [*Andropogon gerardii* Vitman] and indiangrass [*Sorghastrum nutans* (L.) Nash], 25% midgrasses, 13% forbs, 5% switchgrass [*Panicum virgatum* L.], and 4% shortgrasses and annual grasses. All units had been moderately grazed and burned 1 or 2 times in the 5 years previous to initiation of the study.

Methods

The experimental design consisted of a completely randomized design with grazing system and stocking rate as treatments. Six of 12 experimental units were randomly assigned to a rotational grazing system, and the remaining 6 units were assigned to a continuous grazing system. Experimental units ranged in size from 14 to 26 ha. The rotation units were subdivided into 8 pastures. Within each grazing system the units were randomly allocated to 1 of 6 levels of stocking rate. Stocking rates ranged from 127 kg animal live-weight/ha to 222 kg live-weight/ha, which represent moderate to very heavy rates for this range type. The experimental animals were mixed-breed yearling beef cattle with average initial weights of 200-225 kg. Cattle numbers per unit ranged from 10 to 22. The yearlings grazed the units from early April until late September. Cattle in the rotational units remained in a single herd and were moved between pastures every 3 to 7 days. We lengthened the grazing periods as the growing season progressed. Cattle in the continuous units were not moved during the grazing season. All units were burned 1 Apr. 1990 and 20 Mar.1993.

Herbage standing crop was measured in July and September by clipping the total standing crop at ground level in 0.1-m² quadrats. Forty-five quadrats were located systematically in a grid pattern in each pasture. The live:dead herbage ratio was determined according to the technique of Gillen and Tate (1993).

Dependent variables of interest were total, live, and dead standing crop. We analyzed the data as a repeated measures experimental design. Main plot factors were grazing system and stocking rate with year as the repeated factor. Grazing system and year were qualitative variables. Stocking rate was a quantitative variable. Both linear and quadratic effects of stocking rate were included in the statistical model. Because stocking rate was not replicated, Type I sums of squares were used for hypothesis testing (SAS Institute 1985). July and September sampling dates were analyzed separately. When year effects were declared significant, the least significant difference was used for mean separation. When stocking rate interactions with grazing system or year were declared significant, slopes of standing crop versus stocking rate were tested using indicator regression methods (Neter and Wasserman 1974).

Results and Discussion

November-April precipitation was above normal in 4 of the 5 study years (Table 1). May-August precipitation was more than 50% above normal in 2 years, 1989 and 1992. Spring-summer temperatures for these 2 years were relatively cool. May-August precipitation was close to average in 2 other years, 1991 and 1993, and 22% below normal in 1990. Overall weather conditions were favorable during the study period with cumulative precipitation well above average and spring-summer temperatures slightly below average. May-August precipitation correlated well with total standing crop in September (Tables 1, 3).

Year

Year had a significant effect on all standing crop parameters (Table 2). July standing crops were highest in 1991 while September standing crops were highest in 1989 and 1992 (Table 3). Standing crops were lowest in 1990. From minimum to maximum, the data varied over years by a factor greater than 2 for total and live standing crops and a factor of 3.5-4.5 for dead standing crop.

Spring burning probably contributed to lower total standing crops in 1990 and 1993 by removing dead herbage. Burning may have caused a higher proportion of live standing crop in July of 1993. Low early-season precipitation may have masked the effect on live standing crop in July 1990. Precipitation was 38% below normal in May-June but 50% above normal in July-August for 1990. By September, both burn years had higher proportions of live standing crop.

Table 1. Precipitation (mm) and average maximum daily temperature (°C) at the Oklahoma State University Research Range, Payne County, 1989-1993.

	Precipitation		Max Daily Temperature
Year	Nov.-Apr.	May-Aug.	May-Aug.
	------- (mm) -------		(°C)
1989	307	608	29.5
1990	497	281	31.1
1991	204	343	31.9
1992	305	536	28.6
1993	542	361	30.8
Study Average	371	426	30.4
Long-term Average	268	360	31.3

Grazing System

Grazing system did not interact with stocking rate or year for any standing crop parameter (Table 2). There were no significant differences between grazing systems for any standing crop parameter in July (Fig. 1). Total and dead standing crop were significantly higher in the rotation units in September (Fig. 2). The relative difference in total standing crop between grazing systems was 9.5% in July and 19% in September, suggesting the effect of grazing system on standing crop was cumulative over the season. The proportion of live standing crop in July was similar between grazing systems (0.68 versus 0.70 for continuous and rotation, $P>0.05$). The proportion of live standing crop was lower in September but still similar between grazing systems (0.48 versus 0.46 for continuous and rotation, $P>0.05$).

Possible explanations for increased herbage biomass in September in the rotational systems include: (1) enhanced growth due to timing and pattern of defoliation; (2) lower forage intake by cattle; or (3) lower non-consumptive losses. Simple standing crop measurements cannot test these alternative hypotheses. Timing and pattern of defoliation were affected by grazing system with a lower frequency of defoliation on little bluestem in the rotational units (Derner et al. 1994). Additional research will be necessary to fully explain the increased herbage biomass in September in the rotational systems.

Working in tallgrass prairie, Owensby et al. (1973) reported total herbage production was 17% higher under a deferred grazing system compared to continuous grazing. This is similar to the outcome of the current study although the deferred grazing system used only 3 pastures and cattle were moved once or twice during the grazing season.

Table 2. P-values from analyses of variance of herbage standing crop as affected by grazing system, stocking rate, and year.

		July Standing Crop				September Standing Crop			
Source of Variation	df	Total	Live	Dead	% Live	Total	Live	Dead	% Live
(%)									
Grazing System	1	0.32	0.31	0.67	0.39	0.03	0.13	0.03	0.38
Stocking Rate^1	1	0.01	0.01	0.02	0.16	0.01	0.01	0.01	0.62
GSxSR	1	0.77	0.67	0.75	0.60	0.46	0.68	0.38	0.74
Stocking Rate^2	1	0.93	0.71	0.39	0.39	0.98	0.73	0.77	0.53
GSxSR^2	1	0.65	0.41	0.30	0.12	0.96	0.85	0.82	0.83
Year	4	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.01
YearxGS	4	0.61	0.89	0.32	0.35	0.47	0.90	0.18	0.84
YearxSR	4	0.01	0.04	0.01	0.63	0.02	0.37	0.01	0.08
YxGSxSR	4	0.99	0.99	0.78	0.87	0.38	0.52	0.34	0.61
YxSR^2	4	0.25	0.57	0.36	0.76	0.40	0.46	0.30	0.68
YxGSxSR^2	4	0.99	0.93	0.70	0.83	0.56	0.75	0.29	0.16

^{1}Stocking Rate denotes linear effect, Stocking Rate^2 denotes quadratic effect.

Other researchers have seldom reported higher herbage standing crop with rotation grazing. Jung et al. (1985), Pitts and Bryant (1987), Anderson (1988), and Thurow et al. (1988) reported no differences in end-of-season standing crop between continuous and rotation grazing when the systems were stocked at similar rates. Rotation and continuous grazing had equal peak standing crops in exclosures (Gammon and Roberts 1978, Hart et al. 1988, and White et al. 1991) suggesting rotation grazing had little influence on plant vigor. In the study of White et al. (1991), the rotation system was stocked 10-100% higher than the continuous unit while stocking rates were equal between systems in the other studies. Exclosures were moved to new locations each year.

Stocking Rate

Stocking rate was inversely related ($P<0.05$) to total, live, and dead standing crop (Table 2, Fig. 2). More animals per unit area increase total forage demand, so the lower standing crop at the heavier stocking rates was an expected result (Van Poollen and Lacey 1979, Brummer et al. 1988). All standing crop-stocking rate relationships were linear (Table 2). Ralphs et al. (1990) also reported a linear decline in standing crop as stocking rate increased under rotation grazing. They felt the rest periods helped compensate for heavy forage removal at high stocking rates so that the rate of decline in standing crop was lower than expected based on the increase in stocking rate. Stocking rate did not interact with grazing system in this study (Table 2).

Stocking rate interacted ($P<0.05$) with year in 5 of 6 comparisons (Table 2). The slope of total standing crop versus stocking rate varied from -12 to -36 kg/ha per kg live-weight/ha in July and from -12 to -27 kg/ha per kg live-weight/ha in September (Fig 2). The steepest slopes were associated with 1991 and 1992 and were not clearly tied to weather or total forage production for the year. Ralphs et al. (1990) also reported annual variability in slopes, attributing part of the variability to declining vigor at the higher stocking rates because the slopes became more negative over time. Such an effect was not apparent in our study. Additional research is needed to quantify the factors affecting these slopes since intake, trampling, decomposition, or consumption by other animals appeared to vary widely from year to year.

Table 3. Herbage standing crop averaged over grazing system and stocking rate, 1989-1993.

	July Standing Crop				September Standing Crop			
Year	Total	Live	Dead	% Live	Total	Live	Dead	% Live
	———kg/ha———				———kg/ha———			
1989	3490	2510	980	72.0	4470	2340	2130	52.3
1990	1760	1130	630	64.1	1970	1290	680	65.5
1991	4330	2710	1620	62.7	3160	1230	1930	38.9
1992	3320	2300	1020	69.2	4380	1320	3060	30.2
1993	2550	2070	480	81.3	2580	1580	1000	61.1
LSD$_{.05}$	370	370	200	6.6	360	180	280	4.5

Stocking rate did not affect the proportion of live standing crop in

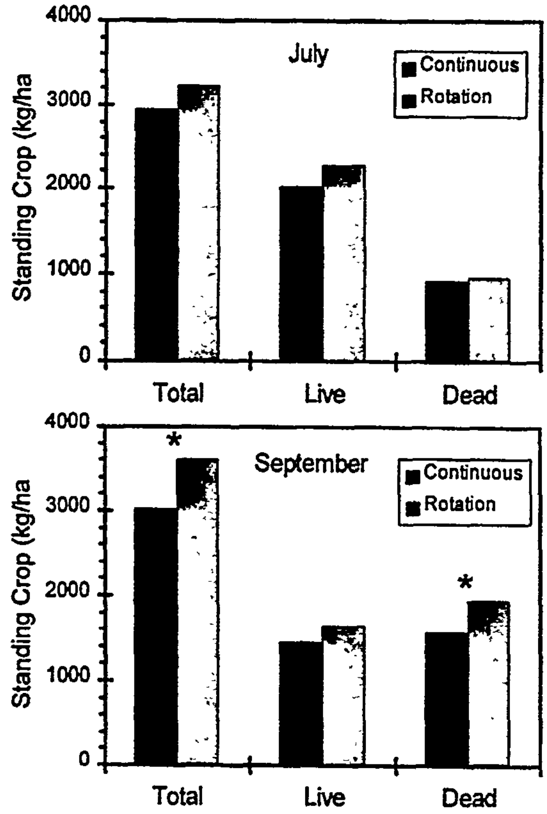

Fig. 1. Herbage standing crop as affected by grazing system averaged over stocking rate and year. Asterisks indicate significant differences ($P<0.05$) between continuous and rotation grazing.

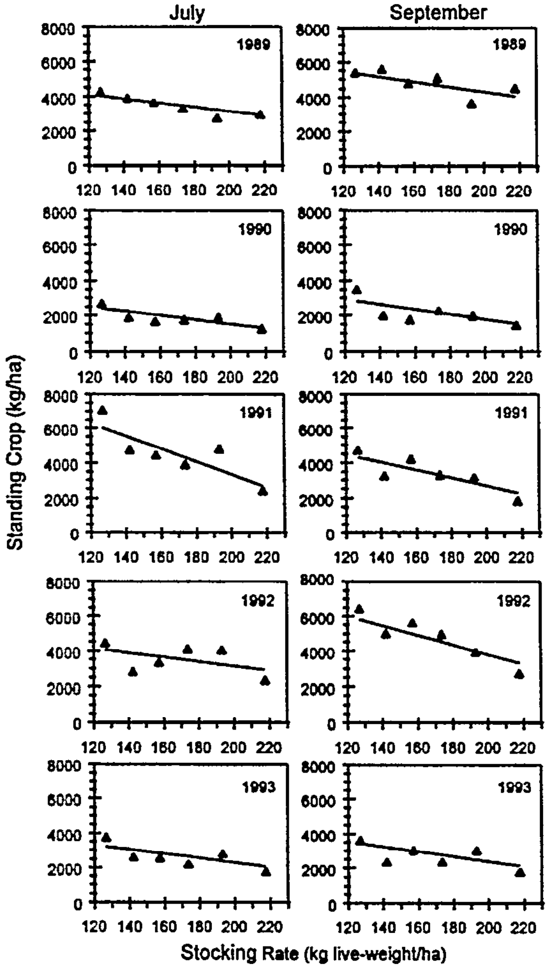

Fig. 2. Total standing crop as affected by stocking rate averaged over grazing system. All lines within sample date are significantly different ($P<0.05$).

July (Table 2). For September , the proportion of live standing crop decreased as stocking rate increased in 1990 and 1992 while the opposite effect occurred in 1989, 1991, and 1993. Under year-round grazing, Heitschmidt et al. (1989) reported a higher proportion of live herbage as stocking rates increased even though total standing crop was lower. Effects may have been variable in our study because of periodic burning and because dead herbage was not consumed during the dormant season (grazing was confined to the growing season).

Conclusions

Weather conditions were generally favorable during the study period. Results could be different under more stressful precipitation patterns. Herbage standing crop in September was about 20% higher in rotation units than in continuous units regardless of stocking rate. Higher total standing crop at the end of the grazing season would mean more forage for winter grazing and higher fuel loading for prescribed burning, and would suggest a lower impact of grazing on plant vigor. However, higher herbage standing crop does not necessarily indicate higher livestock production (Owensby et al. 1973). Livestock gains per head and per acre averaged 13% lower under rotational grazing compared to continuous grazing in this study (Gillen et al. 1992).

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Intermountain West lightning-caused fires: Climatic predictors of area burned

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Abstract

An increase in continuous fine fuels promoted by the expansion of aggressive annual exotic grasses in the Intermountain West has altered the region's fire regimes, with both ecologic and economic ramifications. I examine the predictive nature of seasonal climatic variables, seasonal precipitation and temperature data up to 2 years before the actual summer fire season, to forecast the area burned by lightning-caused fires during the 13 fire seasons (1980-1992). Five climatically-distinct regions in the shadscale, sagebrush-steppe, sagebrush-semidesert, and open pine with grass communities of California, Idaho, Nevada, Oregon, and Utah were included in the analysis. The amount of associated variance ranged from 43 to 62% between area burned and seasonal climatic variables. Results show that the seasonal climate that promotes fire is distinctly regional, even in areas of similar vegetation. However, the area burned increases primarily when the climate favors the growth of annual grasses over perennial species, or promotes either cooler or wetter conditions during the previous summer (fire) seasons. These results provide land managers with additional information for making decisions on presuppression activities.

Key Words: annual grasses, cheatgrass, *Bromus tectorum*, climate, Great Basin, sagebrush

Effective range management in the Intermountain West is, in part, dependent upon the ability to predict the number of fires and the area burned. Natural fire return intervals within the semipristine sagebrush-steppe communities of the Intermountain West range from approximately 32 to 110 years (Wright et al. 1979, Whisenant 1990), but fires are rare (Vale 1982) to non-existent in the shadscale communities (Young and Tipton 1990). The large fire intervals in semipristine areas reflect the lack of continuous fuel to carry the fire across the landscape. The introduction of exotic annual grasses, however, has led to many areas with 100% cover (Stewart and Hull 1949) that has substantially increased the likelihood of fire (Hull 1965, Wright 1985). In addition, the dry atmospheric conditions typical of the Intermountain West allow several years accumulation of the grasses without decomposition, and have led to a large increase in the continuity of fine fuels that promote wildfires.

The central focus of rangeland fire control management has been based on sophisticated models such as the National Fire Danger Rating System, the Lightning-Locating and Fire Forecasting System, and the Fire Behavior Prediction System. The National Fire Danger Rating System and Lightning-Locating and Fire Forecasting System models are designed for low resolution/large scale applications, while the Fire Behavior System model is used for high resolution/small scale applications (Bradshaw et al. 1983, Deeming 1983, Latham 1983, Rothermel 1983, Rothermel et al. 1986). These models rely primarily on a variety of weather observations, live and dead fuel moisture values, and in the case of the Fire Behavior Prediction System, topographical features to produce models of fire behavior.

Neither the National Fire Danger Rating System, Lightning-Locating and Fire Forecasting System, nor the Fire Behavior Prediction System models are designed for long range forecasting. The Lightning-Locating and Fire Forecasting System and Fire Behavior Prediction System are real-time models not designed for predictive application beyond 1 to 2 days, while the National Fire Danger Rating System predicts as well as tracks trends of the fire season for short and medium range (15-30 days) presuppression decisions. National Fire Danger Rating System model outputs are also included for 30 day projections based on the "Severity" system. Some longer range forecasts can be made by examining 1,000 hour (40 day) fuel moisture time lags, but these forecasts are viewed as indicative of trends only, and the length of the time lags (1,000 hours) does not apply to grassland fuel models (Anderson 1982). More recently, works by Latham and Schlieter (1989) examining ignition probabilities of wildland fuels and McRae (1992) examining the prediction of areas prone to lightning based on geographic factors, have shed additional insight on models used for preseason planning and land use.

Given the long term consequences of altered fire regimes, the ability to predict area burned before the onset of the fire season has become increasingly important to rangeland managers involved in presuppression activities (Phillips and George 1991). The purpose of this paper is twofold: first, to demonstrate that the

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incorporation of seasonal climatic variables, lagged as far back as 2 years before a fire season, can provide a modest degree of long range predictive power as to the likelihood of area burned during the fire season; and second, to discuss the regional differences in the climatic variables that influence fire patterns.

Study Area

The Intermountain West of the United States is bordered by the Cascade Mountains and Sierra Nevada on the west and Rocky Mountains on the east. The region (approximately 700,000 km^2) stretches from approximately 38° to 47° N. The terrain is classified as basin and range, marked by hundreds of north-south oriented fault-block mountains separated by broad (often >75 km wide), flat valleys (Trimble 1989). With the exception of the higher elevations, the climate of the region is classified as semi-arid (precipitation totals are 25 to 50 cm/year) north of 41° N. Because of the decreased frequency of Pacific type frontal systems, climate conditions get progressively more arid (precipitation totals of 10 to 25 cm/year) south of 41° N (Houghton et al. 1975), and the climate is classified as arid. The region is characterized by strong seasonal temperature variations with extremes of -40° to 45°C (Western Regional Climate Center 1993).

Three distinct vegetation zones, roughly equal in area, comprise 80% of the Intermountain West study area (West 1983a, b, c, Trimble 1989). The shadscale [*Atriplex confertifolia* (Torr.&Frem.) Wats.] zone represents the lowest elevation and most arid region. Vegetation cover is sparse (typically < 20%) with the dominant shrubs being shadsscale, Bailey's greasewood [*Sarcobatus baileyi* (Cov.) Jeps.], horsebrush (*Tetradymis* spp.), and the dominant grasses being the perennial Indian ricegrass (*Oryzopsis hymenoides* (R & S.) Ricker], and the aggressive exotic annual, cheatgrass (*Bromus tectorum* L.) (Tueller 1989, Knapp 1992a). The shadscale zone is primarily confined to areas south of 41°N and is best represented in the Lahontan and Bonneville basins that lie on the west and east sides of the study area, respectively (West 1983a).

The big sagebrush (*Artemisia tridentata* Nutt.)-steppe zone occurs under semi-arid conditions primarily north of 41° N. Cover varies substantially, ranging from 30% (Knapp 1992a) to over 100% (Daubenmire 1970). Dominant species are the shrub big sagebrush, the perennial grasses bluebunch wheatgrass [*Agropyron spicatum* (Pursh.) Scrib. & Smith], western wheatgrass (*A. smithii* Rydb.), thickspike wheatgrass [*A. dasystachuum* (Hook.) Vasey.], needle grasses (*Stipa* spp.), Idaho fescue (*Festuca idahoensis* Elmer.), and the annual grasses cheatgrass and medusahead [*Taeniatherum caput-medusae* (L.) Nevski] (West 1983b, Whitson et al. 1992). In areas receiving minimal anthropogenic disturbance, equal dominance between sagebrush and bunchgrasses typically occurs (West 1983b).

The third zone is the big sagebrush semi-desert. It is found principally south of 41°N, and although similar to the big sagebrush-steppe zone, is more arid. Additionally, many of the same grasses found in the sagebrush-steppe zone exist, but they comprise less than 30% of the relative cover while sagebrush is at least 70% (West 1983c). Absolute cover of higher plants rarely exceeds 40% (West 1983c).

In the more mesic end (typically higher elevations) of the sagebrush-steppe and sagebrush zones, the plant communities may be characterized as grass-dominated (often cheatgrass) with open timber (e.g., ponderosa pine (*Pinus ponderosa*, Laws), Jeffery pine (*P. Jeffreyi* Grev. & Balf.), and singleleaf pinyon (*P monophylla* Torr. & Frem.). This zone is represented poorly in the Intermountain West, and is not to be confused with singleleaf pinyon and juniper (*Juniperus* spp.) woodlands that, although are substantially better represented in the Intermountain West, (approximately 82,000 km^2) are not grass-dominated.

Data and Methods

Fire statistics were provided by the National Interagency Fire Center (Boise, Ida.). Data for 16 Bureau of Land Management (BLM) districts covered the period 1980 to 1992, and included the annual number of fires and the annual number of acres burned by fuel model classification for both lightning and human-caused fires. Fuel models indicate the type of vegetation that burned. The summed value of lightning-caused fires that burned in the western annual grass, western perennial grass, open pine with grass, and sagebrush with grass fuel model classifications were used for statistical analyses. Human-caused fires (e.g., accidental fires begun by sparks from catalytic converters or campfires) were excluded. Since population density largely influences the level of human activity and population density varies greatly throughout the study area, the data on human caused fires were eliminated from the models used. The 4 fuel models were grouped together (with annual grasses present in all groups) based on the "Grass-Dominated Group" classification set forth by Anderson (1982). The fuel model group is characterized by continuous surface of the herbaceous fuel that promotes rapidly moving surface fires. The BLM districts vary substantially in size and in the potential area burned. To make meaningful comparisons then, the area of lightning-caused fires was converted into Z-scores with a mean of 0 and a standard deviation of 1 (SUMLACRE) (Clark and Hosking 1986).

Climatological data were provided by the Western Regional Climate Center (Reno, Nev.). The data set contained monthly precipitation and temperature values of 91 stations within the Intermountain West from 1978 through 1992. All BLM districts were represented climatically by at least 3 stations, and most commonly by 5 or more stations, that fall within the corresponding BLM district boundary. Station data were averaged by BLM district. Seasonal data were then generated by summing the monthly data for each season (using traditional definitions for seasons: e.g., winter—December, January, February; c.f. Knapp 1992b). Because the fire season for the Intermountain West generally occurs from 1 June through 15 September (L. Mahaffey, pers. comm. 1993), all seasons preceding the summer season were included for the previous 2 years (e.g., for the 1992 summer fire season, climatic variables included would be from summer 1990 through spring 1992). Data included both precipitation and temperature, for a total of 16 independent climatic variables (Table 1).

The original 16 BLM districts were combined into 5 regions: the Northwest, represented by the Lakeview, Burns, and Vale (Ore.) districts, and Boise (Ida.) district; the Southwest, represented by the Susanville (Cal.), and Winnemucca and Carson City (Nev.) districts; the Southcentral, comprised of Battle Mountain, Elko, and Ely (Nev.) districts; the Southeast, consisting of the Cedar City, Richfield, and Salt Lake (Ut.) districts; and the Northeast, represented by the Shoshone, Burley, and Idaho

Table 1. Definitions for independent variables.

Variable Name	Variable Definition
SUMTLAGR[1]	Summer (Jun., Jul., Aug.) temperature lagged 2 seasons
AUTTLAG2	Autumn (Sep., Oct., Nov.) temperature lagged 2 seasons
WINTLAG	Winter (Dec., Jan., Feb.) temperature lagged 1 season
SPRTLAG	Spring (Mar., Apr., May) temperature lagged 1 season
SUMTLAG	Summer temperature lagged 1 season
AUTTLAG	Autumn temperature lagged 1 season
WINT	Winter temperature
SPRT	Spring temperature
SUMPLAG2[1]	Summer (Jun., Jul., Aug.) precipitation lagged 2 seasons
AUTPLAG2	Autumn (Sep., Oct., Nov.) precipitation lagged 2 seasons
WINPLAG	Winter (Dec., Jan., Feb.) precipitation lagged 1 season
SPRPLAG	Spring (Mar., Apr., May) precipitation lagged 1 season
SUMPLAG	Summer precipitation lagged 1 season
AUTPLAG	Autumn precipitation lagged 1 season
WINP	Winter precipitation
SPRP	Spring precipitation

[1] Because the fire season occurs during the summer and before autumn, the first summer and autumn seasons included for analyses (SUMTLAG, AUTTLAG, and AUTPLAG) are for the previous year (i.e., lagged 1 season), while the second summer and autumn seasons (SUMTLAG2, SUMPLAG2, AUTTLAG2, and AUTPLAG2) date back 2 previous years (i.e., lagged 2 seasons).

Table 2. Seasonal climate averages for the 5 study regions.[1]

Seasonal climate averages	Region				
	Northwest	Northeast	Southeast	Southcnt.	Southwest
Temperature			(°C)		
Winter	-0.89	-4.12	-1.59	-1.35	0.28
Spring	8.99	7.45	9.36	7.71	8.92
Summer	19.61	18.93	21.56	19.61	19.66
Autumn	9.33	7.90	10.34	9.11	9.80
Mean	9.26	7.54	9.92	8.77	9.67
Precipitation			(cm)		
Winter	9.67	8.58	7.72	6.14	7.56
Spring	9.65	9.60	11.45	9.16	6.75
Summer	5.18	5.33	6.22	4.59	2.84
Autumn	7.82	7.92	10.03	6.93	6.27
Total	32.32	31.43	35.42	26.82	23.42

[1] Based on years 1980 through 1992. Source: Western Regional Climate Center, 1993.

Falls (Idaho) districts (Figure 1). The total area of the districts is approximately 3.15 million km². The regional groupings were based on 2 climatic criteria that affect vegetation composition. The predominant winter air mass boundary within the Intermountain West, ranging between 40° N to 42° N from Oregon through Idaho (Mitchell 1976, Woodhouse and Kay 1990) was used to separate the northern and southern regions. The coldest winters are in the Northeast region while the Southwest region has the mildest winters (Table 2). Precipitation patterns, based on amounts and timing, were used to separate the regions further. The Northwest and Southwest regions are both characterized by a winter precipitation maximum; and, the Northeast, Southeast, and Southcentral regions by a spring maximum. The driest region is the Southwest, while the wettest is the Southeast (Table 2).

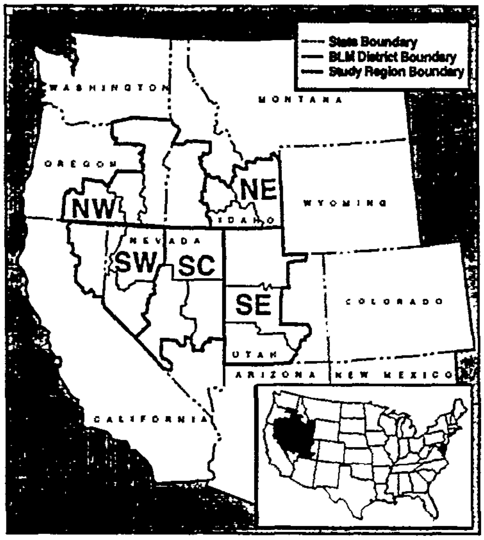

Fig. 1. Location of Intermountain West study regions.

Multiple regression analyses were done by region using the annual area burned by lightning-caused fires as the dependent variable. All models were checked for possible violations of the assumptions of the general linear models (Clark and Hosking 1986). Significance of t-values and F values were checked, residuals were examined using Cook's D and studentized residuals diagnostics, and the Drubin-Watson test was used to check for autocorrelation. The independent variables were checked for collinearity problems examining condition numbers and variance proportions. Finally, the signs (+ or -) of the partial regression coefficients were examined to determine if they were logical. None of the models included violated these assumptions (i.e., failed the tests).

Results

Associated variance (R^2) between lightning-caused fires and climatic variables ranged from 0.43 in the Northwest region to 0.62 in the Southwest region (Table 3). One to 4 independent variables entered into the multiple regression equation.

Regression analyses for the Northwest, Southwest and Southcentral regions showed that a positive SUMPLAG (summer precipitation lagged 1 season) was included in each model, and that the relative contribution of the variable, as shown by the partial coefficient of determination, was substantial for the Northwest and Southcentral regions (Table 3). This indicates that area burned was greater following wet summers the previous year. The Northwest and Southwest regions also included a second common variable, a negative AUTTLAG (autumn temperature lagged 1 year). Autumn temperature lagged 1 year made the greatest contribution to the Northwest model, accounting for approximately one fourth of the total associated variance, but only accounted for approximately one sixth of the total associated variance for the Southwest. This variable suggests that area burned increases following cooler than normal autumns. Minor contributing variables included for the Northwest and Southwest regions were a positive SPRT (spring temperature) and a negative SPRP (spring precipitation), indicating that area burned increases if springtime conditions are warmer and drier than the normal, respectively. A positive SUMPLAG2 (summer precipitation

Table 3. Regression models for Intermountain West regions predicting area burned as a function of seasonal climatic variability[1].

Region	Regression Model	F statistic	R^2
Northwest	[2]SUMLACRE = 2.741 + 0.336 (SUMPLAG) - 0.145 (AUTTLAG + 0.0741 (SPRT) (0.25)[3] (0.12) (0.07)	11.34[3]***	0.43
Southwest	SUMLACRE=3.995 + 0.390 (SUMPLAG) - 0.091 (AUTTLAG) - 0.232 (SPRP) + 0.439 (SUMPLAG2) (0.12) (0.09) (0.07) (0.33)	12.28***	0.62
Southcentral	SUMLACRE=0.342 + 0.519 (SUMPLAG) + 0.245 (SUMPLAG2) - 0.059 (WINT) (0.34) (0.08) (0.08)	10.90***	0.50
Northeast	SUMLACRE=12.861 + 0.283 (SPRT - 0.296 (SUMTLAG) (0.23) (0.30)	19.86***	0.53
Southeast	SUMLACRE=-1.444 + 0.311 (AUTPLAG) (0.51)	33.91***	0.51

[1] Based on period 1980-1992.

[2] SUMLACRE = Z score transformation of the number of acres burned as a result of lightning-caused fires by region.

[3] Partial R^2 are shown parenthetically below the regression coefficients.

[4] *** $P<0.0001$. All t-values for the included independent variables were significant ($p<0.05$).

lagged 2 seasons) was common among the Southwest (contributing to over half the total) and Southcentral models and shows that above normal precipitation amounts as far back as 2 years can lead to greater area burned. In addition, a negative WINT (winter temperature) was included in the Southcentral model indicating that below average winter temperatures are followed by more area burned.

Only 3 variables were used for the Northeast and Southeast region regression models. In the Northeast, the relative contribution of the variables was almost evenly distributed between a negative SUMTLAG (summer temperature lagged one season), indicating that below average temperatures the previous summer are associated with greater area burned and above normal spring temperatures. Conversely, the only contribution to the regression model for the Southeast came from a positive AUTPLAG (autumn precipitation lagged one season), which shows that above average autumn precipitation is positively associated with area burned. This correlation may likely be because seedling production of cheatgrass and medusahead is linked to above average autumn rains (West 1983b, Morrow and Stahlman 1984).

Eight of 16 original variables were used by the regression models. Those variables that were not included in the regression models were WINTLAG, SPRTLAG, AUTPLAG, SUMTLAG2, WINPLAG, SPRPLAG, WINP, and AUTTLAG2 (Table 1). Of the 8 variables used, SUMPLAG was found in 3 models; SUMPLAG2, SPRT, and AUTTLAG were found in 2 models; and the remainder of the variables occurred in only 1 model. In general, the regression models for regions with lower annual precipitation included a greater number of significant explanatory variables.

Results of annual fire statistics summed by region and converted into Z-scores show that area burned is highly variable annually, but less variable regionally (Figure 2). In the Northwest, Southwest, and Southcentral regions, the greatest number of acres burned occurred in 1985, while for the Northeast region it was 1992, and for the Southeast, 1983. The years when the least area burned were 1988 for the Northwest and Southeast, 1984 for the Northeast, and 1982 for the Southcentral and Southwest.

Within a region, the number of years with negative Z-scores (showing less area burned) ranged from 7 to 10, with many of the remaining observations having large (>0.5) positive Z-scores (Figure 2). These Z-scores show that during this study period, fire seasons in the Intermountain West were not characterized by even distributions of area burned yearly, but rather were marked by many years with little area burned punctuated by the occasional season where the total area burned was large.

Discussion

The 5 regression models show that a few climatic variables provide a modest degree of associated variance with acres burned by lightning-caused fires, and that seasonal climatic conditions up to 2 years before the fire season may contribute largely to area burned in a given year. These lags indicate that not only are current weather conditions important in determining the likelihood of area burned, but that the area burned is influenced by the magnitude of precipitation and temperature variations in the proceeding months. These climatic fluctuations are important because they influence the amount of fine fuels (cheatgrass and other annual grasses) that promote fires. In Arizona, fire-climate studies in Sonoran Desert vegetation (Rogers and Vint 1987) and mixed conifer and pine forests (Baisan and Swetnam 1990) have shown that fire occurrence is related to above normal precipitation 2 years before the fire season because the wetter conditions produce an abundance of fine fuels necessary to carry fires. Similar interactions between climate, fuel production, and fire intensities exist in the Intermountain West. Interpretation of the regression models for the Intermountain West are based on those climatic variables that tend to either promote more fine fuel production or temporarily suppress fires, which allow greater accumulations and coverage of fine fuels.

Northwest, Southwest, and Southcentral Models

Common among these models are the contributions of below normal temperatures during either the preceding autumn (AUTTLAG) or winter (WINT) and above normal precipitation the preceding summer (SUMPLAG). Cooler than normal autumns or winters may favor the production of cheatgrass and medusahead for 2 reasons. First, cheatgrass and medusahead may be favored because following the onset of the first autumn rain, growth of

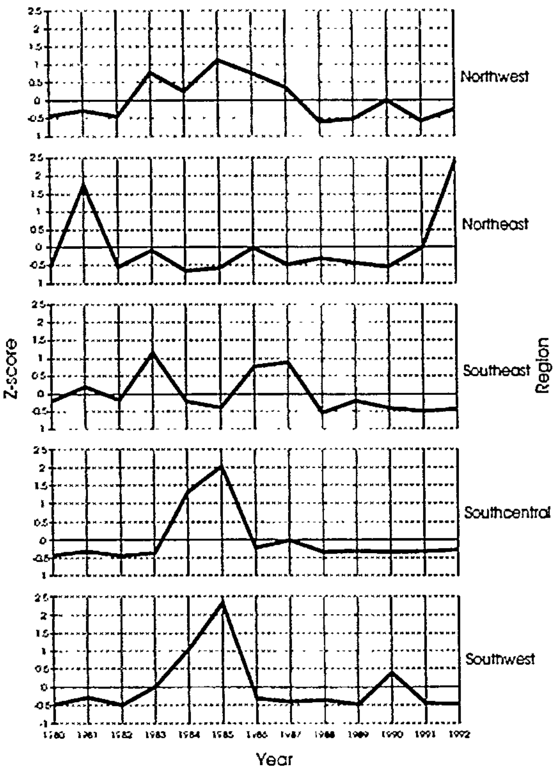

Figure 2. Annual lightning-caused fire statistics by region. The number of acres burned annually as a result of lightning-caused fires were transformed into Z-scores with a mean of 0 and standard deviation 1.

their roots can continue as long as temperatures remain above 0°C. In contrast, native perennial grasses such as *Agropyron spicatum* cannot grow at temperatures below 4°C (Harris 1967, West 1983b). Second, soil moisture retention is greater during colder winters leading to better spring growth. As a result, the annual grasses are able to establish extensive root systems that allow them to extract soil moisture at greater rates than the perennial grasses can in the spring when temperatures are sufficiently warm to promote shoot and leaf growth. The net effect is a relative increase in annual cover (Morrow and Stahlman 1984).

Wetter than normal summers the preceding year (and, in the case of the Southwest region, the previous 2 years) promote fire in several ways. Cheatgrass is effective at removing moisture from the upper soil layers and can outcompete many native species such as needleandthread (*Stipa comata* Trin. & Rupr.) and green rabbitbrush [*Chrysothamnus vicidiflrus* (Hook.) Nutt.] for the available water resources (Melgoza et al. 1990, Melgoza and Nowak 1991). Because summer rains are short-term conductive thunderstorms that rarely soak the soil, cheatgrass, with its shallow, but extensive root system, is well-equipped to benefit from increased soil moisture following summer precipitation.

Much of the native flora in these regions evolved with mechanisms that conferred particular strategies to cope with drought that are generally not conducive to exploiting summer precipitation. Big sagebrush for example, has a deep root system that allows it to extract water from deep soil layers during the summer and to continue growth after the topsoil becomes dry (Mozingo 1987). However, when summers are wetter than normal, annuals are best able to exploit the short-term favorable soil conditions with an increase in their cover since summer rains rarely soak the soil to the point where perennial species proportionally benefit. The net effect is that because of their high degree of phenotypic plasticity (Young et al. 1972), the normally compressed phenological cycle for cheatgrass and medusahead of drying out and casting seed by early summer (West 1983b) can be expanded to a much later date, with more vegetative growth in the intervening period. The result is an increase in the amount of continuous fine fuel required to carry fire. Finally, wetter summers can increase fuel moisture loads, suppressing fires, and subsequently allowing an even greater continuity of fuels for the following fire season.

The remaining variables included for the Northwest and Southwest regions were warmer spring temperatures (SPRT) and below normal spring precipitation (SPRP), respectively. These variables indicate the importance of reduced fuel moisture levels in the season immediately preceding the summer fire season. Bunting et al. (1987) found that abundant precipitation in late winter and spring raises fuel moistures to the point where fires have difficulty carrying. Either dry or warm spring seasons lead to a more rapid drying stage of the spring annuals, and promote the likelihood of fire early in the season.

Northeast

Cooler than normal preceding summer temperatures (SUMTLAG) and above normal spring temperatures (SPRT) were linked with increased fire activity in the Northeast region. Above normal spring temperatures in this region promote the likelihood of fire for the same reasons as the Northwest, Southwest, and Southcentral regions. Cooler summer temperatures in the year preceding the fire season tend to decrease the likelihood of fire because of decreased fuel moisture loads, but also lead to greater continuities of fine fuels for the following fire season. Similar conclusions have been found by Balling et al. (1992) in adjacent Yellowstone National Park where they found positive correlations between both antecedent temperatures (January-June) and wildfires (although in forests in contrast to grasslands), and summer temperatures and wildfires

Southeast

Only one variable, above normal precipitation in the autumn preceding the fire season (AUTPLAG), was included. Above normal autumn precipitation favors the germination and subsequent buildup of annual grasses, particularly *B. tectorum*, that germinate in the fall and establish root systems that provide a competitive advantage to native grasses and shrubs when they resume growth in early spring (Morrow and Stahlman 1984). Consequently, a larger than average amount of continuous fine fuel is produced that increases the chances of fire in the summer season.

Conclusions

These predictive models using climatic variables indicate that the likelihood of fire is increased by events that promote the growth of fine fuels (i.e., primarily annual grasses), by events that delay or suppress fires, thereby allowing even greater continuities of phytomass, or by a combination of the 2 factors. The models suggest that the timing of seasonal climatic variability that promotes fire is distinctly regional, even in areas of similar vegetation. They underscore 2 key points: fire area is often increased primarily when either the climatic conditions favor the growth of aggressive, exotic, annual grasses that provide the continuous fine fuels necessary to carry fire, or when these conditions suppress fire long enough to allow sufficient fuel continuity. Additionally, these models are generally in concert with findings of other fire-climate studies in areas bordering the Intermountain West. In studies of the Giant Sequoia groves of the Sierra Nevada (Swetnam 1993) and the Douglas fir [*Pseudotsuga menziesii* (Mirb.) Franco] and pine (*Pinus* spp.) forests of the Southwestern United States (Swetnam and Betancourt 1990), it was determined that seasonal climate variability (in addition to fire weather) determines the amount of area burned.

Examining regional similarities and differences sheds considerable insight on the models' usefulness. For the Northwest, Northeast, Southwest, and Southcentral region models, the common characteristic was including either above normal precipitation or below normal temperature during the previous summer seasons. In each of these models, one summer variable contributed over one-half of the total associated variance. The importance of these variables suggests that seasonal climatic conditions affecting fuel moisture (increased precipitation or decreased evaporation) during the summer fire season is particularly important in decreasing the area burned. Additionally, real-time climatic data collection allows for this information to be acquired nine months before the fire season and increases the long range predictive value of the models.

The Southeast region model did not include a summer climate variable. This may be a function of the greater amount and consistency of spring and summer precipitation relative to the other regions. The wetter spring conditions promote abundant herbaceous growth that increases fuel moisture loads. This higher moisture level may make the region less susceptible to lightning ignitions even after the fuels dry, since fires have less success burning through combined live and dead fuels (Bunting et al. 1987).

The predictive power of the models was limited by several factors that undoubtedly influence the occurrence of fire, but were not modeled. These factors include grazing intensity (Higgins 1984), the occurrence of fires outside the summer season, the fact that rarely only one fuel type (e.g., western annual grass only) is found within a region, and time since last fire (since a longer fire interval could allow a greater continuous fuel bed to develop). Favorable fuel conditions may also occur in the absence of lightning ignition.

Given the ecologic and economic ramifications (i.e., resource losses, suppression costs, presuppression costs, rehabilitation, and fire management) of increased fire activity there has been an impetus to engage in a variety of fire presuppression activities based on fire danger projections. Increased foot and air patrols, greater emphasis on tracking trends (i.e., projecting out fire probabilities several days in advance), increased fire safety education, and installation of mechanical fire-breaks in areas especially likely to burn are a few presuppression efforts that have been implemented (Pellant 1990, Phillips and George 1991). Prescribed burning is also used as a fire management technique (Bunting et al. 1987). Results from this study suggest that a moderate degree of predictive power can be gained from examining seasonal climatic variability up to 2 years before the actual fire season, and could help establish a baseline estimate of area burned in the Intermountain West that could aid in pre-fire season management decisions.

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Technical Note:
A total urine collection apparatus for female bison and cattle

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Abstract

A urinary collection device is described for use in metabolism studies on female bison *(Bison bison)* and cattle. Separating urine from feces, and collecting all urine produced by female animals in metabolism stalls present difficulties. Catheters are usually used on animals in confinement, but often with varying degrees of success. Thus, an external device designed to divert urine into collection receptacles was developed. The urine collection apparatus was used successfully in six 8-day metabolism trials conducted during 1991 and 1992.

Key Words: *Bison bison, Bos taurus*, metabolism studies

Metabolism studies with ruminants are an important method for determining physiological responses of animals to changes in a variety of environmental stimuli such as, ambient temperature, energy and nutrient levels, and water availability. These studies usually require the measurement of feed offered, and the separation and quantification of urine and feces produced by individual animals. However, total collections of urine and feces are difficult to achieve from females; the proximity of the meatus urinatus and ishio-rectal region causes cross-contamination of samples. Consequently, metabolism studies often use male subjects because of the obvious ease of separating and collecting urine and feces.

If total urine collections from female ruminants are required, the technique most often employed is bladder catheterization. However, catheters present unique problems such as their difficulty of insertion, secondary bacterial infections, and often substantial urine loss.

An apparatus for separating urine and feces from female cattle and bison was developed. This urine collection apparatus was modeled after the urine deflector flap developed for fecal collection bags by Kartchner and Rittenhouse (1979). Unlike the urine deflector flap, however, this apparatus was also designed to collect urine.

Materials and Methods

Urine collection devices were used on 3 Hereford cattle and 3 American bison in six 8-day metabolism trials. The urine collection apparatus was constructed of a 2,000 ml center entry, closed system urinary drainage bag[1], a 500-mm x 250-m strip of burlap, and a 1.2 m length of 7.6 mm inside diameter plastic tubing. The top of the bag was cut open, and the edges around the opening were sewn to the burlap strip using cotton thread in a zigzag pattern. The bag was oriented perpendicular to the burlap, and centered horizontally on the long axis of the burlap (Fig. 1). The edge along the opening of the bag was sewn about 25 mm from the edge of the burlap. An opening to the bag was cut through the burlap in roughly the size and shape of the vulva.

The apparatus was attached to an animal in a squeeze chute. A hypoallergenic biological adhesive[2] was applied to the burlap strip and to the animal; care was taken when applying glue in the area around the vulva, especially below the anus. The apparatus was first attached to the animal around the vulva, and then out around the tuber ischiadica (e.g., the pins).

After 2 to 3 minutes the apparatus was securely bonded, and the animal was placed in a metabolism crate. Once confined, the plastic tubing was connected to the drainage valve at the base of the bag and secured with a number 1-size hose clamp. The end of the tube was placed in a collection bucket outside the crate (Fig. 2). The length and position of this tube were modified for each animal to minimize the possibility of the tube becoming entangled in the animal's legs.

After the first 8-day trial was completed, only the drainage bag

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[1] Order #153504, C.R. Bard, Inc., Bard Urinological Div., 8195 Industrial Blvd., Covington, Ga. 30209.

[2] K-mar Inc., Box 773838, Steamboat Springs, Colo. 80477.

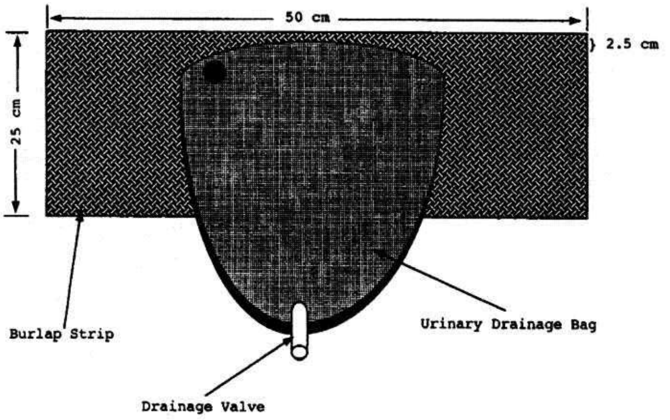

Fig. 1. Urinary collection bag developed for use on female bison and cattle.

portion of the apparatus was removed, while the strips of burlap were left attatched to the animal. This was accomplished by cutting the polypropylene drainage bag with scissors where it was sewn to the burlap. Any free edges of burlap were then trimmed back to the point where it was securely bound to the animal. This allowed animals to urinate freely during the 14-day adaptation periods that preceded each of the subsequent 8-day trials.

Attachment of apparatuses during the second and third trials was similar to the first. However, because the burlap strips of previous apparatuses were still attach over the tuber ischiadica, the next apparatus was glued directly to this burlap. On completion of the last trial, the drainage bag portion of the apparatus was once again removed, and the burlap strips were left in place until they fell off the animals unassisted.

Discussion

Careful application of the urine apparatus resulted in little or no sample loss during the 8-day trials. The most important stage during application was placement of the apparatus around the vulva. The adhesive was developed to bond materials to animal hair; subsequently, the burlap bound tightly to the hair of the hind quarters. However, little hair exists in the area around the anus and vulva. Thus, it was necessary to adequately work the adhesive into the burlap, and the fine hair around the vulva for a sufficient bond to occur. Also, care was needed to prevent the adhesive from getting on the vulva itself, or inside the bag. This sometimes interfered with the normal discharge of urine, and ultimately caused malfunction of the apparatus.

We did experience a problem with using the apparatus on cattle that we did not have with bison. The protruding tuber ischiadica of cattle resulted in a concave surface in the area between these 2 skeletal projections. Thus, if the burlap was stretched out around the tuber ischiadica, it would cause the apparatus to lift away from the animal in the region of the vulva. We prevented this from occurring by following the contour of the body when gluing the burlap, rather than stretching it out over the tuber ischiadica. However, sometimes the bags did loosen in the region of the vulva towards the end of the 8-day trial. Usually, bags could easily be repaired by carefully gluing the loosened area. On 2 occasions, though, enough of the burlap had become detached that we chose to remove the drainage bag portion of the apparatus and attach another. The docile behavior of cattle and their confinement allowed us to easily accomplish this task in the metabolism crates.

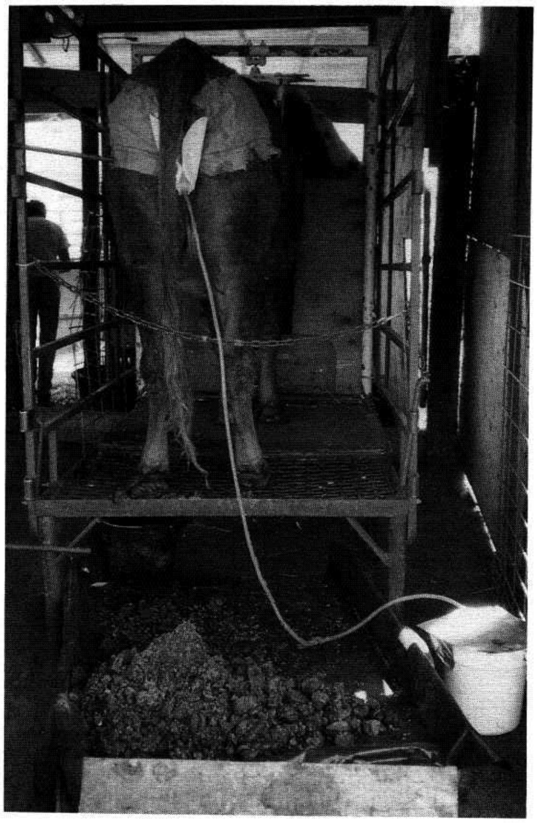

Fig. 2. Complete urinary collection apparatus used on female bison and cattle during metabolism studies.

Removal of only the drainage bag portion of the apparatus between trials, allowed the animals to urinate freely without causing stress by attempting to remove burlap that was bound intimately with hair. Animals did not exhibit any distress beyond that expected during routine handling, and the apparatus did not appear to adversely influence their behavior once in place.

Conclusions

We found the urine collection apparatus to be an effective means for collecting total urine samples from female bison and cattle during metabolism studies. Additionally, the simple construction and application of the apparatus made it easy to use and did not result in additional stress or infection to our study animals. Therefore, we considered it an improved alternative to catheters in our studies requiring urine collections from female animals.

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Book Reviews

Goat Nutrition. Edited by P. Morand-Fehr, with 41 text contributors. 1991. Centre for Agricultural Publishing and Documentation, (Pudoc), Wageningen, Netherlands. Distributed in U.S. by UNIPUB, Lanham, Maryland. 308 p. US$83.00 cloth. ISBN 90-220-1009-0.

This book summarizes presentations at seminars held at Reading, U.K. in 1982, Grangeneuve, Switzerland in 1984, Nancy, France in 1986, and Potenza, Italy in 1988 by scientists under the Programme of the FAO Cooperative Research Sub-Network on Goat Production. Twenty-four major chapters plus an introduction cover both basic research findings and practical applications related to the nutrition, physiology and management of goats. The editor's hope was that the book would be useful to scientists, teachers and students of animal husbandry, and to experts in agricultural development, livestock production, and goat breeding and management. Geographically, the volume focuses on Europe, and to a lesser extent the Middle East and other goat producing regions in content and in literature cited. Several of the chapters cite considerable North American research.

The volume is divided into 4 parts entitled General Goat Nutrition, Evaluation and Utilization of Feeds, Feeding of Adult Goats, and Feeding of Young Goats. Discussions of production systems relevant to the technical research presented are found in many of the chapters. Compared with much research on sheep and cattle, the goat management practices and production systems presented are less intensive, and their descriptions are more readable. Several chapters specifically concern goat management on rangelands or extensively managed pastures. Chapter 14 by M. Meuret *et al.* examines the value and use of rangeland forages by goats. Discussions of goat management practices relevant to production systems involving rangeland are dispersed throughout the book.

All chapters are written in English with abstracts in English and French. In some chapters an English language assistant editor might have smoothed the syntax, which is unrefined in places. Still the messages get through, mostly without pretentious prose or perplexing paradigms to sedate the reader. Some of the chapters do contain considerable technical, nutritional jargon. *Goat Nutrition* does not have unifying introductions to its 4 sections; in content and message some of the individual chapters are better balanced than the book as a whole. The book has no general index.

Goats are major products in some countries. Where they are not, researchers and producers of them seem comfortable as niche players in ranching industries. In the United States and in other developed countries, goats seem to have a secure future as components of sustainable, extensive production systems. The chapters in *Goat Nutrition* are readable syntheses of basic research and applied practices that readers will find relevant to a wide variety of production systems involving goats.—*David L. Scarnecchia,* Washington State University, Pullman, Washington.

The Landscapes of Craters of the Moon National Monument. By R. Gerald Wright and Stephen C. Bunting. 1994. University of Idaho Press, Moscow, Idaho. 103 p. US$24.95 paper. ISBN 0-89301-168-1.

This short book evaluates the vegetational changes in Craters of the Moon National Monument by comparing 34 pairs of contemporary and historic photographs. The monument, located at the northern edge of the Snake River Plain in central Idaho, is a stark landscape of geologically recent basalt flows and cinder cones in a cold desert environment. Because of its harshness, the area saw little documented exploration until the early 1900's. Earliest photographs used in the vegetation comparisons date to the 1920's.

The book begins with some background on the project which produced it, followed by brief descriptions of the history, geology, environment, vegetation, and visitor use of the area. Brief sections discuss the concept of environmental change, the photographic method of evaluation of long-term environmental change, and trends in vegetational change on the Snake River Plain. The black and white photographs come next, followed by a discussion of what the photo comparisons reveal. An appendix of the common and scientific names of relevant plants, a list of literature cited, and a general index complete the book. The book contains five one-page maps including four showing photo locations.

The semi-technical discussions are in a relaxed style that makes the book satisfying reading. That the authors enjoyed working on this project shows in the tone of the book. The black and white photography, necessary in the case of the older photos, seems especially appropriate in this land of gray and black. The unusual landscape makes the observed vegetational changes partly a curiosity, but they still have some relevance to the larger Snake River Plain and bordering foothills. The book's coverage of the history, geology and ecology of Craters of the Moon, combined with its past and recent photographs should answer most of the questions a curious visitor would have about this offbeat area. —*David L. Scarnecchia,* Washington State University, Pullman, Washington.

Rangeland Health: New Methods To Classify, Inventory, And Monitor Rangelands. By National Research Council. 1994. National Academy Press, Washington, D.C. 180 p. US$26.00 paper. ISBN 0-309-04879-6.

Rangeland Health is an important book for those concerned with managing U.S. rangelands because it provides the U.S. Congress and concerned federal land management agencies with guidelines on the direction that federal policy regarding national-level range condition and trend assessments should take. The intended audienced includes the public, special interest groups, and policy makers in the federal land management agencies.

Rangeland Health includes an executive summary, five chapters, an appendix, resumes for each of the 14 panel members, and an index. Chapter 1 provides a definition of rangelands, explains why they are a relevant issue to the public, and introduces the need for a national assessment of rangeland condition and trend. Chapter 2 introduces a new term: *rangeland health,* and a conceptual model of land degradation herein called the health threshold model (HT, Figure 1, p. 38). Chapter 2 also contains illustrative case studies of three different rangeland ecosystems examined in terms of newly introduced ecological concepts. The book lacks a glossary, which should have been added because of the many ecological terms used. Chapters 3 provides a history of data collection methodologies and their ecological bases. Chapter 4 explains the ecological indicators used in range assessments and provides an excellent discussion on the distinction between an ecological assessment and interpretations based on management values and decisions. Although it omits a discussion of Native-American rangelands under the federal jurisdiction of the Bureau of Indian Affairs, chapter 5 provides an excellent historical review of legislative policies, ecological methodologies, and past federal surveys that are the basis for the conduct of national level assessments. The book emphasizes the change in the ecological theory upon which range degradation assessments are based. It also points out that a lack of standard methods and data collection systems among federal agencies has hindered the national-level determination of the ecological condition of the U.S. rangelands. The book recommends that federal agencies cooperate by using a similar sampling framework such as that proposed by the Environmental

Protection Agency's Environmental Monitoring and Assessment Program (EMAP) to determine national-level resource degradation. The recommendation for interagency cooperation has been acted on most recently at a "Rangelands Health Assessment Workshop" in Ogden, Utah.

From the perspective of ecological risk assessment (Suter, 1993. *Ecological Risk Assessment.* Lewis Publishers, Boca Raton), ambiguities are present in chapters 2 to 4. The HT model is presented too early in the text. It would have been better to introduce the model after chapters 3 and 4, where the model's theoretical and practical bases are introduced. The terms *rangeland health* and its derivatives (e.g., unhealthy, Figure 1: x-axis) are problematic because they are ambiguous. Rangeland health is an attempt at specifying an assessment endpoint: a formal expression of the actual environmental value that is to be protected. An assessment endpoint has the following characteristics: social relevance, biological relevance, an unambiguous operational definition, accessibility to prediction and measurement, and susceptibility to a hazard (Suter 1993). The term *rangeland health* does not fit these requirements. In order for rangeland health to be socially relevant or to satisfy values, a linkage would have to be made between ecological and either economic aspects of rangelands and/or human health. The development of the site conservation threshold model (SCT) by the Society for Range Management (Task Group for Unity in Concepts and Terminology. 1991. *New directions in range condition assessment.* Report to the Board of Directors. Denver: Society for Range Management; Figure 1, p. 16), a precursor of the HT model, is consistent with ecological risk-assessment protocols.

The SCT and HT are both presented as 2-dimensional graphs; however, both axes of the HT are ambiguous (i.e., y = capacity to produce commodities and satisfy values and x = a range of healthy range conditions; Figure 1, p. 38). Suter (1993) observed that such terms "are not suitable subjects for assessment because they cannot be measured or modeled from any measurement." The quantification of rangeland commodities (y-axis) is an area of ongoing economic research. The quantification of satisfaction of societal values and their relationship to ecological principles is a new area of fertile and necessary research which is found primarily in the social and political sciences. The quantification of the axes of the SCT model has been carried out by physical scientists. The SCT model's axes are measurement endpoints of range degradation [i.e., soil erosion (y-axis) and vegetation cover (x-axis); Figure 1, p. 16]. A measurement endpoint is a standardized ecological indicator (e.g., percent loss in vegetation cover) that comes from an existing data series, it is correspondent or predictive of an assessment endpoint, is easily measured, is appropriate to the scale of the disturbance, and it possesses particular temporal dynamics and routes of exposure. A measurement endpoint also should have low natural variability, be diagnostic of a disturbance, and be broadly applicable (Suter 1993).

Despite the observational data to support the SCT, neither the SCT nor the HT have been empirically tested as appropriate models of rangeland degradation, whereas Dysterhuis' model (1949. "Condition and management of range land based on quantitative ecology." *J. Range Manage.* 2:104-15) has seen international application. Further, both models lack an explanatory theory as to why the observed changes in plant species' response to environment occurs (e.g., Roberts D. 1986. "A dynamical systems perspective on vegetation theory." Vegetatio 69:27-33; Lockwood, J.A. and D.R. Lockwood. 1993. "Catastrophe theory: a unified paradigm for rangeland ecosystem dynamics." *J. Range Manage.* 46:282-88). It would be better and more interesting to test the validity of the patterns in nature suggested by each model before they are applied. Once this is accomplished, integration of the SCT into the HT model would be appropriate.

Although space and time scales are recognized as legitimate concerns, no serious attempt is made to incorporate them into the discussions in Chapters 2-4. A watershed-bounded ecosystem perspective is suggested as the level of observation to determine rangeland degradation. The recommended measurement endpoints of ecosystem function are point-based or spatially aggregated soil and vegetation-based indices (Table 4.8, p. 130-31). The problems with a watershed view are that it has insufficient resolution to detect changes in phenomena that act at larger and smaller spatio-temporal scales and that the requisite measurement endpoints do not account for location (i.e., they are not spatially explicit). Because observational perspectives are scale-independent, arbitrary boundaries are necessary to detect change at different spatio-temporal scales. This suggests that the appropriate observational perspective for a national-level assessment is the landscape where measurement endpoints such as shape complexity (fractal dimension) have been effective in detecting anthropogenic disturbance (e.g., Krummel et al. 1987. "Landscape patterns in a disturbed environment." Oikos 48:321-24.

Additionally, the SCT axes can be viewed as multi-dimensional, thus measurement endpoints specific to different observational perspectives and spatio-temporal scales can be specified. As suggested in the book, the obvious tool for data collection at large geographic scales is remote sensing. A proactive response at the national level requires that measurement endpoints be incorporated in spatially explicit models. These measurement endpoints are likely to be proxies or surrogates of point-based indices of vegetation and soil degradation that are incorporated within a hierachial Geographic Information System (GIS). This style of data analysis will allow predictive capabilities. National-level assessments that utilize remote sensing and GIS are currently being conducted by the National Biological Survey and FMAP using landscape, ecoregion, and biome points of view. The measurement endpoints used for the landscape perspective (e.g., landscape diversity and fractal dimension; see Turner and Gardner 1991. *Quantitative methods in landscape ecology: the analysis and interpretation of landscape heterogeneity.* Ecological Studies Vol. 82, Springer-Verlag, New York) need to be related to range degradation.

Rangeland Health provides an admirable synopsis of the problems of ecological monitoring of U.S. rangelands. The recommendations made are aimed at decision makers but provide little guidance for theoretical and applied ecologists. The conceptual model presented is ambiguous and not amenable to theoretical specification and, therefore, measurement. Consequently, generalities but no specific guidelines are given to field managers and scientists who are responsible for acting on these recommendations. Therefore, for technical guidance, I would recommend Archer and Smeins (1991. *Ecosystem-level Processes.* pp. 109-139. in R.K. Heitschmidt and J. Stuth (Eds.). 1991. *Grazing Management: An Ecological Perspective.* Timber Press, Inc., Portland, Oregon). For a review of successes and failures of old methods and a discussion of new concepts and methods: West et al. (1994. *Monitoring and Interpreting Ecological Integrity on Arid and Semi-Arid Lands of the Western United States.* New Mexico Range Improvement Task Force, Las Cruces, New Mexico). For a heuristic study, I highly recommend Behnke et al. (1993. *Range Ecology at Disequilibrium: New Models of Natural Variability and Pastoral Adaptation in African Savannas.* Overseas Development Institute for Environment and Development, and Commonwealth Secretariat).–*Robert A. Washington-Allen,* Research Associate, Utah State University, Logan, Utah 84322-5230 and Environmental Sciences Division, Oak Ridge National Laboratory, Oak Ridge, Tennessee.