

Journal of Range Management

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The Trail Boss

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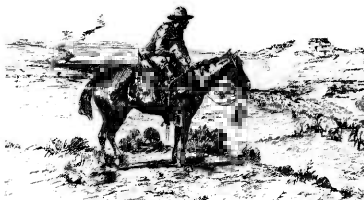
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The economic logic of prescribed burning law and regulation

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Abstract

Prescribed burning has long been recognized as a useful tool in rangeland management, but with it comes the risk of fire and smoke damage to the property of others. All but 2 states have codified laws specifying criminal penalties or liability rules for prescribed burning, but the laws in a number of states have changed in recent years or are under review. We develop an economic model of the incentive and welfare effects of prescribed burning law and regulation in which the likelihood and extent of external damage can be reduced by precautionary effort on the part of both the burner and/or the victim. The model provides implications regarding the comparative advantages to the public of strict liability versus negligence rules. We conclude that the relative effectiveness of a liability rule depends in large part on the relative ability of burners and other landowners to mitigate the probability and extent of damage, as well as the legal costs associated with implementing a given liability rule.

Key Words: fire, natural resources policy, prescribed fire, rangeland fire, rangeland policy

Prescribed burning is an inherently risky rangeland management tool that can result in litigation and considerable liability exposure to the prescribed burner. Through much of the 20th century, prescribed fire was resisted by policy makers and many natural resources managers because fire was considered a detriment to either ecosystem integrity or to ecosystem products (Pyne 1982, Biswell 1989). Even though fire is now widely viewed as a useful vegetation and fuels management tool (Bernardo et al. 1988, Svejcar 1989, Briggs and Knapp 1995, Zimmerman 1997, Babbitt 1995, Pattison 1998), the exposure to liability remains a primary impediment to increased use of prescribed burning in the United States. At the same time, state and federal programs (e.g., U.S.D.A. Environmental Quality Incentive Program) and policies encourage the use of prescribed burning. The Federal government recognized recently the use of prescribed fire as an integral element of wildland fire management, despite the explicit recogni-

Resumen

La quema prescrita ha sido reconocida mucho tiempo como una herramienta útil en el manejo de pastizales, pero con ella viene el riesgo de daño por humo y fuego a otras propiedades. Exceptuando 2 estados el resto ha establecido leyes especificando penalidades criminales o reglas por daños a terceros para la quema prescrita. Desarrollamos un modelo económico de los efectos del apoyo de gobierno e incentivos de la ley y regulación en quema prescrita, en el cual los daños a los vecinos y lo extenso del daño externo pueden ser reducidos por un esfuerzo precautorio tanto del que quema como de la víctima. El modelo provee implicaciones relacionadas a las ventajas comparativas para el público estricto en daños a terceros versus reglas por negligencia. Concluimos que la efectividad relativa de una regla de daños a terceros depende en gran parte de la habilidad relativa de los que queman y de otros propietarios para mitigar la probabilidad y extensión del daño, así como de los costos legales asociados con la implementación de una regla de daños a terceros dada.

tion that it is among the most risky activities of federal land management agencies (U.S. Department of the Interior, U.S. Department of Agriculture 1995).

The relative incentives for individual prescribed burners (and society as a whole) versus the potential victims (individuals) of escaped fire differ widely because of the widely varying liability rules among states in the U.S. Virtually all states have codified civil or criminal statutory law for prescribed burning, but the structure of these laws varies substantially across states (Yoder et al. 2003). Only 4 states impose strict liability on prescribed burners. Under strict or unlimited liability, defendants are liable for the damage caused by an escaped prescribed fire even if there is no evidence of negligence on their part and regardless of the precautions taken to contain the fire. Most states with prescribed fire statutes impose negligence rules of some form on the prescribed burner, but again, these negligence rules vary substantially across states (Yoder et al. 2003). Not only do prescribed burning laws vary substantially across states, but these laws currently are in flux. The laws in most states have been revised since 1990, and a number of statutes are currently under review.

We build on a model adapted from the law and economics literature and developed in Yoder et al. 2003 to compare the capacity of the different liability rules to induce the economically appropriate level of precaution by prescribed burners and their neighbors. The intent of this paper is to provide a conceptual framework for assessing the economic efficiency and incentive effects

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of prescribed burning liability law so that rangeland resource managers can more knowledgeably articulate to policy makers the relative merits of alternative liability statutes.

A Model of Liability for Prescribed Burning

We will examine 2 neighboring property owners. One neighbor applies prescribed burning to his land, and a neighbor's property would suffer damage if the fire escaped onto his land. Suppose the probability of an escaped fire depends on precaution effort by the burner, and the extent of damage—given that a fire escapes—depends on precautionary effort taken by the victim. The following model is adapted from Brown (1973) and developed for this scenario by Yoder et al (2003).

First, consider the efficient (wealth-maximizing) levels of precaution; we will then examine the effectiveness of various liability rules for inducing this allocation. The total net value of a prescribed burn, Π , is the value of the benefits from the burn minus the precaution costs and expected value of damage incurred by the burner and victim:

$$\Pi = R - D(V) \cdot P(B) - W^v V - W^b B \quad (1)$$

where

- $R > 0 \equiv$ the value of the burn to the burner (including society in general),
- $D(V) \equiv$ damage to the victim if fire escapes (potential damage),
- $P(B) \in (0,1) \equiv$ probability of an escape that results in damage,
- $V \equiv$ the level of precaution invested by the victim,
- $B \equiv$ the level of precaution invested by the burner,
- W^v and $W^b \equiv$ Cost of a unit of precaution for the victim and burner, respectively.

A central component of the analysis that follows is "expected damage," defined here as the statistical expectation of damage: $P(B) \cdot D(V)$. Notice that if either the probability of damage increases or potential damage increases, then expected damage increases. Examples of V (precaution by the victim) include the use of fire resistant construction materials in buildings and fuel reduction around structures (e.g., defensible space). Examples of B (precaution by the burner) include fire planning, constructing fuel breaks, notifying neighbors and fire officials, and utilizing sufficient manpower. Burning under narrow fire prescriptions, such as highly restrictive windows of air temperature and relative humidity, is an important factor that

also can be considered a costly precaution by the burner (Roberts et al. 1999).

The economically efficient levels of precaution invested by the burner (B) and the victim (V) are those that maximize Π , the total net expected value of a burn. Assuming that the probability of an escape ($P(B)$) and damage to the victim ($D(V)$) decline at a diminishing rate with increases in precaution by the burner and victim (B and V) respectively, the model provides a number of implications regarding the optimal precaution of the burner and the victim. Economic efficiency requires that both the burner and the victim take precautions to reduce potential damage except in special cases. First, if precaution by either the burner or the victim (B or V , respectively) is very costly or ineffective at reducing either the risk of escape ($P(B)$) or damage to the victim ($D(V)$), then it may be optimal for one, the other, or even both parties to expend no precautionary effort even when the use of prescribed fire is beneficial to the burner or to society in general (i.e. $\Pi(B = 0, V = 0) > 0$). Second, if the probability of escape that leads to damage is very low for optimal levels of B (precaution by the burner), then it may be optimal for the victim to expend no precautionary effort. Similarly, if potential damage is very low for even low levels of V (precaution by the victim), then it may be optimal for the burner to take no precautionary effort (see Yoder et al. (2003) for mathematical justification of these results).

This model provides a framework for understanding how different liability rules influence incentives for prescribed burners to practice precaution and for potential victims to mitigate potential damage. Strict liability will be considered first, followed by an analysis of negligence rules.

Strict liability

Consider 2 scenarios: (1) the burner is not liable for (not required to pay for) damage suffered by the victim, and (2) the burner is liable for damage suffered by the victim.

Scenario (1) represents the case where no restrictions or responsibilities were placed on burners with regard to damage and burning. The victim bears all of the damage costs from an escaped fire, and will therefore exert the economically efficient level of precaution. On the other hand, the burner bears none of the damage costs if a fire escapes, and will therefore exert no effort to reduce the likelihood of escape. If the burner has cost-effective means of reducing the probability of escape, this level of precaution ($B = 0$) is inefficiently low ("cost-effective" means here that benefits exceed the cost for some level of precaution). Therefore, the probability of escape will be inefficiently high and expected damage from prescribed fire will be inefficiently high.

In scenario (2), The burner bears all the damage costs of an escaped fire in addition to his own precaution costs, and will therefore exert the efficient level of pre-

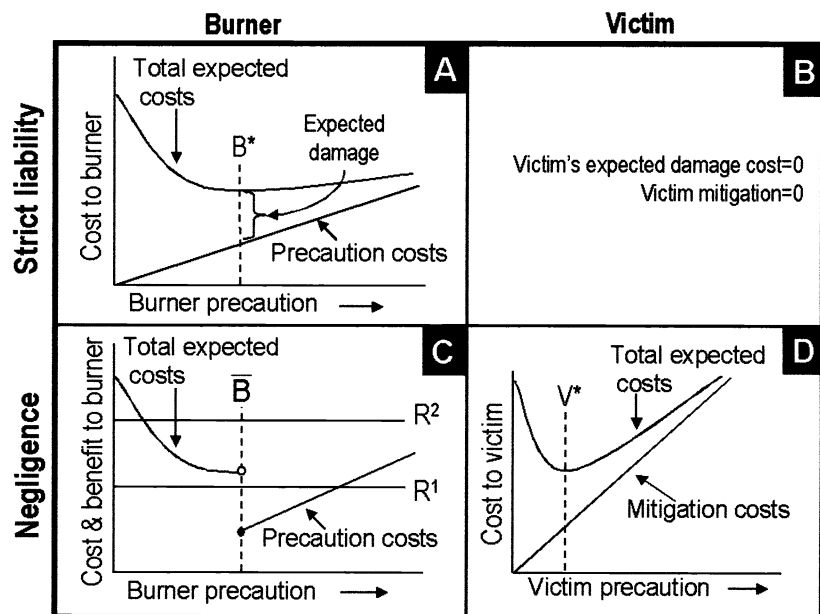


Fig. 1. Benefits and costs for the burner (left) and victim (right) under strict liability (top) and negligence (bottom).

caution for any given level of victim precaution. The top row of Figure 1 shows benefits and costs for the burner (left) and victim (right) under strict liability. The burner bears precautionary costs and expects to pay for damage regardless of his precaution level. He therefore expends precautionary effort B^* , which minimizes total expected costs—the sum of expected damage and precaution costs (panel A). The burner will choose to burn only if total expected costs at B^* are lower than the benefits (benefits are not shown in panel A). There is one crucial weakness of a strict liability rule such as this: the victim bears none of the damage costs of an escaped fire, and therefore has no incentive to exert effort to reduce potential damage to his property (panel B). If the victim has cost-effective means of reducing the extent of potential damage, this level of precaution ($V = 0$) is inefficiently low. Therefore, expected damage, $P(B) \cdot D(V)$, will be inefficiently high for any level of B . This was the case scenario (1) as well. This time, however, it is because potential damage to the victim's property, $D(V)$, is too high rather than $P(B)$ being too high. This discussion highlights 2 implications of the model.

Implication 1. Strict burner liability is more appropriate when the burner has cost-effective means to reduce expected damage but the victim has no control over potential damage.

Implication 1 suggests that when prescribed fire is, for any reason, uncommon in the vicinity, it makes less economic sense for potential victims to expend effort to prepare for it, and therefore efficiency losses from imposing strict liability on the burner are low. Strict burner liability is more likely to be more appropriate when and where the expected net social benefits of burning tend to be very low or negative and burning is an uncommon activity. Exceedingly costly precaution technologies available to the victim have the same result. If victims can not mitigate potential damage in an economical way, then strict liability results in no efficiency losses. Nonetheless, in fire-prone environments, inadequate precaution by the victim can result in great damage to the victim when wildfire occurs.

Implication 2. Strict victim liability is more appropriate when the victim has cost-effective means to reduce expected damage but the burner has no control over the probability of escape.

Implication 2 simply flips Implication 1 on its head. This result provides an illustration of one of the central arguments of

Coase (1960) in his seminal paper "The Problem of Social Cost." That is, in our use of the label "victim" and "burner," the distinction between victim and culprit turns on the ability to reduce expected damage, and is but a matter of degree. It would not be unusual for a burner to suffer significant financial loss should his fire escape even if prescribed burning provides value to society in general (e.g., fuel reduction, wildlife habitat enhancement, increased water yield, etc.). Using fire-resistant construction as well as fuels reduction around homes are examples of victim actions that can reduce expected damage from escaped fire. Indeed, the increase recently in voluntary (e.g., Firewise, the national wildland/urban interface program) and mandated (e.g., Florida's fuel reduction statute) programs is indicative of the view that victims possess the ability to reduce expected damage from wildfire regardless of the fire's cause.

Negligence

With strict burner liability, the burner expects to bear both the costs of precaution and the value of damage to the victim. Now consider a negligence rule such that the burner is not liable for damage if precaution by the burner is greater than or equal to some negligence standard, \bar{B} . If the burner satisfies the negligence standard ($B \geq \bar{B}$), he will accrue only his costs of precaution even if the fire were to escape and cause damage.

The second row of Figure 1 illustrates a negligence rule. In panel C, the standard, \bar{B} , is set to minimize the total expected cost of the prescribed burn, which is the economically efficient negligence standard (that is, \bar{B} in panel C is equal to B^* in panel A). The burner minimizes his costs by exactly satisfying the negligence standard; anything less and he will be found liable, but the burner does not benefit from exerting effort beyond that point. The victim then faces some probability of damage costs and therefore exerts precaution effort V^* (panel D). R^2 and R^1 in panel C represent different levels of benefit to the burner. If $R = R^2$ it is economically efficient to burn and the burner will do so. If $R = R^1$ total expected costs are greater than the benefits, but the burner will perform the burn because he does not expect to bear damage costs.

Given that the burner satisfies the negligence standard, the liability will fall on the victim; thus there is a discontinuity in the burner's cost function at \bar{B} . Assuming complete information, the victim knows

that the burner has an incentive to satisfy the negligence standard, and therefore expects to bear the costs of any damage resulting from an escaped fire. This therefore induces the victim to exert the optimal level of care as well (Fig. 1, panel D).

An important characteristic of a negligence rule is that the burner will choose to apply precautionary effort at exactly \bar{B} (Fig. 1, panel C shows that the level of precaution that minimizes total expected costs *borne by the burner* is exactly at \bar{B}). If the negligence standard is not set at the efficient level of precaution ($\bar{B} \neq B^*$, where total expected social costs are at their minimum as in Fig. 1 panel A), it will induce the burner to choose the wrong level of precaution. Accuracy of the negligence standard is therefore crucial to the success of a negligence rule as a means to induce efficient precaution.

Implication 3. A negligence rule is likely to be superior to strict liability when both burner and victim can substantially affect the value of expected damage.

It is possible to set a negligence rule so high that it effectively becomes a strict liability rule. Specifically, if the precautionary costs of reaching \bar{B} are higher than the expected damage given no precautionary effort, then it would make sense economically for the burner to disregard the negligence standard and simply act as if he faces strict liability. Furthermore, given that the victim is aware of this incentive, the victim will expend no precautionary effort, and the result of an exceedingly high negligence standard is identical to strict liability in terms of both party's precautionary effort.

To burn or not to burn

The results above relate to the allocation of effort given that a prescribed fire is set by the burner. Rules that result in damage being borne by the burner and rules that result in damage being borne by the victim may affect the burner's decision to perform a prescribed fire.

Under a negligence rule, a burner may decide to burn even if total costs outweigh benefits. Figure 1 panel C suggests that a negligence rule may result in too many prescribed fires. R^2 represents a level of benefit that, at \bar{B} , covers both the costs of precaution and expected damage. From an efficiency perspective a prescribed burn should be conducted in this case. In contrast, R^1 at \bar{B} covers the costs of precaution borne by the burner in order to satisfy the negligence rule, so the burn will be conducted. However, because total expected costs (i.e., precaution costs + expected

damage) are larger than R^1 at \bar{B} , efficiency dictates that the burn should not be conducted. Thus, a burn will be conducted when it is inefficient to do so if the benefits to the burner lie between the costs of the optimal level of precaution (W^bB^*) and the total expected costs ($P(B)D(V)+W^bB^*$). For any given distribution of R , this is more likely if the net benefits to the burner are positive but small, and when expected damage is large relative to the precaution costs. Indeed, benefits from a single prescribed burn on rangelands are often small relative to the risk to others (or at least not easily quantified).

In contrast, strict liability requires the burner to pay for damage in every case, and therefore is induced to provide efficient precautionary effort and start fires only when the total expected costs are outweighed by the benefits for any given level of precaution by the victim. The victim, on the other hand, has no incentive to expend precautionary effort. If R (the gross value of benefits) falls above the minimum total expected costs given efficient levels of precaution by the burner and victim, but *below* the minimum total expected costs given no victim effort ($V = 0$), the burn will not be performed even though it would be efficient to do so given efficient precaution by the victim. This case is shown in Figure 2 with $R = R^3$. As shown in the figure, under strict liability, $V = 0$. Total expected damage, and total expected costs (TC) for the burner are therefore higher for any level of B than the efficient level resulting from $V = V^*$. If the benefits of the burn fall between the minima of these 2 cost curves (e.g., R^3), a fire will not be set even though it would be set if the victim were performing precautionary effort. It follows from this discus-

sion that if the net benefits of prescribed burning tend to be small, as is often the case on rangelands, a strict liability rule will tend to result in too few prescribed burns if the victim could (but does not) mitigate potential damage to his property.

The previous 2 paragraphs suggest the following implication about the relative efficiency of strict liability versus negligence based on the size of the benefits from prescribed fire:

Implication 4. A negligence rule is likely to be superior to strict liability when the expected net benefits of a prescribed burn (including expected damage) tend to be high.

The usefulness of prior regulation and value-based rules

At least 2 approaches might be used to address the incentive (discussed above) to conduct too many burns under a negligence standard. The first approach is to add a second type of negligence rule. Recall that the negligence rule discussed previously imposes a standard on the amount of precaution, B , given that a fire is performed, and that this standard is in principle chosen based on the costs and benefits of precautionary effort. For purposes of comparison, call this an "input-based" negligence standard; it imposes no restriction or requirement on whether a fire should be performed in the first place. A second negligence rule could be based on the total net expected social value of conducting a burn. Call this a "value-based" negligence rule. It requires a burner to be found negligent if he conducts a burn when the expected total net benefits (including expected damage) are negative (Feldman and Frost 1998). Whereas an

input-based negligence rule cannot ensure that burns will not be performed too often, a rule based on the value of the burn cannot induce efficient precautionary effort. The 2 standards must be used together to address both problems. However, in order to implement a value-based standard, the court needs information about the benefits of a fire, as well as information about expected damage and the costs of precaution. To implement an input based rule, only information about damage and precaution costs are needed.

The second approach is to reinforce the input-based negligence rule with prior regulation such as requiring burners to acquire a permit before burning. Presumably, this permit would only be issued if the expected social net benefits of the burn are positive. Acquisition of these permits may also be contingent on evidence of some level of preparation such as a written prescribed burn plan. Permitting also may be used as explicit elements of a negligence standard if litigation ensues, thereby facilitating pretrial settlement and minimizing court costs. Thus, a permit system acts as a check on the problem inherent in negligence rules, that burners may tend to use prescribed burning too often.

Implication 5. Input-based negligence standards may be complemented by value-based negligence rules or a priori regulation.

For prescribed burns on rangeland, benefits to a larger group of society must be demonstrated, because benefits to a single land owner, manager, or for a single rangeland use often will be insufficient to justify a negligence rule over strict liability. Value-based negligence rules could provide a decided advantage to input-based negligence rules over the long term by focusing public attention on benefits as well as requiring burners to justify burns. As with many environmental regulations, valuing the benefits of prescribed burns is often a subjective process. Valuing the benefits of a prescribed burn that enhances non-game habitat, for example, remains a challenge even to theoreticians (Tietenberg 2000).

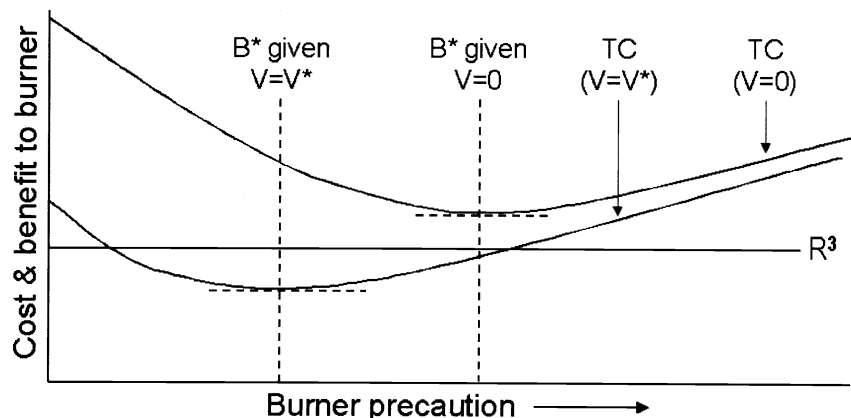


Fig. 2. The reduced incentive for victim precaution may lead to higher potential damage, more precaution by the burner, and fewer burns than is economically efficient. TC represents total costs and R^3 represents benefits.

The importance of Information and transaction costs for liability rules

The costs of gathering information and the effects of inconsistent or inaccurate negligence standards play a role in the relative effectiveness of a strict liability rule versus a negligence rule because enforcement of the 2 rules requires different information (Cooter 1991). A negligence rule

requires information on the extent of damage only after the burner is found negligent by the court. In contrast, a strict liability rule requires information about the value of damage in order to settle every litigation event. If damage is not easily or credibly monetized, then a strict liability rule is at a comparative disadvantage for 2 reasons. First, over the course of numerous litigation events, the cumulative costs of generating damage estimates will be higher than with a negligence rule in which damage estimates are only required after a finding of negligence. Second, the outcome of litigation events may be different in a setting of imperfect information as compared to a setting with perfect damage information, leading the burner or victim to alter their patterns of care if the accuracy and precision of damage estimates is questionable.

The difference between smoke damage and physical fire damage provides an example. The extent of suffering by smoke inhalation from smoke exposure is likely to be more difficult to credibly verify than fire damage to a home. If victims tend to be able to extract excessive compensation, burners will be "too careful" from an efficiency perspective. As Cooter (1991) notes, this type of error will have more pronounced effects on the level of care under a strict liability rule because the effects will be felt every time litigation is brought, whereas under a negligence rule misspecified damages only matter when the burner is found negligent.

Perfectly specified negligence standards lead to efficient effort for any prescribed fire, but misspecified negligence standards will result in inefficient precaution by both parties. Consider Figure 1 again. Because the burner minimizes his expected costs at exactly \bar{B} (or $B = 0$ if \bar{B} is set extremely high), the burner's behavior will be highly responsive to a consistently misspecified negligence rule. On the other hand, if the legal standard is vague and applied inconsistently by the courts, a negligence rule is likely to induce either too much or too little precautionary effort on the part of the burner even if the standard is on average applied correctly (Kolstad et al. 1990, Cooter and Ulen 1988). Both imprecise and inaccurate negligence rules reduce the benefits of negligence standards relative to strict liability, and both imprecision and inaccuracy follow from imperfect information about the cost and damage functions in a given case of prescribed burning.

If a negligence rule is imposed, information deficiencies also will shape the *structure* of a negligence rule. A statutory negli-

gence rule may be vague, such as "a landowner is not liable for damage caused by a prescribed fire unless the landowner failed to exercise due care." This rule relegates the definition of "due care" to the courts. It may be associated with substantial a priori uncertainty as to the actual standard that will be imposed by the court. On the other hand, it allows a court to adjust to event-specific variation in the productivity and costs of precaution on a case-by-case basis. When the efficient precaution level is relatively invariant across events, a clear statutory standard may reduce litigation costs in terms of case-specific misspecification. This characterization of statutory ambiguity relates closely to the problem of incomplete contracts, which are those contracts for which all details cannot possibly be specified. Incomplete contracts are applicable to prescribed burning because specifying appropriate weather conditions inclusive of every potential prescribed burning objective and every rangeland setting is impossible. Three implications follow from this discussion.

Implication 6. A negligence rule is superior to a strict liability rule when damage $D(V)$ is difficult to measure.

Implication 7. Statutory negligence standards should be precisely specified when precaution productivity and costs are relatively invariant (at the margin) across events.

Implication 6 applies to most rangeland burning for many reasons. Damage to rangeland properties is difficult and costly to assess and often subjectively determined. Moreover, rules-of-thumb that have been used to reduce costs of assessment are likely fraught with error (e.g., Engle and Bidwell 2001). Implication 7 suggests that for the sake of tractability, statutory negligence rules cannot cover all possible scenarios, and policy makers inevitably must search for the optimal mix of specific negligence standards (e.g., neighbor notification requirements) and ambiguous standards ("burners must exert due care").

The next section examines current prescribed fire law in the United States in the context of the model. However, one point about the applicability to the incentives of public land managers is worth noting. Prescribed fire use on many public lands has been increasing in the last decade, and the May 2000, Los Alamos fire in New Mexico is a well-known illustration of the grave consequences of the issue discussed here. It was started as a prescribed fire by the National Parks Service and resulted in approximately 24.5 million dollars in con-

trol costs, damage, and rehabilitation costs (Interagency Burned Area Emergency Rehabilitation Team 2000).

Federal agencies are liable under state common law and state statutory law in basically the same way that private citizens are, but agency personnel are not held personally liable as are private citizens, except for violation of the constitution (Chalifour 1999). As a result, there is a disconnect between federal agency personnel and liability in terms of burner incentives. They may bear costs of negligence in the use of prescribed fire, but these costs will not be directly tied to the value of damage associated with their negligence. Rather, the costs they face are tied to agency-imposed penalties such as employment termination or other punitive agency responses. Furthermore, unlike a private landowner performing prescribed burning, agency personnel do not directly gain from the benefits of prescribed burning, because they do not own and have rights to utilize and gain from the land and its attributes to the extent a landowner does. Because of these disconnects between the agency personnel and the costs and benefits of burning, the model as developed here does not strictly apply, except to the extent that the costs and benefits of burning are felt by the decision-makers through agency rules and incentive structures.

Application to Current Statutory Law

Strict liability versus negligence rules

Our model implies that strict liability is likely to induce efficient precaution if burners have most or complete control over the likelihood of damage due to prescribed fire, and it is not cost-effective for potential victims to reduce potential property damage from fires (implication 1). In the U.S., 22 states explicitly impose negligence rules and only 4 impose strict liability on burners (Yoder et al. 2003). This suggests policy-makers recognize that potential victims generally have some control over the extent of damage that might be sustained as a result of prescribed burning.

Two specific elements common to a number of negligence standards also support this conclusion. First, some states have a 2-part negligence standard: (a) the burner must notify all adjacent landowners of his intentions, and (b), the burner must use all due caution to prevent the fire from escaping the property. The first element is

very specific, and (at least in principle) easily verifiable. The second element leaves the definition of "due caution" for the court to define on a case-by-case basis. The point is that if neighbors have no means to mitigate potential damage, there would be no apparent motivation for the notification requirement.

Second, states can have a contributory negligence element in their statute. No rangeland state has such an element in their statutes (only Connecticut and Illinois have such). The statute has merit in that if victims do not expend reasonable effort to mitigate potential damage to their own property, the prescribed burner from whose land the fire originated will not be held liable. This contributory negligence rule recognizes a precautionary role for potential victims. The model suggests that strict liability provides little incentive for potential victims to exercise precautionary effort. Given that potential victims of escaped fire have an ability to mitigate damage, these specific requirements of notification and contributory negligence are consistent with the finding that most states with prescribed fire statutes rely on negligence rules rather than strict liability (Yoder et al. 2003).

Four states, including 2 rangeland states (North Dakota and Oklahoma), impose strict liability on the burner. Oklahoma's liability law was enacted in 1890 (prior to statehood) and last revised in 2001. North Dakota's was enacted in 1877 (last revised in 1943). The other 2 states, New Hampshire and Connecticut, are in the northern eastern seaboard states, where prescribed burning is relatively uncommon (implying a relatively low net value). This distribution of strict liability rules is consistent with our model (implication 4) in that states with strict liability rules tend to be in states where the net benefits of burning tend to be relatively low.

Specificity of negligence rules

Statutory rules relating to prescribed fire often contain an ambiguous statement requiring "due care", as well as more specific rules that are necessary (but not sufficient) to satisfy due care. The economic logic behind one common specific rule, the requirement to notify neighbors, is as follows. If landowners expect to be notified of their neighbor's intentions of prescribed burning, they need only be on alert for an escaped prescribed fire when such a fire is planned (and reported). This undoubtedly lowers their overall precaution costs, because time-sensitive precautionary effort (clearing dry vegetation near

a house that might contribute to the extent of damage, for example) may then be performed only when the potential for an escaped prescribed fire exists, and need not be applied at other times. Furthermore, the cost to a burner of notifying adjacent landowners is likely to be relatively low. As a result, notification of neighbors will reduce the overall expected costs of a prescribed burn. Of course, the threat of wild-fire still exists, but this probability is separate from that of prescribed burns from neighbors. It should be noted that not all precautionary effort need be time-specific. For example, using fire-resistant building materials does not necessarily require timely notification.

It would also be possible for a notification requirement to extend beyond adjacent landowners. However, notifying nearby landowners is not costless, and the potential gains from prior notification are likely to be lower because landowners further away will most likely have more time to react to the news of an escaped fire. Also, the probability of a fire crossing an adjacent landholding and onto landholdings further away are lower, so the expected costs to distant landowners are lower. Thus, the expected net benefits from a notification requirement for distant landholdings is not as compelling. Indeed, no landowner notification requirements extend to non-adjacent landowners. Notification requirements to non-adjacent landowners could be justified in some situations. For example, in some states small land holdings are common and fire spread is sufficiently rapid that non-adjacent landowners might not have time to react.

In some states, a burner must notify a related regulatory agency before burning in order to escape potential criminal penalties or civil liability. Colorado statutes state that a person who starts a fire is not liable for the expenses of extinguishing an escaped fire if he notifies the sheriff of the time and place of the burn. To the extent that prior notification reduces the cost or increases the effectiveness of public fire-fighting effort, this negligence requirement does so at only a small cost to the burner (a telephone call, perhaps).

Another common specific requirement among state statutes is that burners must remain with the fire until it is completely extinguished (i.e., "dead out"). On one hand, the cost to a landowner (or the landowner's agent) for remaining an additional hour or day on a burn site is likely to be relatively low compared to the expected costs of an escape from an unattended smoldering fire. The crucial point

here that leads to such a requirement is that without such a negligence standard, the costs of a burner leaving a site prematurely would likely be borne at least to some extent by a neighboring landowner rather than the burner. But this is yet another example of an incomplete contract in that specifying every indicator of "dead out" fires would be impossible. Moreover, the "dead out" requirement assumes low cost to the burner when in some cases, practicality in assessing "due care" in regard to attaining this standard would result in high cost to the burner. This is especially true on rangelands in which large burns, complex fuel involvement, rough topography, and other factors, limit the burner's ability to completely and accurately assess the fire's status. Moreover, the probability of fire escape may be very low. The specifics of the level of certainty of "safe-to-leave" decisions (i.e., mopping up including thorough "cold trailing") are not well defined in the rangeland fire literature and are beyond the scope of this paper.

Specific negligence rules for cost-effective inputs such as notification and on-site presence are consistent with implication 7, because it is unlikely that the costs of such precautions will outweigh their expected benefits (i.e. reductions in expected damage). Even though limitations to their cost-effectiveness exist, statutory specification of these rules will provide a higher degree of certainty about negligence requirements, thereby more effectively inducing proper precautionary incentives and reduce transaction costs of court proceedings.

The productivity and costs of many precautionary inputs, however, depend on the specific circumstances of a case. Attempts to impose a priori statutory requirements for input levels may lead to improperly specified negligence rules for many cases, and therefore should on efficiency grounds be left for a case-by-case analysis. Indeed, all statutory negligence standards for prescribed fire allow the courts the leeway to define "due care" (implication 7). Common elements considered by the courts in setting due care standards include starting fires during excessive dryness and foreseeable windiness, failure to build adequate firebreaks around the burn area, burning too close to neighboring property or buildings, and lack of sufficient accessible water (25ALR5th 391). The appropriate use of each of these inputs is relatively case dependent. Specification of statutory limits to be used in all cases would likely induce inappropriate precau-

tionary levels in many cases. Specifying a complex set of statutory requirements based on a broad set of possible states of nature would arguably be more difficult (costly) than addressing these issues on a case by case basis.

An important characteristic of court negligence findings is that courts usually distinguish between foreseeable factors and abnormal or unforeseeable factors contributing to the spread of fire, such as abnormal change in wind speed or direction. Our model suggests that the probability of the fire spreading to neighboring lands should be considered when establishing negligence. This probability is in turn based in part on expectations about exogenous factors such as wind. When deciding whether a burner started a fire negligently, courts generally base their decisions on the information that was available to burners at the time the fire was started. A burner may be found negligent if prevailing winds were unsatisfactory when the fire was ignited, but generally would not be found negligent for the spread of fire resulting from an abnormal and unforeseen change in the wind patterns (25 ALR5th 391).

Permits and regulatory requirements

Regulatory restrictions and permits are property rules providing landowners with the right to burn only if they satisfy a set of requirements delineated by statute and regulatory agencies. Otherwise, the burner may be subject to criminal penalties. These are different from liability rules, where burners have the right to perform prescribed burns but must bear the liability associated with the burn. As is the case with many environmental issues, *a priori* regulation and *ex post* liability are used simultaneously in many states to address prescribed fire externalities.

Property rules for prescribed burning are imposed for 2 general types of activities: for burning without a permit or contrary to permit stipulations, and for leaving a fire unattended or for negligent escape and failure to extinguish. Most states maintain a permit system for prescribed burning under some circumstances. In some states, satisfaction of permit requirements is necessary to avoid potential fines and other criminal penalties. To acquire a permit, the landowner may have to show sufficient knowledge, preparation, and notification of neighbors or public fire-fighting entities. Colorado's statute, for example, states that permits are to be issued based on the proximity of the planned burn to

buildings, the potential contribution of the fire to air pollution, climatic conditions, and other related factors. These requirements, when used in conjunction with a negligence rule, are consistent with implication 5. Pre-fire acquisition of a permit is necessary to be eligible for public fire-suppression support in some states, and the acquisition of a permit is an element of a negligence rule in some states as well.

A new generation of prescribed fire statutes

A new generation of prescribed fire statutes have been developed in the southeastern states beginning with Florida in 1990 (Brenner and Wade 1992). The Florida statute goes to great length to recognize prescribed burning as a useful land management tool. The legislation explicitly recognizes ecological benefits, and benefits from reducing the likelihood and severity of wildfires. It explicitly recognizes prescribed burning as a property right, subject to a relatively detailed set of precautionary requirements. Finally, it specifies that landowners are not liable for damage or injury caused by escaped fire or smoke unless found to be grossly negligent. Other southern states to explicitly recognize prescribed burning as a beneficial property right include Georgia, Louisiana, Mississippi, and North Carolina. In the context of our model, the explicit recognition of the value of prescribed burning acts to emphasize the possibility that R^1 in Figure 1 is high, arguably increasing the likelihood that a value-based rule is found by the courts to be satisfied. The requirement of gross negligence arguably lowers the negligence standard, B , relative to not requiring gross negligence. These statutes are therefore consistent with an apparent attempt to reduce the likelihood of prescribed burner liability.

If land and demographic characteristics of southern states result in relatively large benefits from prescribed fire, our model predicts more widespread use of negligence rules in these states (implication 5). One conjecture regarding the relative support of prescribed burning in these new statutes is that these statutes are a response to an apparent growing recognition of the role of prescribed fire as a wildfire management tool.

To the extent that reduction of fuel loads resulting from controlled burning reduces the likelihood and severity of wildfires, prescribed burners may contribute positive externalities by reducing potential fuel accumulation that would contribute to fire

spread across numerous landholdings in a region. If this conjecture is correct, we would expect this type of statutory response in areas where prescribed burning can reduce the total social costs of fire generally (that is, the net cost of prescribed fires plus the costs of wildfires and their control).

Conclusions

Prescribed fire is a land management tool with long historical roots in rangelands of North America, Australia, and elsewhere. A resurgence in interest from scientists, land managers, and legislators has led to substantial changes in the statutory law of many states in recent years. This paper examines the economics of liability for prescribed fire. Using a graphical representation of a mathematical model developed in Yoder et al. (2003), we provide a conceptual framework for improving existing policy at a time when prescribed burning policy is in a state of flux.

The risk of fire escaping to neighboring landholdings always accompanies the use of prescribed fire, and burners therefore may not bear all of the potential costs of their prescribed burning decisions. Criminal and civil liability rules specified by legislation and enforced by the courts work to internalize these costs. The relative effectiveness of a liability rule depends in large part on the relative ability of burners and other landowners to mitigate the probability and extent of damage, as well as the transaction costs associated with implementing a given liability rule.

All negligence rules rely on an ambiguous requirement of due care that is left to be defined more specifically by the courts, but many states include specific negligence standards as well. Most of the recent changes in statutory law relating to prescribed fire provide substantial support for prescribed fire as a land management tool despite the risks associated with its use. These changes may result more from the increasing evidence that prescribed fire can be a cost-effective means of reducing the incidence and intensity of wildfires.

This paper is about tradeoffs in the design of law. State prescribed fire law varies across states, and these laws affect the amount of precautionary effort expended by burners and their neighbors. Strict liability induces appropriate precaution from the person conducting the burn if a prescribed fire is performed, but neighbors have little incentive to reduce potential damage. Negligence standards, if

properly set, induce appropriate precaution by both burners and neighbors for any prescribed fire, but prescribed fires may be performed too often from an economic perspective. Strict liability is likely to result in fewer escaped prescribed fires than a properly set negligence rule, but this comes at a cost as well, including excessive precaution costs by the burner, potentially higher damage for any escaped fire, and less aggregate benefits from fires because fewer prescribed fires will be performed. If one of the objectives of liability law in this context is to promote total social welfare and economically efficient resource management, these tradeoffs must be addressed when tailoring law to a given environment.

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Research Observation: Effects of rangeland ecological condition on scaled quail sightings

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Abstract

Scaled quail (*Callipepla squamata*) numbers were evaluated during and after a 2-year drought period using strip census techniques on 2 pastures in late seral rangeland ecological condition and 2 pastures in mid-seral rangeland ecological condition. This study was conducted on the Chihuahuan Desert Rangeland Research Center (CDRRC) in south-central New Mexico on 4 adjoining pastures that were similar in size and terrain. During part of the study (August 1994 to April 1997) all 4 pastures were destocked due to depletion of perennial grass cover and biomass from a combination of drought and heavy cattle grazing. Scaled quail sightings pooled across sampling periods (9) were different ($P = 0.08$) on high and low rangeland ecological condition treatments. They averaged 10.72 birds per pasture on late-seral and 4.22 birds per pasture on mid-seral rangeland ecological condition treatments. Autumn perennial grass cover and standing biomass levels was higher ($P < 0.10$) on late seral than on mid-seral rangeland ecological condition pastures during both years of study. Availability of scaled quail foods such as leatherweed croton and broom snakeweed did not differ ($P > 0.10$) between treatments. Our study indicates that during extended dry periods livestock grazing at moderate intensities may adversely affect scaled quail populations in the Chihuahuan Desert by depleting perennial grass cover. However, in years of above average precipitation there is evidence scaled quail prefer mid-seral pastures over late-seral pastures. Maintaining a mosaic of conservatively (late-seral) and moderately (mid-seral) grazed pastures should best meet the habitat needs of scaled quail in the Chihuahuan Desert.

Key Words: upland game birds, wildlife, arid lands, cattle grazing, rangelands

Scaled quail (*Callipepla squamata*) are important upland game birds in the Chihuahuan Desert region of the southwestern United States and northern Mexico. However, a 50% decline has occurred in scaled quail populations over their range during the past 30 years (Brennan 1993). Although reasons for the decline are not well understood, poorly controlled livestock grazing could be a contributing factor.

Research is lacking on how different cattle grazing intensities influence scaled quail populations in the Chihuahuan Desert.

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Resumen

El número de "Scaled quail" (*Callipepla squamata*) se evaluó durante y después de un periodo de sequía de 2 años mediante técnicas de censo en franjas, la evaluación se realizó en 2 potreros de condición ecológica del pastizal de etapa seral terminal y en 2 potreros de condición ecológica del pastizal de etapa seral intermedia. Este estudio se condujo en el Centro de Investigaciones de Pastizales del Desierto Chihuahuense (CDRRC) localizado en el centro-sur de New Mexico en 4 potreros adyacentes que fueron similares en tamaño y características del terreno. Durante parte del estudio (Agosto de 1994 a Abril de 1997) se removió completamente la carga animal de los cuatro potreros debido al abatimiento de la biomasa y cobertura de zacates perennes a causa de la combinación de la sequía y el fuerte apacentamiento por el ganado. Los avistamientos de "Scaled quail", promediadas a través de todos los periodos de muestreo (9), fueron diferentes ($P = 0.08$) en los tratamientos de condición ecológica de pastizal alta y baja. El promedio de aves por potrero fue de 10.72 en el tratamiento de condición seral final y 4.22 aves en el de condición seral intermedia. En ambos años del estudio, la cobertura de zacates perennes en otoño y los niveles de biomasa en pie fueron mayores ($P < 0.10$) en los potreros de condición seral final que en los de condición seral intermedia. La disponibilidad de alimento para el "Scaled quail", como "Leatherweed croton" y "Broom snakeweed", no difirieron ($P > 0.10$) entre tratamientos. Nuestro estudio indica que durante periodos de prolongada sequía el apacentamiento de ganado a intensidades moderadas puede afectar adversamente las poblaciones de "Scaled quail" en el desierto Chihuahuense al agotarse la cubierta de zacates perennes. Sin embargo, hay evidencia que años con precipitación arriba del promedio el "Scaled quail" prefiere potreros en condición ecológica de pastizal de etapas serales intermedias sobre los de condición seral final. Manteniendo un mosaico de potreros apacentados conservadoramente (condición seral final) y apacentados moderadamente (condición seral intermedia) debe ser lo mejor para satisfacer las necesidades de hábitat del "Scaled quail" en el desierto Chihuahuense.

There is evidence that moderate grazing intensities may benefit scaled quail under some conditions by creating more structural diversity in plant communities with dense stands of grass (Campbell et al. 1973, Saiwana et al. 1998, Nelson et al. 1999). However, during drought periods even moderate livestock grazing may adversely impact scaled quail populations by depleting cover and food (Brown 1978). On early seral rangelands any benefits of livestock grazing on scaled quail habitat are doubtful.

(Saiwana et al. 1998). We compared the effects of late-seral and mid-seral rangeland ecological condition resulting from conservative and moderate cattle grazing on scaled quail sightings in southcentral New Mexico during and after a 2-year period of drought.

Materials and Methods

Study Area Description

Our 4 study pastures were located on the NMSU Chihuahuan Desert Rangeland Research Center (CDRRC) (32° 32' 30" N 106° 52' 30" W) operated by New Mexico State University, 37 km north of Las Cruces, N.M. in Dona Ana County. This flat to gently rolling area is in the southern portion of the Jornada del Muerto Plains between the San Andres Mountains to the east and the Rio Grande Valley to the west. Elevation varies from 1,188 to 1,371 m. Soils of the Research Center are fine loamy, mixed, thermic, typic haplargids of the Simona-Cruces association (Soil Conservation Service 1980) underlain by calcium carbonate hard pan (caliche) at depths varying from a few centimeters to 1 m or more (Valentine 1970). In areas where the ground cover is sparse, sand dunes form around the invading mesquite (*Prosopis glandulosa* Torr.) plants (Wood 1969).

Climate

The climate on the Research Center is arid with an average of 200 days in the frost free period. The only permanent water sources are wells and pipelines provided for livestock use. Temperatures are high with a mean maximum of 36°C during June, and a mean maximum of 13°C during January (Pieper and Herbel 1982). Temperature differences are substantial between day and night. Strong winds in the spring cause severe erosion and water stress plants.

Annual precipitation is bimodal. Summer precipitation (July–September) is from localized convectional storms of high intensity, but low frequency. Winter precipitation (December–February) is relatively gentle and evenly distributed. Mean annual precipitation is 230 mm with 52% of the annual rainfall occurring during summer.

Annual precipitation in 1996 was 208 mm (89% of \bar{x}) (Table 1). In 1994 and 1995 annual precipitation was 76% and 64% of the mean, respectively. Prior to the 1994–1996 period of below average precipitation, several years of above average precipitation had occurred.

Table 1. Average monthly precipitation (cm) on the Chihuahuan Desert Rangeland Research Center in south central New Mexico for 1994 to 1998 period.

Month	64 yr. Avg 1930–1998	1994	1995	1996	1997	1998
Jan.	1.27	0.76	1.65	0.71	1.47	0.38
Feb.	1.04	0.30	0.97	0.10	1.63	0.91
Mar.	0.66	0.35	0.05	0.00	1.55	1.04
Apr.	0.55	0.55	0.00	1.55	0.28	0.13
May	0.88	1.32	0.00	0.00	1.50	0.00
Jun.	1.27	0.63	1.24	2.90	5.38	0.41
Jul.	4.24	2.48	2.18	5.26	2.94	4.62
Aug.	4.62	1.57	3.43	2.64	6.63	3.78
Sep.	3.58	0.93	4.72	5.41	2.49	0.94
Oct.	2.23	2.28	0.00	1.88	1.32	4.98
Nov.	1.19	3.25	0.23	0.38	1.40	1.45
Dec.	1.85	3.53	0.58	0.00	3.25	0.76
Total	23.52	17.78	15.03	20.83	32.87	19.48

Vegetation

Primary grass species on our study areas include black grama (*Bouteloua eriopoda* Torr.), dropseeds, (*Sporobolus* sp.), three-awns (*Aristida* sp.), bush muhly (*Muhlenbergia porteri* Kunth.), fluffgrass (*Erioneuron pulchellum* Tateoka), and tobosa (*Hilaria mutica* Buckley). The most commonly encountered shrub species is honey mesquite. It dominates the overstory and has been increasing over the past 100 years (Pieper and Herbel 1982). Other shrubs include broom snake-weed (*Gutierrezia sarothrae* Pursh), soap-tree yucca (*Yucca elata* av.), and creosote-bush (*Larrea tridentata* [Pursh] Nutt.). Leatherweed croton (*Croton pottsii* Lam.) the primary forb, is an important food for livestock and pronghorn antelope (*Antilocapra Americana*).

Experimental Procedures

During 1991, 4 adjoining pastures arranged from west to east with similar soils (sandy loams), topography (flat), water availability and size (1,098 ± 126 ha) were delineated and fenced. These pastures had previously (1970–1991) been grazed year-long at a moderate intensity by cow-calf pairs. At the beginning of our study in 1996 pastures 1 and 4 were in late seral ecological condition (57 and 64% of climax respectively) while pastures 2 and 3 were in mid seral ecological condition (37 and 32% of climax respectively) using the quantitative climax approach of Dyksterhuis (1949) (Nelson et al. 1997). In autumn 1992, 2 pastures (1 and 4) were stocked with cattle to obtain 30–35% use on key forage species while 2 pastures (2 and 3) were stocked to obtain 40–45% use of key species (Nelson et al. 1997). Cattle were removed from pastures due to

drought from August 1994 to April 1997. Pastures were partially restocked in April 1997 and fully stocked to obtain 30% and 40% use levels in autumn of 1997 (Holechek 1988).

Foliar cover data were collected in autumn 1995, 1996, and 1997 at 10 key areas spaced evenly across each pasture (Molinar 1999). Foliar cover on each key area was evaluated on 2, 61-m transects separate from those used for biomass evaluation. A modification of the line-intercept procedure of Canfield (1941) was used to determine percent foliar cover. A meter stick was used instead of an extended line. Measurements were made approximately every 6.1 meters along 2, 61 m transects at each key area. The meter stick was placed perpendicular to the transect and the intercept of the plants measured according to Bonham (1989). Standing crop biomass was also evaluated in autumn 1996 and 1997. Autumn forage standing crop was determined by clipping 20, 0.5 m² quadrats at 10-m intervals along 2, 100-m lines on each key area.

In June 1993, 5 transects 1.6 km long were systematically placed in each pasture to monitor scaled quail densities (Nelson et al. 1997). With some exceptions transects were placed 1 km from boundary fences to minimize any ecotone effects where pastures adjoined. All transects were separated by at least 0.8 km. Scaled quail sightings were recorded seasonally from winter 1996 through winter 1998 along the 5 transects in each of the 4 pastures using strip census techniques (100 m x 1.6 km transects). Two observers walked adjacent transects within the same pasture on the same day. This technique was used due to the difficulties of enumerating scaled quail through standard line transect

procedures (Brennan and Block 1986, Saiwana et al. 1998). Scaled quail typically run rather than hold or flush when encountered by people or dogs (Saiwana et al. 1998). Because of the chaotic nature of encounters, observers found it difficult to accurately measure sighting angles and distances to birds encountered. Two observers well trained in wildlife population sampling techniques walked transects. Each observer was limited to 2 transects per day. Observers rotated between grazing intensity levels on each sampling day (2 transects late-seral pasture, 2 transects mid-seral pasture). These inventories were taken seasonally from winter 1996 through spring 1998. Quail inventories were conducted between the hours of 0700 and 1100. Only scaled quail observed within 50-m on either side of the observer were recorded.

One problem with the enumeration technique we used is some birds previously counted can move ahead of the observer and potentially be counted again. The low level of quail encounters relative to distance traveled, the sparse nature of the vegetation, and the relatively flat terrain minimized this problem.

Brush cover was similar in height on the 4 pastures. However, ground visibility was impaired on the late-seral pastures where perennial cover was more dense and could have caused underestimation of scaled quail. Nevertheless, we believe our methods provided a reasonable estimation of relative quail numbers among pastures. All experimental pastures were open to hunting and all were equally accessible by roads. Autumn enumerations were made before hunting season.

Statistical Analysis

A repeated measures analysis of variance using the mixed model procedures of SAS (Littell et al. 1996) was used to compare scaled quail sightings across rangeland ecological condition levels (2), seasons (4), and years (2 years). This same type of analysis was used to compare standing herbage biomass and foliar cover among rangeland ecological condition levels (2) and years (2). Pastures 1 and 4 were used as replicates for late-seral treatments and pastures 2 and 3 were used as replicates for mid-seral treatments.

Results and Discussion

Scaled quail sightings pooled across seasons and years averaged 10.72 birds per pasture on late-seral (conservatively

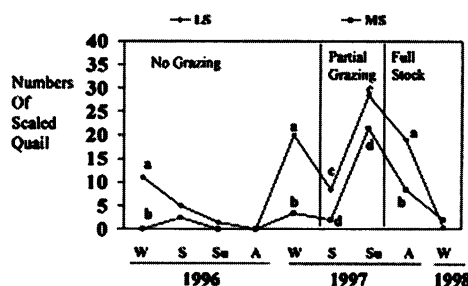


Fig. 1. Mean number of scaled quail observed per pasture on late-seral (LS) and mid-seral (MS) treatments on the Chihuahuan Desert Rangeland Research Center from winter 1996 to spring 1998. Pooled standard errors across treatments and time were ± 3.99 quail per pasture. Letters a and b differ $P < 0.05$ and letters c and d differ $P < 0.10$.

grazed) and 4.22 birds per pasture on mid-seral (moderately grazed) treatments ($P = 0.08$) (Fig. 1). Scaled quail sightings differed ($P = 0.04$) among years. Scaled quail sightings were higher in 1997 than 1996 when the same seasons were compared with the exception of spring. A total of 268 scaled quail were observed.

Autumn total vegetation cover and perennial grass cover differed between range condition treatments (Table 2).

condition treatments (Table 3). Perennial grass standing crop pooled across seasons and years averaged 213 kg ha⁻¹ on late-seral (conservatively grazed) and 172 kg ha⁻¹ on mid-seral (moderately grazed) pastures. Year effect was significant ($P = 0.09$) with autumn perennial grass standing crop lowest in the dry year of 1996 and highest in the wet year of 1997. The higher perennial grass standing crop in 1997 is related to 58% more precipitation

Table 2. Vegetation foliar cover (%) on late-seral (LS) and mid-seral (MS) grazed pastures on the Chihuahuan Desert Rangeland Research Center in autumn 1995, 1996, 1997.

	1995		1996		1997	
	LS	MS	LS	MS	LS	MS
----- (% Cover) -----						
Grasses						
<i>Bouteloua eriopoda</i>	1.3 ^a	0.5 ^b	1.4 ^a	0.8 ^b	1.8 ^a	0.6 ^b
<i>Sporobolus</i> spp.	1.0 ^a	0.4 ^b	0.6 ^a	0.2 ^b	1.1 ^a	0.3 ^b
<i>Aristida</i> spp.	0.2 ^a	0.8 ^b	0.1 ^a	0.5 ^b	0.2 ^a	0.8 ^b
Other grasses	0.4	0.1	0.1	0.1	0.7	0.2
Total grasses	2.9 ^a	1.8 ^b	2.2 ^a	1.6 ^b	3.8 ^a	1.9 ^b
Forbs						
<i>Croton pottsii</i>	0.2	0.	0.2	0.2	0.4	0.3
Other forbs	0.8	0.8	0.2	0.4	1.6	0.1
Total forbs	1.0	1.1	0.4	0.6	2.0	0.4
Shrubs						
<i>Gutierrezia sarothrae</i>	0.4	0.2	0.4	0.3	0.4	0.2
<i>Prosopis glandulosa</i>	4.2	4.3	3.4	3.0	4.5	4.7
Other shrubs	< 0.1	< 0.1	< 0.1	< 0.1	< 0.1	< 0.1
Total shrubs	4.6	4.5	3.8	3.3	4.9	4.9
Total vegetation	8.5 ^a	7.4 ^b	6.4 ^a	5.5 ^b	10.7 ^a	7.2 ^b

^{a,b} Rows within years with different letters differ ($P < 0.10$).

Perennial grass cover ($P = 0.07$) was higher on late-seral than mid-seral pastures in all 3 years of study. This also occurred for black grama and mesa dropseed cover. Other cover components showed no differences ($P > 0.10$) between grazing treatments. Year effects and year by treatment interactions were generally non-significant ($P > 0.10$).

Total autumn standing crop of perennial grasses differed ($P = 0.04$) between range

than in 1996 (Table 1). Treatment by year interactions were not significant ($P > 0.10$) for total perennial grass standing crop and biomass components with the exception of broom snakeweed ($P = 0.09$).

Range condition levels on the 4 pastures in our study were the same as in Nelson et al. (1997). However in contrast to our study, Nelson et al. (1997) reported average scaled quail sightings were twice as high on mid-seral compared to late-seral

Table 3. Standing biomass (kg ha⁻¹) on late-seral (LS) and mid-seral (MS) treatments in October 1996 and October 1997.

Plant Species	1996		1997	
	LS	MS	LS	MS
Grasses	(Kg ha ⁻¹)		(Kg ha ⁻¹)	
<i>Bouteloua eriopoda</i>	122 ^a	58 ^b	139 ^a	100 ^a
<i>Sporobolus</i> spp.	38 ^b	48 ^b	80 ^a	40 ^b
<i>Aristida</i> spp.	18 ^b	22 ^b	21 ^b	58 ^a
Other grasses	4 ^a	6 ^a	4 ^a	12 ^a
Total grasses	182 ^c	134 ^d	244 ^a	211 ^b
Forbs				
<i>Croton pottsii</i>	24 ^c	38 ^{bc}	43 ^{ab}	51 ^a
Other forbs	29 ^a	27 ^a	1 ^b	7 ^b
Total forbs	43 ^a	65 ^a	41 ^a	58 ^a
Shrubs				
<i>Gutierrezia sarothrae</i>	28 ^c	50 ^c	148 ^a	98 ^b
Total vegetation	258 ^c	249 ^c	433 ^a	367 ^b

^{a,b} Rows within years with different letters differ ($P < 0.10$).

pastures in 1993 and 1994 (16.2 versus 8.1 birds, respectively; $P = 0.14$) (Fig. 2). Their study was at the end of a 10-year-period in which precipitation was about 30% above the long-term average. Perennial grass standing biomass was higher on the 4 pastures during their study than during ours because of several consecutive years of above precipitation (Nelson et al. 1997, Winder et al. 2000) (Fig. 2).

Moderate livestock grazing may benefit scaled quail populations in years of average or above average precipitation on Chihuahuan Desert rangelands in mid or late seral ecological condition (Campbell et al. 1973, Nelson et al. 1997, Saiwana et al. 1998). However, Brown (1978) reviewed evidence that scaled quail and several other gallinaceous gamebirds in arid environments can experience major population declines in drought years because of reduced cover and food. There is conjectural evidence these declines can be magnified by excessive livestock grazing (Brown 1978).

Scaled quail on our study pastures were seldom encountered in dense shrublands lacking perennial grass cover or in dense grassland areas devoid of shrubs. Scaled quail were primarily observed in areas with a mixture of mesa dropseed, black grama, threeawns, bare ground, broom snakeweed and scattered shrubs. Saiwana et al. (1998) and Nelson et al. (1999) made this same observation regarding scaled quail use of habitat in the Chihuahuan Desert. Mesa dropseed is a bunchgrass that grows to a 45–70 cm height with interspaces between individual plants. It is important in meeting the cover needs of scaled quail because it provides overhead concealment for scaled quail

without obstructing their mobility (Saiwana et al. 1998). Mesa dropseed dominates Chihuahuan Desert sites in a mid to late seral stage while black grama dominates those in climax ecological condition (Holechek et al. 1994). Neither black grama nor mesa dropseed are important food sources for scaled quail (Davis and Banks 1973).

Both honey mesquite and broom snakeweed are important scaled quail foods in New Mexico (Davis et al. 1975). Broom snake-weed and honey mesquite availability was not different between late-seral and mid-seral pastures (Table 2 and 3). Similarly forb availability did not differ ($P > 0.10$) between treatments. Our data (Table 2) show perennial grass cover was the primary scaled quail habitat component that differed between late-seral and mid-seral pastures.

Since 1992 perennial grass cover and total vegetation cover on Chihuahuan Desert rangelands in southern New Mexico has been trending downwards due to several drought years (Galt et al. 1999). Perennial grass cover doubled between 1961 to 1992 due to average precipitation,

but was reduced by 68% from 1992 to 1999 due to below average precipitation.

Our highest sighting of scaled quail occurred in summer 1997 (Fig. 1). In this period we observed a large proportion of small recently hatched birds. We attribute the higher number of quail sightings in summer and autumn 1997 compared to 1996 to more favorable precipitation in 1997. Campbell (1968) found scaled quail reproductive success in New Mexico was positively correlated with precipitation levels in April through August. We cannot well explain why relatively high scaled quail numbers were observed in winter 1997 and few scaled quail were observed in winter 1998. We believe this is probably a sampling aberration. Scaled quail coveys join together in late autumn to form large winter groups while they disperse into nesting pairs in early spring (Schemnitz 1961). The high numbers of scaled quail observed in winter 1997 in the late-seral treatment are the result of one chance encounter with large quail groups in pasture 1.

We recognize some limitations of our study. The 4 experimental pastures are contiguous and scaled quail can readily move from one pasture to another. Therefore, our data may more reflect scaled quail preference rather than actual survival and productivity under mid-seral and late-seral ecological condition levels. A useful follow up study would evaluate trends in scaled quail numbers on similar Chihuahuan Desert rangelands where late-seral and mid-seral treatments are widely separated.

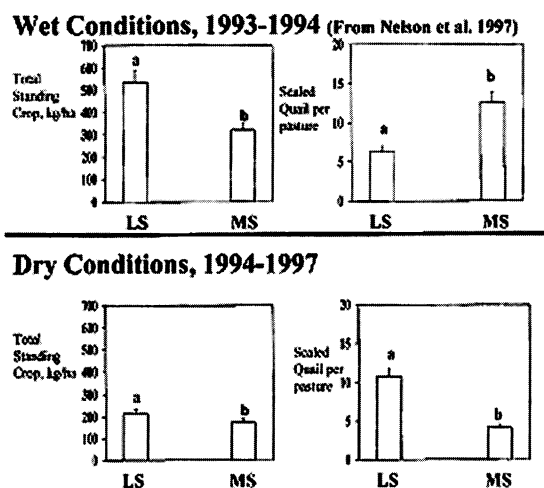


Fig. 2. Mean number of scaled quail observed per pasture and total standing crop of perennial grasses (kg ha⁻¹) in pastures of late-seral (LS) and mid-seral (MS) ecological condition on the Chihuahuan Desert Rangeland Research Center. The years 1993-1994 were wetter than normal in the Chihuahuan desert (Nelson et al. 1997) and the years 1994-1997 were more dry than normal. Letters a and b differ $P < 0.05$.

Management Implications

Our study indicates that extended dry periods and livestock grazing at moderate intensities may interact to adversely impact scaled quail populations in the Chihuahuan Desert through reduction in perennial grass cover and biomass. Conservative grazing has shown several benefits over moderate grazing in the Chihuahuan Desert. Benefits include: less soil erosion, accelerated plant succession, higher forage productivity, higher livestock productivity, higher financial returns, and lower ranching risk (Paulsen and Ares 1962, Valentine 1970, Holechek et al. 1994, 2000, Winder et al. 2000). Results from our study suggest that conservative grazing may improve habitat conditions for scaled quail during dry periods. During wet periods scaled quail appear to prefer moderately grazed pastures in mid seral condition while in dry periods they prefer conservatively grazed pastures in late seral condition. A mix of seral stages and grazing intensities should insure scaled quail habitat needs are best met.

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Sustainability of Inner Mongolian Grasslands: Application of the Savanna Model

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Abstract

The sustainability and resilience of an Asian typical steppe grazing ecosystem was assessed by determining thresholds and stable states with an ecosystem simulation model. This analysis used the Savanna model to simulate spatial climate, vegetation, and livestock grazing dynamics, at 14 different stocking rates (5.5–59.8 AU km⁻²). Grazing effects on vegetation were assessed, including effects on primary production, vegetation composition, and root biomass. Simulations were run for 100 years: 50 years to examine sustainability and 50 years to examine resilience of the system. Results showed that a grazing intensity (1-g/u; g = biomass in grazed area, u = biomass in ungrazed area) of 0.49 was sustainable for this particular system. This region was resilient to grazing up to the intensity of 0.49, where the system remained dominated by herbaceous production. Grazing intensities higher than 0.49, in combination with low precipitation events, resulted in decreased herbaceous net primary production and root biomass, and increased shrub net primary production and root biomass. Herbaceous vegetation was unable to gain a competitive advantage over shrubs in areas where grazing intensities were above 0.49; consequently, the system shifted to a stable shrub-dominated state that could not return its original composition even without further grazing.

Key Words: grazing management, modeling, thresholds, sustainability and resilience, typical steppe, Inner Mongolia

The long-term sustainability and resilience of Asian grassland ecosystems may be under threat as a result of changes in grazing management patterns and intensification of land use. In Inner Mongolia, Peoples Republic of China, the predominant land use pattern has shifted, over the last 50–60 years, from one of mobile, extensive range utilization, to sedentary livestock operations, increased stocking rates, and expansion of dryland cultivation.

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Resumen

La sustentabilidad y resiliencia de un ecosistema de pradera Asiática típica para apacentamiento fue evaluada con modelos de simulación de ecosistemas para determinar los umbrales y los estados estables. Este análisis uso la Savanna para simular la variabilidad espacial del clima, vegetación y dinámicas de apacentamiento con 14 diferentes cargas animal (5.5 – 59.8 UAA km⁻²). Se evaluaron los efectos del apacentamiento sobre la vegetación, incluyendo los efectos sobre la producción primaria, composición de la vegetación y la biomasa de raíces. Las simulaciones se corrieron para 100 años: 50 para examinar la sustentabilidad y 50 para examinar la resiliencia del sistema. Los resultados mostraron que a una intensidad de apacentamiento de (1-g/u; g = biomasa en el área apacentada, u = biomasa en el área sin apacentar) 0.49 fue sustentable para este sistema particular. Esta región fue resiliente al apacentamiento hasta una intensidad de 0.49, donde el sistema permanece dominado por la producción herbácea. Intensidades de apacentamiento mayores de 0.49, en combinación con eventos de baja precipitación, resultaron en reducciones de la producción de primaria neta herbácea y biomasa de raíces y aumento la producción primaria neta y biomasa de raíces de los arbustos. La vegetación herbácea fue incapaz de ganar ventaja competitiva sobre los arbustos en áreas donde la intensidad de apacentamiento fue superior a 0.49; consecuentemente, el sistema es desviado a un estado estable dominado por arbustos que puede no regresar a su composición original aunque este no se someta mas a apacentamiento.

Results include land degradation in the form of activated sand dunes in heavily degraded regions and altered vegetation structure in other areas (Jianguo and Loucks 1992, Chen and Xiao 1993, Williams 1996a, Renzhong and Ripley 1997, Sneath 1998). These changes in management style and increases in demand for livestock products have contributed to improved economic returns to livestock production in the short run. However, many scientists believe that present exploitation rates are unsustainable in the long run and that major declines in ecosystem production and/or irreversible changes in vegetation state are probable.

Grassland systems are subject to shifts among stable states due to threshold effects in grazing systems (Noy-Meir 1975, Westoby et al. 1989, Friedel 1991). The recent shifts in vegetation and increases in livestock populations on the Asian typical steppe, a bunch-grass steppe with many or few forbs in a semi-arid climate (Lavrenko and Karamysheva 1993, Zhu 1993), demonstrate a

lack in understanding of grazing management and an urgent need to determine appropriate grazing regimes (National Research Council 1992). Models can be used to understand interactions between abiotic and biotic factors to determine which grazing practices and intensities of use are sustainable and do not lead to degradation (Caughley et al. 1987, Agren et al. 1991, Ellis et al. 1993, Hall and Day 1997). We chose the Savanna ecosystem model (Coughenour 1993) to examine these interactions.

The Savanna model is a spatial and dynamic model that simulates ecosystem processes including vegetation and livestock production. The model takes a process-oriented approach to represent grassland ecosystems including flows of biomass, nitrogen, and organisms, and subsequent changes in system states. The capabilities of the model to simulate interactive responses to grazing can be used to further our understanding of the sustainability and resilience of semi-arid grasslands. Sustainability is defined as the non-degradative use of ecosystems that maintains system health for present and future generations (Lubchenco et al. 1991, Lele and Norgaard 1996) and resilience is defined as the amount of disturbance an ecosystem can experience before it shifts to an alternate state (Holling 1973, Gunderson 2000). Here we used this model to examine plant competition and grazing on the typical steppe of Northern China to determine the implications of different grazing regimes to ecosystem sustainability and resilience.

Methods

Study area

This study was focused on the Baiinxile livestock farm, which is located on the typical steppe of Inner Mongolia, China (43.5°N, 116.5°E). The farm is 3,680 km², divided into an administrative village and 12 branches. A branch is an administrative division of land, ranging in size from 79 km² to 655 km². Herders are sedentary with the majority of their land allocated to grazing. The farm is grazed predominately by a mixture of cattle, sheep, and horses.

Long-term mean annual precipitation at Baiinxile is 360 mm but varies between 180 mm and 500 mm. Mean annual temperature is -0.4° C, ranging from -27.0° C to 28.6° C (Li 1989, Xiao et al. 1997). The 3 main soil types in this area are kastanozems, chernozems, and eolian sandy soils (FAO 1991). Dominant grasses

include *Stipa grandis* and *Leymus chinensis*, which have a C3 photosynthetic pathway. Dominant forbs include *Artemisia frigida* and *Potentilla* sp., while the primary shrubs are *Caragana microphylla* and *Astragalus melilotoides* (Li 1978).

Model description

The Savanna model (Coughenour 1993) is a spatially explicit, process-oriented model of grassland, shrubland, savanna, and forested ecosystems. The model simulates processes at a landscape through regional spatial scales over annual to decadal time scales. The model is composed of site hydrology, plant biomass production, plant population dynamics, ungulate herbivory, ungulate spatial distribution, ungulate energy balance, and ungulate population dynamics submodels (Fig. 1).

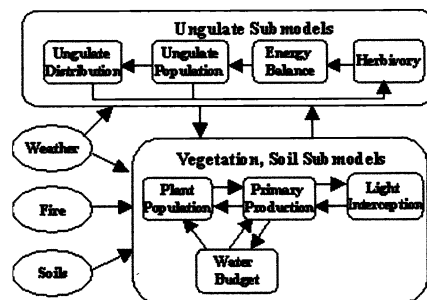


Fig. 1. Savanna model structure (Coughenour 1993).

The Savanna model has a nested spatial structure that is spatially explicit (representing spatial position) at the landscape scale. Grid-cell size is scaled to the spatial extent of the simulated ecosystem. A landscape is covered by grid-cells. The model is spatially inexplicit at sub-grid patch scales. The model represents the proportions of each grid-cell that are covered by vegetation patches or "facets". Patch locations are not modeled, but the model does represent the fractions of ground area covered by patches of herbaceous plants, shrubs, and trees in each grid-cell. Since plant growth is simulated, patch cover is a dynamic outcome of simulated vegetation growth and mortality. The results are scaled-up to the grid-cell level by multiplying the fractions of the grid-cell area covered by each patch type.

Water is redistributed by modeling runoff and runon. By simulating water movements among landscape positions, the model accounts for effects of patch-

scale landscape structure on soil water storage and subsequent plant growth. Runon potentially recharges deeper soil layers, thus affecting the balance between deep and shallow rooted plant species, and the length of the period during which water is available to support plant growth.

The Savanna model is driven by monthly weather data. Precipitation data may be from multiple weather stations, or it may simply be comprised of data from a single station. Monthly temperature data from a base station at known elevation are corrected for grid-cell elevations according to temperature lapse rate. A snowmelt submodel simulates snow water content and depth, and snow crusting is stochastically related to temperature.

The water budget submodel simulates soil moisture dynamics and use on each patch type on each grid-cell. Soils map data are used, in conjunction with soil properties for each soil type, to determine soil water holding capacities of each subarea on each grid-cell. The water budget includes terms for precipitation, interception, runoff, runon, infiltration, deep drainage, bare soil evaporation, and transpiration.

The net primary production (NPP) submodel simulates plant biomass dynamics. Plant biomass production is affected by light, water, temperature, nitrogen, and herbivory. The NPP submodel is explicitly linked to the water budget submodel through an empirical relationship between carbon assimilation rate and stomatal conductance (Ball 1988). Biomass is allocated to leaves, stems, and roots. Plant tissues die due to water or temperature stress or phenological state, and they turn over at a nominal rate that reflects their maximal longevities. The NPP submodel also simulates losses due to herbivory and tissue mortality.

Plant population submodels simulate plant establishment, size, and mortality. Plant establishment is affected by herbaceous standing crop, water and temperature. The population models simulate either a single variable-size class or up to 6 fixed-size classes of plants. Mortality occurs at a nominal rate accentuated by water and temperature stress. Competition between plants occurs at the functional group level, based on water, nutrient, and light resources. When demands for soil resources exceed availability, plants acquire the available resources based upon relative demands in each of 3 rooting layers. The plant population submodels are explicitly linked to the NPP model.

Simulated forage biomass and nutrient content are used to predict forage offtake

and ungulate distribution across the landscape. Forage intake then affects ungulate energy balance, which subsequently affects ungulate population dynamics, which are modeled separately for each type of livestock. Forage offtake is affected by forage quantity and availability, and ungulate diet composition and preference, maximal species intake rates, and stocking rates, which are unique to each ungulate type. Ungulate weight dynamics are derived by modeling herbivore energy intake and expenditure, and resultant changes in body mass. An animal condition index is then calculated, and can be used to affect ungulate population distribution. The Savanna model distributes ungulate populations based on habitat locations of suitable forage and management practices. For this analysis sheep, horses, and cattle per km² were entered as model input.

The model's structure includes rasterized GIS maps of vegetation, soil, elevation, slope, and aspect for the Baiinxile farm. Spatial analyses and model output are provided at the scale designated by the grid-cell size. A 1-km² grid-cell size was used for this analysis. Management strategies are incorporated into the model by limiting and restricting livestock movements with forcing and boundary maps created in a GIS. The model therefore has the ability to simulate ecosystem responses to alternative livestock management practices involving movements of animals amongst pastures.

The Savanna model has been used to simulate vegetation and ungulates in a wide variety of ecosystems such as Rocky Mountain National Park, Colo. (Weisberg 2000); Yellowstone National Park, Wyo. (Coughenour and Singer 1996a, 1996b); Ngorongoro Conservation Area, Tanzania (Boone et al. 2002); and Kruger National Park, South Africa (Kiker 1998).

Model parameterization/verification

Fieldwork conducted in Inner Mongolia was used to parameterize the vegetation and soil portions of the model (Xiao et al. 1996, Christensen et al. 1998). Vegetation biomass and percent cover data from lightly grazed plots were used in Savanna initialization parameter files to describe the vegetation at the Baiinxile farm (Christensen et al. 1998). The purpose was to use the model to simulate vegetation in a non-disturbed state. Both percent cover and vegetation biomass of each functional group were used in model initialization files. Other plant parameters specific to this region, such as plant physiological

Table 1. Vegetation categories used in Savanna simulation runs, simplified from Xiao et al. (1997).

Vegetation classification	
1	meadow steppe
2	typical steppe
3	<i>Artemisia frigida</i>
4	desertified land
5	saline alkaline land
6	wetland
7	cropland
8	fallow cropland
9	sand dunes with <i>Ulmus</i> sp.

characteristics, were taken from several chapters in Yang (1987). The base vegetation map consists of 9 vegetation types (Table 1) modified from a vegetation classification of Landsat TM imagery (Xiao et al. 1997). Biomass data from 1980 to 1989 (Xiao et al. 1996) were used for model verification analysis.

Field soil texture data from soil samples were used to parameterize soil water holding capacity and water infiltration rates. A digitized soil map of China (scale 1:4 million) was used as the soil base vegetation map.

Simulated livestock species included sheep, horses, and cattle, the primary grazers on the livestock farm. Information needed for model parameters such as livestock height, weight, and diet were gathered from livestock data specific to the typical steppe (Yang 1987). Herbaceous plants were selected as the preferred forage type due to the overall dominance of grass and forbs in this ecosystem.

On the typical steppe, areas of grassland are reserved for hay cutting and winter grazing. To reproduce this spatial effect in model simulations, "force maps" were used. Force maps blocked use of specified areas during summer months, and were then removed during winter months to make the areas available. Vegetation cells classified as meadow steppe were blocked from grazing during April through November to simulate areas reserved for fodder growth during the growing season. Grid-cells classified as meadow steppe were chosen because these areas were more productive, higher in elevation, and further away from water holes, and were therefore reserved for fodder growth (personal communication with local herders). Areas classified as sand dunes were reserved for winter grazing because of the shelter they provided against winter climate events.

Climate data from the Inner Mongolia Grassland Ecosystem Research Station (IMGERS), centrally located in the Baiinxile Farm, and 6 surrounding weath-

er stations were used in Savanna simulations. Nineteen years of maximum and minimum temperatures, precipitation, wind speed, humidity, and radiation data collected at the station were used in model analyses. Random years were chosen from the original 19 to create a weather data set for 50 years. Precipitation data from 6 surrounding weather stations were used in the weather interpolation submodel of Savanna.

Model validation

Model validations compared satellite imagery, not used in model parameterization, to final model output to determine model simulation accuracy (Jorgensen 1994). Eleven years, 1982–1992, of Normalized Difference Vegetation Index (NDVI) bimonthly composites derived from satellite imagery (Tucker 1979, Justice et al. 1985, Tucker et al. 1985, Malingreau 1986), totaling 66 images, were used to validate Savanna simulation output (Christensen et al. 1999). The NDVI data were analyzed in Idrisi (IDRISI 1997). The Idrisi software was used to extract time series of mean NDVI values for each branch of the farm. These trends were plotted and compared to Savanna green vegetation biomass outputs, which were also averaged over cells for each branch. A regression analysis of NDVI data versus simulated model results was used to test the model. The Savanna model green vegetation biomass output included summation of green leaf mass of herbaceous, shrubs, and trees and green herbaceous stem biomass. The 11-year cyclic trend in NDVI compared directly to model output rather than biomass values derived from NDVI. Ideally conversions to biomass would be used, if corrections could be made for errors in the Advanced Very High Resolution Radiometer data arising from satellite orbital drift and volcanic aerosols (Privette et al. 1995, Malmstrom et al. 1997, Asner 2000). However, since these errors were poorly characterized, added errors could result from conversions of NDVI values to biomass (Asner 2000). Due to these complications, NDVI was not converted to biomass in this analysis.

The NDVI data are from a region that is grazed. Therefore it was necessary to incorporate grazing activity in the Savanna model runs for an accurate comparison. A light grazing treatment of 14.65 animal units per year (AUY km⁻²) was included in simulation runs for the validation analysis to incorporate realistic grazing activity on the grasslands. Vegetation data from heav-

ily grazed plots were compared to Savanna output data in grazing scenarios with heavy grazing.

Model experiments

The first goal of this analysis was to determine through model experiments, the stocking rates that were sustainable on the typical steppe. For the purpose of this paper, the system was defined sustainable if herbaceous plants remained the dominant vegetation and could support grazing as a form of land use. This was accomplished by modeling the effects of different stocking rates on vegetation. A stocking rate analysis is only 1 of many different types of management that could be tested, but was chosen based on the scale and type of this analysis. Fourteen different stocking rates were chosen for model runs, ranging from extremely low to extremely high rates (Table 2). The model

Table 2. Livestock composition of each density (km^{-2}) and its total animal unit per year (AUY) equivalent used in model experiments. Animal unit equivalents: cow = 1, sheep = 0.14, horse = 1.8.

Stocking rate	Sheep	Horse	Cow	AUY
1	5	1	3	5.55
2	7	2	4	8.65
3	10	2	6	11.10
4	15	3	7	14.65
5	20	4	8	18.20
6	23	5	12	24.45
7	25	6	15	29.55
8	27	7	17	33.65
9	30	8	20	38.90
10	33	8	22	41.35
11	35	8	25	44.65
12	40	8	30	50.40
13	43	9	32	54.65
14	45	10	35	59.75

averages stocking rate over the entire grid-cell area, so at any particular moment, some grid-cells could have a higher number of specified animals, whereas others could have fewer. Proportions of animals in each livestock species group were based on typical herd sizes in that region. Therefore there were proportionally more sheep than cattle, and very few horses. Population numbers of sheep, horses, and cattle were converted into AUY km^{-2} for analysis. Grazing intensity, otherwise known as the proportion of vegetation removed, was used to describe effects of stocking rate on vegetation. McNaughton (1979) defined grazing intensity as:

$$GI = 1 - (g/u) \quad (1)$$

where g = biomass in grazed area and u = biomass in ungrazed areas. Grazing intensity data were averaged for the growing season May through October for analysis.

Each model run was 50 years in length. Model output of herbaceous and shrub above ground net primary production (ANPP); grass, forb, and shrub live roots, averaged from May through October, and then averaged in 10-year increments; and percent vegetation offtake, averaged May through October, from each stocking rate were used in grazing intensity analyses to determine the effect of stocking rate on the simulated grassland. Vegetation that remains dominated by herbaceous plants while grazed exists as an herbaceous stable state system. If vegetation composition changes with grazing, to one dominated by shrubs, then the system has shifted to a different stable state.

To examine the resilience of the system, animal populations were removed from model runs to simulate grasslands recovering from grazing. State variable outputs from each stocking rate run were saved and used to initialize a set of "resilience" runs to examine if vegetation composition and production could return to an herbaceous dominated stable state. Stocking rate was set at 0 for each of the 14 resilience runs and vegetation production was modeled for 50 years following removal of grazing (Burke et al. 1995). If herbaceous vegetation does not recover, then the system was not resilient to that intensity of grazing. The same weather file was used in this analysis as the previous set of runs. Herbaceous and shrub ANPP, grass, forb, and shrub live roots were used in the resilience analysis.

Results

Validation analysis

Monthly Normalized Difference Vegetation Index (NDVI) images were compared to Savanna green vegetation biomass output for the growing season, May through October, to validate vegetation biomass model predictions. For analyses, NDVI images and Savanna output were averaged for each branch and plotted over time (Fig. 2). Accuracy in Savanna's predictions of green vegetation biomass varied depending on branch. Correlations between predictions and NDVI data ranged from $R^2 = 0.34$ ($P = 0.00021$) at branch 9 to $R^2 = 0.57$ ($P < 0.0001$) at branch 3 (Table 3).

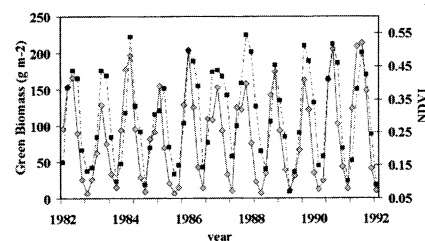


Fig. 2. Validation data of Savanna output from branch 3. Continuous line represents green biomass data (g m^{-2}) from Savanna, dotted line represents NDVI data, rescaled to the interval -1 to 1. Values from May to October are shown on graph.

Sustainability

Mean seasonal grazing intensity in 50 year simulations increased as stocking rate increased (Fig. 3). Animal units per year

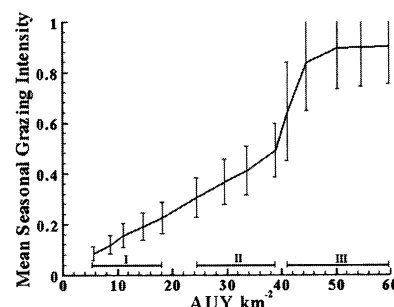


Fig. 3. Relationship between stocking rate (AUY km^{-2}) and grazing intensity (± 1 SD). Line I represents 5.6–18.2 AUY km^{-2} (light grazing), line II represents 24.5–38.9 AUY km^{-2} (moderate grazing), and line III represents 41.4–59.8 AUY km^{-2} (heavy grazing).

(AUY) values are averaged over entire simulated area. Effects of grazing intensity on annual herbaceous above ground net primary production (ANPP_h) varied (Fig. 4). The ANPP_h decreased slightly as grazing intensity increased from 0.09 to 0.49 (5.6–38.9 AUY km^{-2} , refer to Table 2). Grazing intensities 0.09 to 0.23 (5.6–18.2 AUY km^{-2}) had the least effect on ANPP_h where trends did not differ from ANPP_h with no grazing. Grazing intensities 0.30 to 0.49 (24.5–38.9 AUY km^{-2}) caused a proportionally higher decrease in ANPP_h than lower grazing intensities, but still followed a similar trend as ANPP_h with no grazing. When ANPP_h dropped below 100

Table 3. Regression statistics for branches 1-12 comparing simulated biomass from May through October to 11 years of NDVI Global Area coverage (4 km²) data (n = 65).

Branch	1	2	3	4	5	6	7	8	9	10	11	12
Area (km ²)	196	334	323	212	301	130	655	208	609	412	141	79
Adjusted R ² ***	0.343	0.532	0.574	0.385	0.410	0.560	0.467	0.397	0.340	0.431	0.429	0.543
Standard Error	0.082	0.090	0.090	0.092	0.086	0.091	0.092	0.081	0.081	0.082	0.090	0.078

***Significant at the 0.001 level.

g m⁻² year⁻¹ with grazing intensity 0.49, annual shrub above ground net primary production (ANPP_s) increased to ~ 65 g m⁻² year⁻¹ as compared to 18.5 g m⁻² year⁻¹ at low grazing intensities (Fig. 5). This grazing intensity did not suppress herbaceous biomass to the point that shrubs were able to gain a competitive advantage.

A grazing intensity of 0.64 and higher (41.4–59.8 AUy km⁻²) on herbaceous vegetation was not sustainable and caused a sharp decline in ANPP_h subsequently followed by an increase in ANPP_s (Fig. 5). After 43 years of grazing with intensity 0.64, ANPP_h dropped to an average of 10 g m⁻² year⁻¹ and the system shifted to a shrub dominated state (Fig. 4). This shift was reached more rapidly with higher grazing intensities, where ANPP_h was reduced to an average of 9.0 g m⁻² year⁻¹ after 18 years with intensity 0.84 and after 11 years with intensity 0.89–0.90. This switch from grass-dominated vegetation to shrub-dominated vegetation demonstrates a key state change with the new system being inferior for livestock that graze herbaceous plants. There was a rapid replacement of the herbaceous community by a shrub-dominated one due to shrub's access to water in deep soil layers and lack of browsing on shrub vegetation in this simulation.

Biomass output data from grazing intensity 0.64 was compared to field data (Christensen et al. 1998) to check model accuracy in a heavy grazing simulation. Heavily grazed areas were randomly chosen within a 2 km radius of herder's households. Herbaceous biomass collected in the field during the month of August 1997 ranged from 26.5 g m⁻² to 98.1 g m⁻² in heavily grazed plots, with an average of 63.85 g m⁻². These values closely matched modeled herbaceous biomass data (45.2 g m⁻²) from areas grazed with intensity 0.64, during August of the same year.

Grass root biomass ranged from 328.0 g m⁻² to 476.0 g m⁻² with grazing intensities 0.09 to 0.49, but contrary to ANPP, root biomass increased as grazing intensity increased with grazing intensities 0.09–0.23 (Fig. 6). Herbaceous live root biomass decreased as grazing intensity increased from 0.30 to 0.49, averaging a

24 g m⁻² decrease with each intensity increment of 5 AUy km⁻². Although root biomass decreased, their dynamics followed the same trend as roots with lighter grazing intensities. Grazing intensities of 0.49 and higher resulted in a sharp decline of grass root biomass.

Shrub root biomass with grazing intensities 0.09 to 0.49 remained stable, between

12.9 g m⁻² and 19.8 g m⁻² (Fig. 7). Biomass values are low because model output expresses shrubs as g per total area in the steppe. Shrubs cover only 12 percent of the total area in the typical steppe vegetation, therefore reported shrub biomass is lower than data, which is expressed in terms of grams per meter squared of shrub-patches. Shrub root biomass in areas grazed with

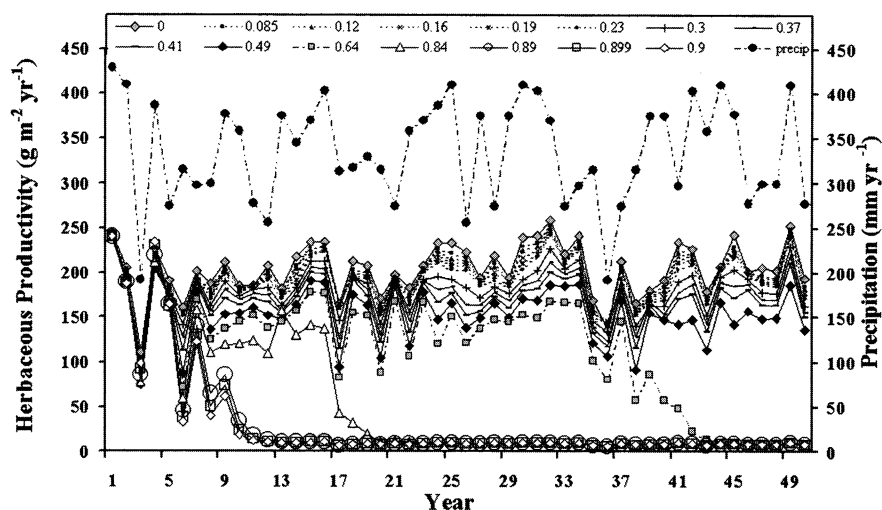


Fig. 4. Annual herbaceous ANPP from 50-year simulation runs with no grazing (0) and 14 different grazing intensities (5.6– 59.8 AUy km⁻²) and annual precipitation data.

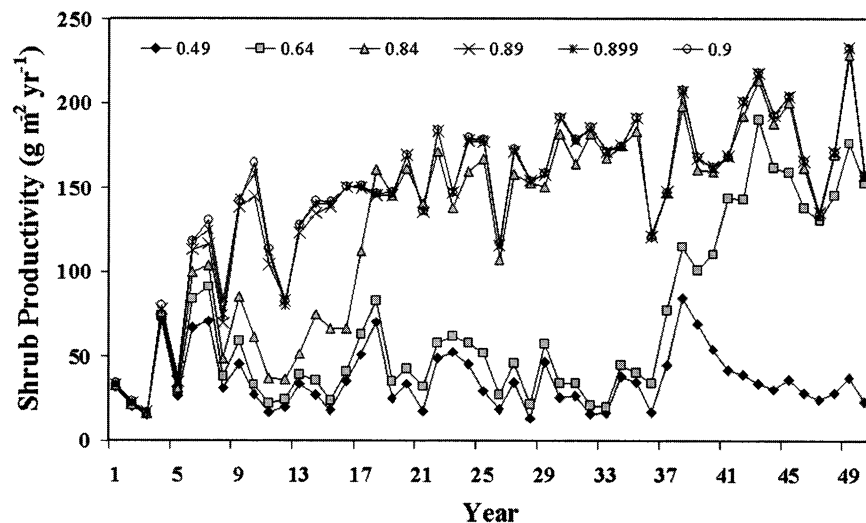


Fig. 5. Annual shrub ANPP in areas grazed with intensities of 0.49 to 0.9 (38.9 to 59.8 AUy km⁻²).

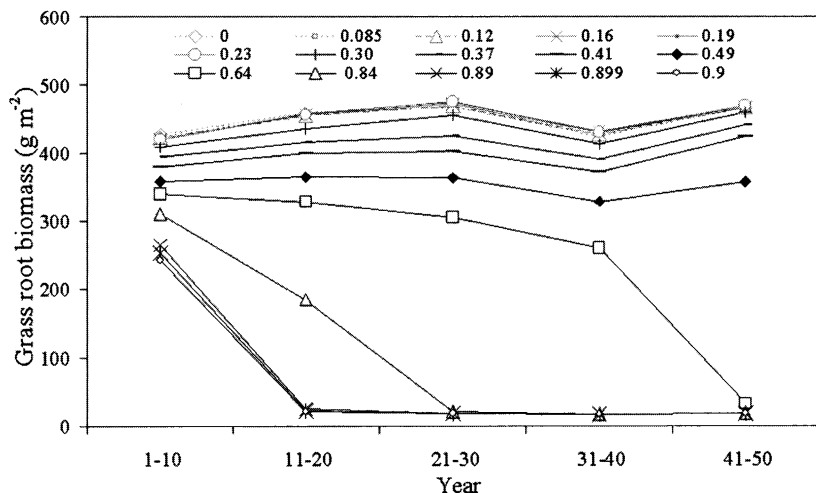


Fig. 6. Root dynamics from grass vegetation (g m^{-2}) averaged for the growing season May through October, then averaged in 10-year increments. Each line represents different grazing intensities (stocking rates 1–14).

intensity 0.64 and higher gained a competitive advantage over herbaceous root biomass and increased to levels ranging from 179.8 g m^{-2} to 238.7 g m^{-2} .

Based on results from Savanna output, grazing intensities were categorized into 3 groups: light, moderate, and heavy (Fig. 3). A light grazing intensity included grazing intensities of 0.09–0.23 (the 5 lowest stocking rates of 5.6–18.2 AUy km^{-2}). Light grazing intensity did not have a large effect on root biomass dynamics as annual average root biomass slightly increased as grazing intensities increased from 0.09 to 0.23 (Figs. 6 and 7). There was a slight decrease in ANPP_h as grazing intensity increased, but ANPP_h under light grazing intensity followed closely the trend of ANPP_h without grazing. Moderate grazing occurred at grazing intensities of 0.30 to 0.49 (24.5–38.9 AUy km^{-2}), a range where the herbaceous system was sustained. Averaged annual root biomass decreased as grazing intensity increased within the moderate intensity category. Heavy grazing occurred at grazing intensities above 0.49, and herbaceous production was not sustainable at these levels (the five highest grazing rates of 41.4–59.8 AUy km^{-2}).

Thresholds in herbaceous production, or point where higher grazing intensities result in a shift to a shrub dominated system, occurred with heavy grazing only when there were repeated years with below average precipitation and herbaceous production dropped below $70 \text{ g km}^{-2} \text{ yr}$ and root biomass fell below 200 g m^{-2} (Figs. 4 and 6). Average annual precipita-

tion at the Baiinixile farm for these simulations was 334.7 mm . In the 5th year of simulation, annual precipitation dropped to 274.3 mm and ANPP_h began to decrease as grazing intensity increased. The following 3 years, annual precipitation was below average (315.6 mm , 297.6 mm , and 299.2 mm respectively) and ANPP_h grazed at intensities 0.89 to 0.9 dropped to $10 \text{ g m}^{-2} \text{ year}^{-1}$ (Fig. 4). Subsequent to year 8, the threshold was passed and shrub production increased and became dominant at these grazing intensities (Fig. 5). In the 12th year of simulation, ANPP_h at grazing intensity 0.84 dropped, but the following

year had above average precipitation and ANPP_h recovered. Starting with the 17th year, there were 3 consecutive years with below average precipitation and ANPP_h dropped to $43 \text{ g m}^{-2} \text{ year}^{-1}$. This grazing intensity passed the threshold of $70 \text{ g m}^{-2} \text{ year}^{-1}$ in ANPP_h and 200 g m^{-2} in grass biomass, and shrubs became dominant. The drop in ANPP_h with grazing intensity 0.64 occurred after simulation years 36–38, all of which had below average annual precipitation (192.5 mm , 274.3 mm , and 315.6 mm respectively). While herbaceous vegetation was dominant and grazing intensity was light, shrub production remained low. When herbaceous vegetation was removed by heavy grazing intensity, which coincided with low precipitation years, the threshold was passed and shrub production increased to maximum values.

Resilience

Results from simulation runs that examined resilience of the system were similar to results from sustainability runs. The herbaceous above ground net primary production (ANPP_h) in areas previously grazed with intensities 0.085 to 0.49 (5.6–38.9 animal units per year (AUy) km^{-2}) returned to levels similar to runs with no grazing. The ANPP_h associated with a grazing intensity of 0.49 took 46 years to recover to the same biomass levels as with no grazing, but the reduction in ANPP_h was small, therefore the system was resilient with this grazing intensity. The ANPP_h that was grazed with intensities 0.64 to 0.9 was unable to recover, and

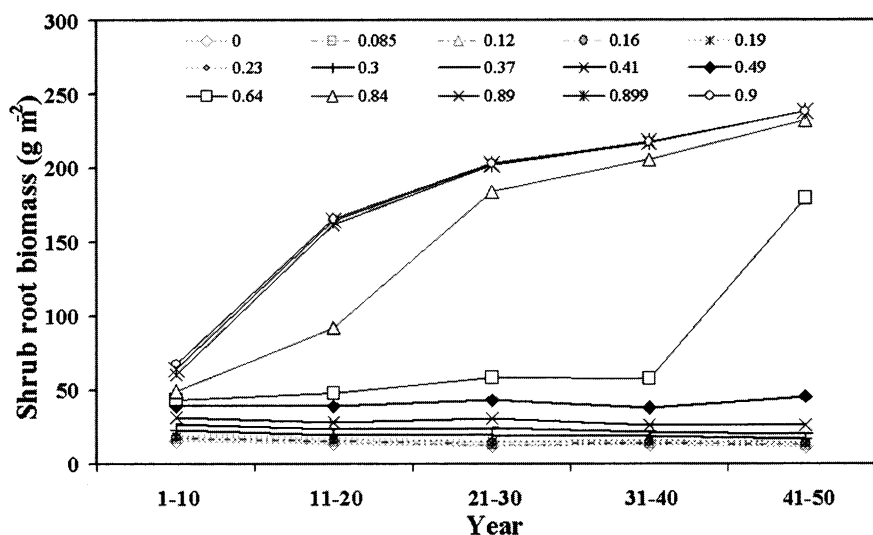


Fig. 7. Shrub root dynamics from grass vegetation (g m^{-2}) averaged for the growing season May through October, then averaged in 10-year increments. Each line represents different grazing intensities (stocking rates 1–14).

shrub above ground net primary production (ANPP_g) remained high. Herbaceous vegetation grazed with intensity 0.64 slightly increased ANPP_h to 32.5 g m⁻², but was unable to compete with shrubs and did not return to the original biomass level.

Root biomass from simulation runs examining resilience of the system was analyzed in a similar fashion as sustainability runs. Grass root biomass ranged from 405 g m⁻² to 467 g m⁻² in runs that had previously been grazed with intensities 0.085 to 0.49. Grass root biomass decreased as grazing intensity increased from 0.085 to 0.49 and followed a trend similar to grass root biomass with no grazing. Shrub root biomass was not affected by the removal of grazing. Shrub root biomass in areas that had been grazed with intensities 0.085 to 0.49 remained stable, while in areas previously grazed with intensity 0.64 to 0.9, shrub root biomass ranged from 201.9 g m⁻² to 253.7 g m⁻². Shrub root biomass maintained the competitive advantage over grass root biomass in areas that had grazing intensities of 0.64 and higher for 50 years after grazing was removed.

Discussion

Ecosystems that are grazed are subject to change due to shifts in human and livestock population levels, changes in climate, changes in land use from grazing to agriculture, alteration of management technologies, and changes in management such as the change from nomadic to sedentary grazing practices (Archer et al. 1995, Walker and Abel 1999). Management changes have occurred in the Inner Mongolia region without an understanding of their consequences and therefore have left the system vulnerable to change, and the arid climate of this region makes the system more likely to exhibit vegetation state changes under grazing (Ellis and Swift 1988). Despite the aridity of the system, present day herders maintain a style of management where livestock numbers are kept constant or gradually increased, despite varying weather patterns (Bilik 1996, Williams 1996b). As a result of these increases, grassland degradation is increasing (Li 1989, Sheehy 1993, Chen 1996) and the number of livestock die-offs is increasing (Chen 1996). Heavy grazing during low precipitation years may bring this system to a threshold beyond which there can be a shift to an alternate stable state (Holling 1973, Sheehy 1993), and

grazing should be managed with this in mind (Ellis and Swift 1988, Ellis et al. 1993). It is vital to recognize these thresholds in order to devise sustainable management regimes (Cowling 2000).

Westoby et al. (1989) proposed the State-and Transition model for range management. This model recognizes the dynamics of rangelands by describing different vegetation states, and the importance of understanding the mechanisms causing transitions among states. 'Transitions' occur when thresholds in a particular stable state are passed and the system shifts to an alternate stable state. Grazed landscapes are vulnerable to shifts between stable states when subject to poor management or the combination of intensified grazing pressure and extreme climate events (Friedel 1991, Laycock 1991, Ellis et al. 1993, Rietkerk and van de Koppel 1997). For these reasons, a systems approach was used to more specifically address the problems of grazing management at a particular site. From modeling results, this system was hypoth-

esized as having the potential to switch from a grass to a shrub dominated stable state when heavy grazing is combined with below average precipitation events. In model simulations above a certain grazing intensity, herbaceous plants could not recover from grazing removals and shrubs were able to capitalize on available resources once the herbaceous vegetation was suppressed (Archer 1995). Because shrubs were not browsed they displaced the overgrazed herbaceous plants and became the dominant functional group.

The Savanna model determined what combinations of grazing intensities, precipitation, and vegetation patterns were sustainable for the Xilingol region and found where thresholds and stable states exist. Results of the model analysis helped to explain how heavy grazing intensities, above 0.49, in combination with 2 or more years of below average precipitation events surpassed the threshold of sustainability and caused a sharp decline in grass vegetation. Angell (1997) conducted a 4-year study in the Northern Great Basin

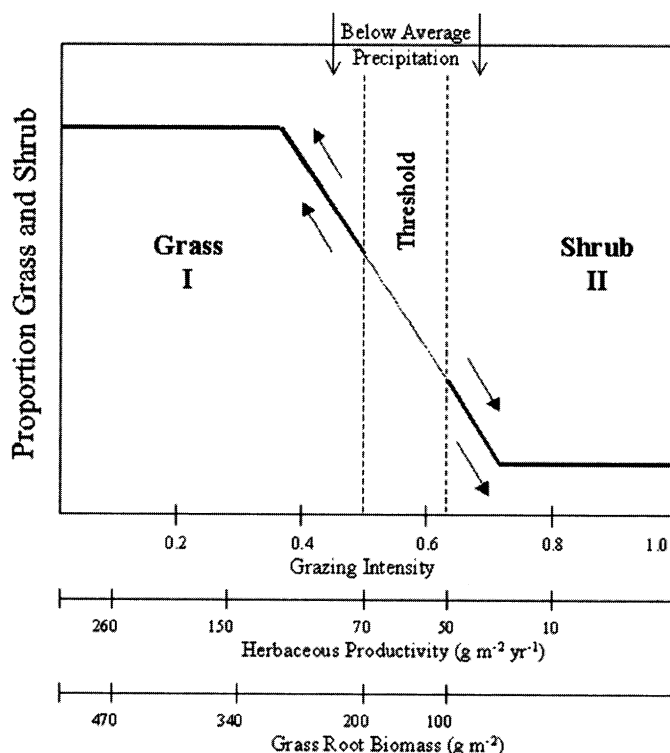


Fig. 8. Grass/shrub stable state system, one dominated by grass (region I) and the other shrubs (region II). Horizontal lines (above Grass and below Shrub) represent systems in a stable state. As grazing intensity (GI) increases, the system increases in shrubby biomass (horizontal line shifts diagonally). The system is resilient if grazing intensity is below threshold zone (GI 0.49–0.63) and will return to a grass stable state if grazing is removed (arrows) despite precipitation being below average. If GI is higher than threshold zone (GI > 0.63) and precipitation is below average, the grassland system is not resilient to grazing and will gradually move towards a shrub stable state (arrows). The higher the GI, the shorter amount of time it takes for the system to move towards a shrub stable state.

Experimental Range, Oregon, on the effects of grazing on grass and shrub vegetation. His results were similar to this study in that grass standing crop decreased in years 2, 3, and 4 with heavy grazing, and low precipitation events limited grass regrowth after grazing. Standing biomass in heavily grazed sites (1.2 animal units (AU) ha⁻¹) was reduced by 43% as compared to continuously grazed (0.6 AU ha⁻¹) sites. He also found an increase in juvenile sagebrush survival due to heavy grazing on herbaceous vegetation. Gillen et al. (1998) also found decreases in standing crop due to heavy as compared to light grazing, decreasing by as much as 50% during 1 growing season. Although these were short-term studies, they show a similar trend to the first 10 years of model simulations in this analysis.

Field data from the Inner Mongolian Grassland Ecosystem Research Station (Christensen et al. 1998) in the high-stocking rate areas did not show an increase in shrubs as predicted by the model. Possible explanations are that the fieldwork was conducted in 1 season, while the increase in shrubs in the modeling experiments occurred over a 38-year period. Also, live-stock numbers have only recently increased at the Baiinxile farm, whereas the modeling results are predictions of what could happen after many years of heavy grazing. Soil information was limited at the scale used, which could potentially affect shrub growth and/or effects of grazing on shrub growth (Rietkerk and van de Koppel 1997, van de Koppel et al. 1997). There is uncertainty in how fast shrubs in this region can spread, based on seed production and establishment rates, which could also affect responses to grazing (Archer 1995).

Model simulations included only grazers because sheep, horses, and cattle dominate the current system in Inner Mongolia. If goats, which browse shrubs, were simulated, then results from model simulations would likely be different. In neighboring Mongolia, increases in shrubs are not seen with heavy grazing (Fernandez-Gimenez and Allen-Diaz 1999, Fernandez-Gimenez 2000), possibly because goats, which consume shrubs, are a major component of livestock herds in that region. Fire does not occur naturally in this area, but it could suppress shrubby encroachment (Ellison 1960, Archer 1995, Scholes and Archer 1997) and could potentially suppress the competitive advancement of shrubs with heavy grazing in model scenarios.

A graphical representation of the dynamics of the system in regard to

thresholds and stable states describes 2 steady state systems divided by a threshold zone where section I is dominated by grass vegetation and section II is dominated by shrubby vegetation (Fig. 8). The angled line between the 2 stable-state regions represents a transitional system. As grazing intensity increases towards the threshold isocline (grazing intensity = 0.49, herbaceous productivity = 70 g m⁻² year⁻¹, root biomass = 200 g m⁻²) the proportion of shrubs increases. But when grazing is removed, the system is resilient to these levels of grazing and is capable of returning to a grass steady state (represented by arrows) despite precipitation being below average. If grazing intensity increases above a threshold value (grazing intensity = 0.49–0.64, herbaceous productivity < 70 g m⁻² year⁻¹, and root biomass < 200 g m⁻²) the system shifts to a shrub dominated stable-state (region II). When grazing intensity ranges from 0.64 to 0.89 during below average precipitation events, the grassland system is not resilient. These levels of grazing will eventually result in a shrub dominated system, represented by the vertical line in region II.

The Savanna model experiments identified potential grazing thresholds in this system, providing better understanding of sustainability and resilience for future successful management. Understanding thresholds in grazing systems has important policy implications in the Inner Mongolian region. Because of the highly variable climate pattern, it is important not to overstock grazing areas and/or to maintain grazing reserves for use during periods of climate stress (Cowling 2000). This simulation analysis as well as other research has shown the negative impact of high grazing intensities. To avoid negative impacts on this grassland region, policy-makers must limit the amount of livestock or limit high levels of grazing intensity in certain areas to maintain sustainable livestock production.

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Utilization and grazing distribution of cattle at 4 stocking densities

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Abstract

The relationship between stocking density and grazing distribution was studied in eastern Nebraska pastures seeded to a warm-season, tall-grass mixture and grazed at 4 stocking densities: 9, 18, 27, and 54 steers ha⁻¹. Each of 4 pastures was divided into 4 paddocks ranging in size from 0.18 to 1.12 ha. Paddocks within each pasture were grazed rotationally by 10 steers averaging 282 kg during 3 consecutive cycles (12, 36, and 24 days) from early June to late August in 1995 and 1996. Transects 12-m long were established in a grid pattern in each paddock. Six tillers each of big bluestem (*Andropogon gerardii* Vitman) and switchgrass (*Panicum virgatum* L.) were marked permanently in each transect. Height and leaf length of marked tillers were measured before and after grazing in the last 2 grazing cycles in both years. Utilization was estimated by the reduction in tiller height or leaf length. Estimates of grazing distribution were based on a uniformity index, which was calculated by summing the absolute differences of tiller height or leaf length between adjacent transects. Stocking density generally did not affect ($P > 0.05$) tiller height reduction which ranged from 19 to 22 cm and from 29 to 38 cm among the stocking densities in 1995 and 1996, respectively. In most grazing cycles, leaf length reduction for big bluestem was greater ($P < 0.05$) than for switchgrass while tiller height reduction was similar between species. Spatial grazing distribution was not affected ($P > 0.05$) by stocking density but big bluestem was grazed more evenly ($P < 0.05$) than switchgrass in the last cycle in each year. Stocking densities as high as 54 steers ha⁻¹ on warm-season, tall-grass mixtures do not appear to be a major factor in affecting spatial grazing distribution or forage plant selection.

Key Words: big bluestem, switchgrass, uniformity index, herbage allowance

Plant cover of grazing land is heterogeneous because management and environmental characteristics affecting plant growth (e.g., soils, topography, climate) are discontinuous spatially and temporally (Greig-Smith 1983). Given this heterogeneity, grazing animals are unlikely to make uniform use of a grazing unit; some areas are used heavily and others receive little or no use (Edwards et al. 1997). This uneven utilization affects the nutritional status of grazing animals as well as the dynamics of plant communities. When carrying capacity is not exceeded, range condition may improve when herbivores are more evenly distributed (Provenza 1991).

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Resumen

Se estudio la relación entre la densidad de carga y la distribución del apacentamiento en praderas del este de Nebraska sembradas con una mezcla de zacates altos de verano y apacentadas con 4 densidades de carga animal: 9, 18, 27 y 54 novillos ha⁻¹. Cada una de las 4 praderas fueron divididas en 4 potreros variando en tamaño de 0.18 a 1.12 ha. Los potreros dentro de cada pradera se apacentaron rotacionalmente con 10 novillos, (promediando 282 kg) durante 3 ciclos consecutivos, (12, 36, y 24 días), de inicios de Junio a fines de Agosto en 1995 y 1996. En cada potrero se establecieron transectos de 12 m de largo en un patrón cuadrículado. En cada transecto se marcaron permanentemente 6 hijuelos de Big bluestem” (*Andropogon gerardii* Vitman) y 6 de “Switchgrass” (*Panicum virgatum* L.). La altura y la longitud de las hojas de los hijuelos marcados se mido antes y después del apacentamiento en los dos últimos ciclos de apacentamiento de ambos años. La utilización se estimo mediante la reducción en la altura de los hijuelos y la longitud de la hoja. Las estimaciones de la distribución del apacentamiento se basaron en un índice de uniformidad, el cual fue calculado sumando las diferencia absolutas de la altura del hijuelo y la longitud de las hojas entre transectos adyacentes. La densidad de carga generalmente no afecto ($P > 0.05$) la reducción de altura de los hijuelos, la cual vario de 19 a 22 cm y de 29 a 38 cm entre las densidades de carga en 1995 y 1996 respectivamente. En la mayoría de los ciclos de apacentamiento, la reducción de la longitud de las hojas de “Big bluestem” fue mayor ($P < 0.05$) que la de “Switchgrass”, mientras la reducción de la altura del hijuelo fue similar para ambas especies. La distribución espacial del apacentamiento no fue afectada ($P > 0.05$) por la densidad de carga, pero en el último ciclo de cada año, el “Big bluestem” fue apacentado más uniformemente ($P < 0.05$) que el “Switchgrass”. Densidades de carga tan altas como 54 novillos ha⁻¹ en praderas de mezclas de zacates altos de verano no parece ser un factor principal que afecte la distribución espacial o la selección del forraje de la planta.

The consequence of uneven utilization has been reported regularly in the literature and recommendations to alleviate this problem have been developed (Gammon and Roberts 1978, Vallentine 2001). Strategies used to improve grazing distribution include reduction of paddock size, improved water distribution, strategic placement of salt and supplements, and increasing stocking density. A common practice used to increase stocking density is intensive subdivision of grazing units (Gerrish and Morrow 1999, Vallentine 2001).

Increased stocking density is reported to improve grazing distribution because of the role animal density plays in modifying

herbage allowance (Roth et al. 1986, Bailey and Rittenhouse 1989). The relationship between stocking density and grazing distribution has been investigated with experimental designs that do not allow for isolation of stocking density from other grazing variables (Kirby et al. 1986, Walker et al. 1989). Most of these studies arrived at different stocking densities by using various grazing systems that caused confounding with management strategies and stocking rates (Smith and Owensby 1978, Senock et al. 1993). Most studies also have been conducted under extensive conditions where treatment replication is difficult and labor constraints limit sampling intensity and rigorous evaluation of the variables observed (Kirby et al. 1986, Pierson and Scarnecchia 1987, Hart et al. 1993). Moreover, stocking densities studied were relatively low (less than 15 AU ha⁻¹) because of low carrying capacity (Kirby et al. 1986, Pierson and Scarnecchia 1987, Walker et al. 1989).

Studies conducted in small paddocks may isolate responses to stocking density more effectively by eliminating the effect of distance to water and other variables related to grazing distribution. The objectives of this study were to use small paddocks to determine spatial variability in utilization of big bluestem (*Andropogon gerardii* Vitman) and switchgrass (*Panicum virgatum* L.) and the effect of stocking density on utilization of a warm-season grass mixture.

Materials and Methods

Study site

The study was conducted in 1995 and 1996 at the University of Nebraska Agricultural Research and Development Center near Mead, Neb. (96° 33' W, 41° 11' N, 315 m elevation) at the western edge of the tallgrass prairie region. Climate is continental, characterized by wide seasonal variations. Average maximum daily temperatures range from 0.1° C in January to 31.5° C in July. Average minimum daily temperatures range from -11.4° C in January to 18.9° C in July. The long-term (1960 to 2000) annual precipitation averages 741 mm, and about 75% of this falls during the growing season (April through September) (HPRCC 1997). The topography varies from nearly level to slopes of less than 3%. The prominent soil in the study site is a Sharpsburg silty clay loam (fine, montmorillonitic, mesic, Typic Argiudoll), and most of the

Table 1. Description of 4 stocking density treatments.

Stocking density (steers ha ⁻¹)	Paddock size (ha)	Number of animals	Grazing period length		
			Cycle 1	Cycle 2	Cycle 3
			------(days)-----		
9	1.12	10	6	18	12
18	0.56	10	3	9	6
27	0.37	10	2	6	4
54	0.18	10	1	3	2

parent material is loess of Peorian age (Soil Conservation Service 1965).

Four pastures of seeded warm-season grass and averaging 2.23 ha were used. These pastures were grazed from mid-June through August at about 7 AUM ha⁻¹ during the previous several years by cattle as part of a rotational grazing system. Big bluestem, switchgrass, and indiangrass [*Sorghastrum nutans* (L.) Nash] were the dominants in the pastures. Smaller amounts of little bluestem [*Schizachyrium scoparium* (Michx.) Nash] and sideoats grama [*Bouteloua curtipendula* (Michx.) Torr.] were present. To reduce the heterogeneity of the canopy structure, all pastures were burned in early May 1995. Pastures were fertilized in May 1995 and 1996 with 90 kg N ha⁻¹.

Grazing treatments

Each of the 4 grazing units represented 1 replication and was divided into 4 paddocks ranging in size from 0.18 to 1.12 ha (Table 1). The paddocks in each grazing unit were grazed rotationally by 10 cross-bred yearling steers, averaging 282 kg (0.63 AU), for 72 days from early June to late August in both 1995 and 1996. Treatments were 4 stocking densities, resulting from the 4 paddock sizes. Stocking rate was identical at 324 steer days ha⁻¹ (204 AUD ha⁻¹) for each of the 4 treatments because larger paddocks had proportionally longer grazing periods (Table 1). Steers were grazed rotationally through the paddocks of each grazing unit in 3 grazing cycles of 12, 36, and 24 days in length from the beginning to the end of the grazing season. A grazing cycle refers to 1 rotation through the paddocks in a grazing unit. Different cycle lengths were used to match forage availability and growth rates during the different periods in the growing season. The first cycle was rapid to reduce differences in maturity of plants in the paddocks within each grazing unit. Previous research (Anderson 1997) indicated that a 36-day cycle was well suited to a warm-season tall-grass pasture during the growing season. At the end of the 36-day cycle in both years, we finished with a 24-day cycle because the amount of

available forage was too low to support a 36-day cycle.

Within each grazing unit, the grazing cycle began in a different sized paddock to balance differences in plant growth stages during the grazing season across grazing units (Fig. 1). Thus, steers began grazing the 1.12-ha paddock in 1 grazing unit, the 0.56 ha in another, the 0.37 ha in the third, and the 0.18 ha in the fourth grazing unit. Direction of rotation always was from the larger paddock to the next smaller one, except when animals were rotated from the 0.18-ha paddock to the 1.12-ha paddock. Cattle were moved in mid-morning when rotation was scheduled. Fresh water and trace mineralized salt blocks were available in each paddock. The cattle grazed smooth brome (*Bromus inermis* Leyss.) during the 45 days before being moved to the study site.

Sampling and variables measured

Transects, 12-m long, were arranged in a grid pattern in a north-south and east-west direction in each pasture. There were 17, 14, 11, and 8 transects in each of the 1.12, 0.56, 0.37, and 0.18-ha paddocks, respectively. Ends of each transect were permanently marked with wooden stakes identified with metal tags. Along each transect, 6 tillers each of big bluestem and switchgrass were marked with colored, 14-gauge solid-core copper wire loosely wrapped around the tillers' bases. Marked tillers were approximately 1 m apart and species alternated. Tiller measurements, taken before and after grazing, were height (from the soil surface to the tip of the highest fully extended leaf) and total length of green leaf blades per tiller. The same transects and sampling procedures were used during each grazing cycle and year. Tiller measurements were not made in the first cycle because the measurements required more time than available in the short, first cycle.

Tiller height reduction and leaf length reduction were estimated by subtracting post-grazing from pre-grazing tiller height and leaf length, respectively. Tiller height reduction and leaf length reduction were adjusted for growth during the grazing

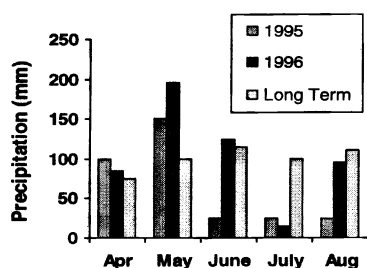


Fig. 1. Monthly precipitation during the growing season for 1995, 1996, and 30-year average at Mead, Neb.

period using a modification of the method described by Morris (1969). Growth rate adjustments were made independently for each grazing unit and species. Growth rate was obtained by marking 10 tillers of each species in each of 3 exclosures (1.2 x 1.5 m) placed randomly in the largest paddock of each grazing unit and measuring these tillers at the beginning and end of each grazing period. Daily growth increment was calculated by dividing the difference of final minus initial tiller height or leaf length by the number of days of grazing. Daily growth increment then was multiplied by the days of grazing in each paddock to determine the amount of increase in tiller height or leaf length for the average tiller in each paddock. Reduction in tiller height or leaf length in a grazed paddock was adjusted by adding the growth occurring during the grazed period.

A uniformity index (Ahuja and Schachter 1983, Hacker et al. 1988) was used to analyze treatment differences in spatial distribution of defoliation intensity of big bluestem and switchgrass. Within each paddock, the uniformity index was calculated by summing the absolute differences in mean tiller heights, or leaf lengths, between adjacent transects along the north-south and east-west grid pattern. This arrangement used 22 differences for the 1.12-ha paddocks, 17 differences for the 0.56-ha paddocks, 12 differences for the 0.37-ha paddocks, and 8 differences for the 0.18-ha paddocks. The sum of absolute differences in each paddock was divided by the number of differences to obtain the uniformity index. This index does not have a unit and higher values imply less uniformity for the variable evaluated. Uniformity indices were calculated for tiller height before grazing, tiller height after grazing, tiller height reduction, leaf length before grazing, leaf length after grazing, and leaf length reduction.

Herbage biomass was estimated before each grazing period by hand clipping the

current year's growth at ground level in randomly placed 0.55-m² quadrats. Samples were dried in a forced-air oven at 60° C until weight was constant. Number of samples collected in each paddock varied according to the size of the paddock and ranged from 5 in the smallest paddocks to 10 in the largest.

Experimental Design

The experimental design was a modification of the standard procedure for a Latin square (Lenter and Bishop 1993) arranged in a split plot (Table 2). The major sources of variation were stage (i.e., order in which paddocks were grazed in each grazing unit), grazing unit, and treatment (i.e., stocking densities and species). Paddocks were the main plot and grass species the split plot (Anderson et al. 1995). Cycle was included as a split factor in the analysis to determine the consistency of the variables studied through the grazing season. Analyses of tiller data included cycles 2 and 3 only because tiller height data was not collected in the first cycle, whereas analysis of standing crop yield data included all 3 cycles. When statistical analysis for a variable resulted in interactions with year, analysis was conducted within individual years (Table 2).

Analysis of the data was conducted using the Statistical Analysis System with the Mixed Procedure (SAS 1995). The

error term used to test each variable is shown in Table 2. Least significant difference (LSD) was used to separate means when analysis showed significant ($P < 0.05$) treatment effects.

Results and Discussion

In 1995, precipitation in April and May was higher than the long-term average, whereas precipitation in June, July, and August was much lower than the long-term average (Fig. 2; HPRCC 1997). Distribution of precipitation followed a similar pattern in 1996 except that the wet spring extended into June before giving way to a relatively dry July and August. Precipitation from April through August in 1995 and 1996 was 344 and 465 mm, respectively, compared to the long-term average of 453 mm. Average monthly maximum air temperature from April through August 1995 was generally higher than the long-term average whereas the average maximum air temperature in 1996 was lower than the long-term average through June before increasing above the long-term average in July and August. Effect of year on utilization or grazing distribution likely was related to differences in weather patterns between 1995 and 1996.

Table 2. Components of the analysis of variance used to test effects of stocking density (SD), grazing units (GU), stage of grazing (ST), species (SP), cycles (CY) and years (YR) on tiller height and leaf length reduction and on uniformity indices in paddocks grazed by cattle.

Over years		Within year	
Source of variation	df	Source of variation	df
YR	1	GU	3
GU	3	ST	3
YR*GU	3	SD	3
ST	3	GU*ST*SD (error a)	6
YR*ST	3	SP	1
SD	3	SP*SD	3
YR*SD	3	GU*ST*SD*SP (error b)	12
YR*SD*GU*ST (error a)	12	CY	1
SP	1	CY*SD	3
SP*SD	3	CY*GU*ST*SD (error c)	12
YR*SP	1	SP*CY	1
YR*SP*SD	3	SP*CY*SD	3
YR*SP*SD*GU*ST (error b)	24	Error d [†]	12
CY	1	Corrected Total	63
YR*CY	1		
YR*CY*SD	3		
YR*CY*SD*GU*ST (error c)	24		
CY*SP	1		
YR*CY*SP	1		
CY*SP*SD	3		
YR*CY*SP*SD	3		
Error d [†]	27		
Corrected Total	127		

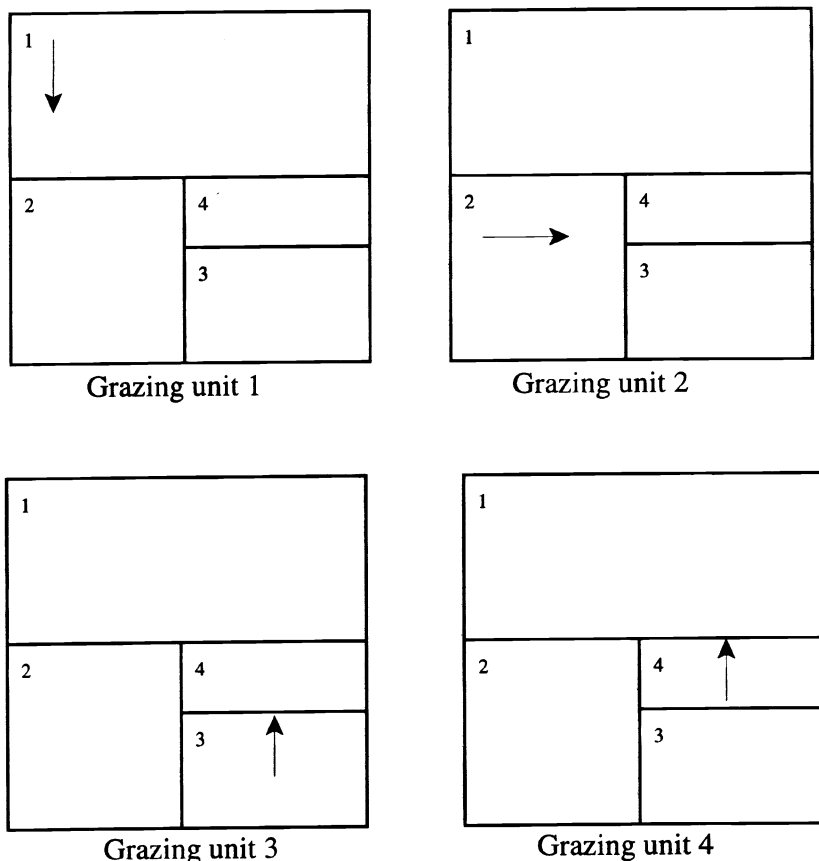


Fig. 2. Paddock arrangement and starting point (↑) in the rotation of each grazing unit.

Utilization

Stocking density did not affect ($P = 0.47$) tiller height reduction in 1995, whereas tiller height reduction in 1996 for the 27 steers ha^{-1} treatment was less ($P = 0.04$) than for the lower 2 stocking density treatments (Table 3). This difference was largely due to the unexplainably low tiller height reduction for the 27 steers ha^{-1} treatment in cycle 3 in 1996, where height reduction was much lower in 1 grazing unit (15 cm) than the average for the other grazing units (29 cm). When data were analyzed across years, but without data from cycle 3 in 1996, there were no differences ($P = 0.44$) among stocking densities. Leaf length reduction was not affected in either year by stocking density ($P > 0.60$). Realizing that tiller height reduction and leaf length reduction are indices of utilization, stocking density did not affect utilization nor did it likely affect the efficiency of harvest of the available forage in the experimental pastures. In addition, there was no stocking density \times species interaction ($P = 0.66$) for tiller height reduction or leaf length reduction indicating that stocking density had no effect on species selectivity.

Animal preference for switchgrass and big bluestem was different in 1995 than in 1996. Tiller height was reduced more ($P = 0.01$) in 1995 for switchgrass than for big bluestem while tiller height reduction was not different ($P = 0.10$) for the 2 species in 1996 (Table 3). Leaf length reduction was similar ($P = 0.73$) between species in 1995 but was 70% greater ($P = 0.01$) for big bluestem than for switchgrass in 1996 (Table 3).

Table 3. Tiller height reduction (THR) and leaf length reduction (LLR) in 1995 and 1996 by stocking density and species averaged over cycles 2 and 3 in warm-season grass paddocks¹.

Source of variance	1995		1996	
	THR	LLR	THR	LLR
----- (cm) -----				
Stocking density (steers ha^{-1})				
9	19a	50a	38a	95a
18	22a	57a	35a	92a
27	21a	57a	30b	86a
54	22a	60a	34ab	95a
LSD (0.05)	5.0	14.8	4.3	8.9
Species				
Big bluestem	19a	57a	36a	116a
Switchgrass	23b	56a	33a	68b
LSD (0.05)	3.3	6.7	4.8	18.6

¹Different letters within a column and source of variance indicate means are different at $P < 0.05$.

Species selectivity changed by cycle for tiller height reduction ($P = 0.01$) and leaf length reduction ($P = 0.01$) in 1995. Tiller height was reduced 35% more for switchgrass than for big bluestem in cycle 2, but tiller height reduction did not differ between switchgrass and big bluestem in cycle 3 (Table 4). In 1996, tiller height reduction was not different ($P > 0.70$) for the 2 species within either cycle. Leaf length reduction was greater for big bluestem than for switchgrass in cycles 2 and 3 of both years except in the second cycle of 1995 when leaf length reduction of switchgrass was greater. In the third cycle, big bluestem tended to be shorter and more leafy with relatively few elongated or reproductive tillers while switchgrass tillers were mostly reproductive, tall, and less leafy. Based on leaf length reduction as an indicator of utilization, the cattle preferred big bluestem in the third cycle of both years.

Grazing Distribution

Uniformity indices, based on grass tiller heights ($0=6.4$, $SD=1.3$) and leaf lengths ($0=17.3$, $SD=1.8$), were similar for all treatment paddocks before the first grazing cycle in 1995. Uniformity indices were lower at this time than for any other collection period in the following 2 years, indicating relatively uniform stands in terms of tiller height and leaf length at the initiation of the study. Prescribed burning in late spring 1995, before initiation of the study, helped develop this uniformity. Fire on tallgrass prairie reduces heterogeneity of community and canopy structure because it minimizes the effect of previous patch grazing and promotes uniform growth of grass communities (Andrew 1986, Collins 1989).

Indices for tiller height before grazing, tiller height after grazing, and tiller height

Table 4. Tiller height reduction (THR) and leaf length reduction (LLR) for big bluestem (BB) and switchgrass (SW) in grazing cycles 2 and 3 averaged over stocking densities during 1995 and 1996.¹

Cycle	THR			LLR		
	BB	SW	LSD (0.05)	BB	SW	LSD (0.05)
1995	----- (cm) -----					
2	23a	31a	2.9	72a	82b	7.9
3	15a	15a	3.5	41a	29b	5.6
1996						
2	43a	41a	5.8	153a	99b	24.3
3	28a	24a	4.5	78a	38b	10.1

¹Different letters within row and plant measurement indicate means are different at $P < 0.05$.

reduction did not vary among stocking densities ($P = 0.52$, $P = 0.64$, and $P = 0.56$, respectively) but indices for tiller height after grazing ($P = 0.01$) and tiller height reduction ($P = 0.01$) were greater in 1996 (11.9 and 11.5, respectively) than in 1995 (8.7 and 8.5, respectively). The lack of differences in tiller height indices among stocking densities indicates that stocking density did not influence utilization or spatial distribution of defoliation at the patch or paddock level. The higher indices for tiller height after grazing and tiller height reduction in 1996 suggest that the increased spatial variability in tiller height over the 2 years was the cumulative effect of selective grazing in the paddocks. Because paddocks were not burned in year 2 before grazing, unevenness established in year 1 due to patch grazing was carried over and accentuated by selective grazing during the second year.

Differences in tiller height indices between cycles were not consistent ($P = 0.01$) by species. The indices for tiller height after grazing and tiller height reduction were greater ($P = 0.01$) for big bluestem in cycle 2 than in cycle 3; whereas, these same indices did not differ between cycle 2 and cycle 3 for switchgrass. Moreover, the indices for tiller height after grazing and tiller height reduction for big bluestem and switchgrass were not different in cycle 2, but in cycle 3 the indices were 59 to 95% greater ($P = 0.01$) for switchgrass than for big bluestem (Table 5). As mentioned earlier, a high proportion of switchgrass tillers was reproductive by the third cycle. Field observations indicated that leaves were stripped from reproductive tillers leaving

the culms largely intact while vegetative tillers were grazed close to ground level. This grazing pattern resulted in a wide range of extended tiller heights. Big bluestem tillers were mostly vegetative in the third cycle and were utilized more heavily and evenly than switchgrass.

Like the tiller height reduction index, the leaf length reduction index was not affected by stocking density ($P = 0.87$) but increased ($P = 0.04$) from 1995 (19.5) to 1996 (24.2). These differences were not consistent between species ($P = 0.02$). During 1995, the leaf length reduction index for switchgrass and big bluestem did not differ but the index was greater for switchgrass (27.4) than for big bluestem (21.1) in 1996. The index for leaf length after grazing varied similarly to the leaf length reduction index.

The leaf length reduction index was greater ($P = 0.01$) for both species in cycle 2 than in cycle 3 (27 vs. 17 averaged over the 2 years). Steers apparently had the opportunity to graze more selectively in cycle 2 than in cycle 3 because of higher herbage allowance. Herbage mass (Table 6) peaked in cycle 2 in both years. Herbage allowance at the beginning of cycle 2 ranged from 100 to 820 kg DM AUM⁻¹, whereas herbage allowances in cycle 3 were 60 to 380 kg DM AUM⁻¹.

Stocking densities, at identical stocking rates, had little influence on level of utilization or spatial distribution of defoliation of switchgrass and big bluestem in a mixed sward. Hart et al. (1993) concluded that pasture size and distance to water were key variables affecting livestock grazing distribution in eastern Wyoming. Percentage use of standing herbage did not differ among locations within small pas-

tures (24 ha) whether they were grazed continuously or grazed rotationally (Hart et al. 1993). Walker et al. (1989) found that uniformity of grazing was not affected by a 74-fold change in stocking density (0.17 vs 12.5 AU ha⁻¹) on rangeland in the Rolling Plains of Texas. Both Walker et al. (1989) and Stuth et al. (1987) reported that cattle were more selective for plant communities or preferred sites in rotationally-grazed (higher stocking density) pastures than in continuously-grazed (lower stocking density) pastures. Kirby et al. (1986) also found no relationship between stocking density and uniformity of utilization on mixed prairie in North Dakota.

Studies (Senock et al. 1993) reporting stocking density effects on utilization and/or grazing distribution generally included confounding factors, such as distance to water, topography, or stocking rate, which does not allow an explicit test of stocking density and livestock grazing behavior relations. In our study, distance to water was less than 240 m in all pastures, which is less than the distance reported to affect grazing distribution (Gerrish and Davis 1999). Furthermore, pasture relief was nearly level in all pastures, thus removing topography as an influential feature on animal foraging behavior (Cook 1966). In addition, stocking rate was kept constant for all treatments by manipulating the length of grazing period.

The principal factors that varied among stocking density treatments in our study were paddock size, initial herbage allowance (Table 6), and grazing period length. Paddock size primarily affects distance to water and, as already stated, distance to water in our study always was less than the critical distance reported to affect grazing distribution (Gerrish and Davis 1999). High herbage allowance and longer grazing periods commonly are given as reasons for development of poor or patchy distribution (Kothmann 1984, Vallentine 2001) because animals have more opportunity to select preferred forage sites and plants and then return to those sites later in the same period to graze regrowth of grazed plants. In our study, herbage yields at the beginning of a grazing cycle generally did not differ

Table 5. Uniformity indices for tiller height before grazing (THBI), tiller height after grazing (THAI), and tiller height reduction (THRI) for big bluestem (BB) and switchgrass (SW) in 2 grazing cycles averaged across 4 stocking densities and 2 years.¹

Cycle	THBI			THAI			THRI		
	BB	SW	LSD (0.05)	BB	SW	LSD (0.05)	BB	SW	LSD (0.05)
2	7.6Aa	8.0Aa	1.08	9.5Aa	11.4Aa	228	10.2Aa	11.4Aa	2.11
3	6.0Ab	9.5Bb	1.31	6.9Ab	13.4Ba	1.93	6.9Ab	11.7Ba	1.53

¹Different uppercase letters within row and index and different lowercase letters within column indicate means are different at $P < 0.05$.

Table 6. Standing crop yields in warm-season grass paddocks at 4 stocking densities in 1995 and 1996 at the beginning of each grazing cycle.¹

Stocking density	Cycle 1		Cycle 2		Cycle 3	
	1995	1996	1995	1996	1995	1996
Steers ha ⁻¹	(kg ha ⁻¹)					
9	2,650a	2,780a	4,640a	3,310a	2,180a	1,790a
18	3,500a	3,100a	4,640a	3,590ab	2,090a	1,760a
27	3,150a	3,280a	3,880a	4,420b	2,170a	1,990a
54	2,430a	3,290a	3,400a	3,650ab	2,180a	2,290a
LSD (0.05)	1,234	648	1,372	1,055	915	925

¹Different letters within a column indicate means are different at $P < 0.05$.

among stocking densities in either year (Table 6); therefore, herbage allowances were lower for high stocking density paddocks because of the higher concentration of cattle. The herbage allowances in the highest stocking density paddocks (60 to 110 kg DM AU⁻¹) did not appear to be at a level where patchiness of grazing was affected significantly relative to the paddocks at low stocking densities. The variable length of grazing periods used in this study also did not appear to be a factor in affecting grazing distribution. Even though the development of patchiness would appear to be favored in low stocking density paddocks with longer grazing periods, no differences among stocking density treatments were detected.

Spatial distribution of defoliation may be affected by very high stocking densities in homogeneous (e.g., monocultures and level terrain) management units and at low herbage allowances. Volesky (1994) reported that with frontal grazing, at stocking densities of 80 to 170 steers (282 kg) ha⁻¹, 98% of the tillers were defoliated in a pasture of >Plains = Old World bluestem [*Bothriochloa ischaemum* (L.) Keng]. These stocking densities are achievable only on productive grazing land and with rapid movement of livestock over the grazing land as could be obtained with frontal grazing or strip grazing. Thresholds at which grazing distribution is affected by stocking density, or herbage allowance, have not been identified for various pasture types. Thresholds would appear to be much higher than what is practical for all but the most management-intensive systems.

Conclusion

Correctly identifying factors affecting the spatial utilization of vegetation in grazed pastures is critical in managing for herbage yield, harvest efficiency, and animal performance. Stocking densities ranging from 9 to 54 steers ha⁻¹ did not affect

the grazing uniformity or utilization of big bluestem and switchgrass in a mixed warm-season pasture. Other factors, such as distance to water and topography, are more likely the principal variables affecting grazing distribution in situations with moderate to high herbage allowances. Spatial uniformity of use between key species, however, may change over time. Uniformity indices were similar for big bluestem and switchgrass in the first half of the grazing season but big bluestem was utilized more uniformly than switchgrass late in the grazing season.

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Cattle distribution patterns and vegetation use in mountain riparian areas

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Abstract

To quantify the effects of season of use on beef cattle distribution relative to the riparian area, 52 cow/calf pairs were used to evaluate 1) early summer grazing (mid-June to mid-July), and 2) late summer grazing (mid-August to mid-September) during the summers of 1998 and 1999. Within a block, cow/calf pairs used during early summer were also used during late summer grazing periods. Pastures were stocked to achieve 50% utilization of herbaceous vegetation after a 28-day grazing trial. Livestock location and ambient air temperature were recorded hourly during two, 4-day periods in each season of use. Locations were transcribed to a geographical information system for the study area. Ocular vegetation utilization estimates, forage quality, and fecal deposits within 1-m of the stream were recorded post-grazing. During early summer, cattle were further from the stream ($P < 0.01$) than late summer, averaging 161 and 99-m, respectively. Cows were observed closer ($P < 0.01$) to the stream when ambient air temperatures were higher. Fecal deposits within 1-m of the stream were similar ($P = 0.13$) following early and late summer grazing. Forage quality varied ($P < 0.01$) between seasons, with early summer forages having lower dry matter, greater crude protein, lower fiber, and greater in situ dry matter disappearance compared with late summer forages. Utilization of riparian vegetation was lower and use of upland vegetation greater during early summer than late summer ($P < 0.05$). In summary, season of use affected cattle distribution relative to the riparian area, with late summer pastures having more concentrated use of riparian vegetation.

Key Words: Beef cattle, distribution patterns, riparian areas, season of use, vegetation utilization

Ecological degradation of riparian ecosystems is one of the greatest contemporary concerns for livestock grazing on western rangelands. Excessive use of riparian areas by livestock can result in removal of woody vegetation, over utilization of streamside vegetation, soil compaction, increased soil erosion, reduced water

Resumen

Durante los veranos de 1998 y 1999 se utilizaron 52 pares de vaca-becerro para cuantificar los efectos de la época de uso en la distribución del ganado en un área ribereña y para ello se evaluaron los siguientes tratamientos: 1) apacentamiento a inicios de verano (mediados de junio a mediados de julio) y 2) apacentamiento a finales de verano (mediados de Agosto a mediados de Septiembre). Dentro de un bloque, los pares de vaca-becerro utilizados a inicios de verano también se usaron en los periodos de fines de verano. Los potreros se cargaron para alcanzar una utilización de 50% de la vegetación herbácea en un periodo experimental de 28 días. La ubicación del ganado y la temperatura ambiente se registraron cada hora durante dos periodos de 4 días en cada época de uso. Las ubicaciones se introdujeron a un sistema de información geográfica para el área de estudio. Después del periodo de apacentamiento se registraron estimaciones oculares de la utilización de la vegetación, calidad del forraje y depósitos fecales dentro de un área de 1 metro de la corriente. A inicio del verano el ganado se alejó más de la corriente que a fines del verano ($P < 0.01$) promediando 161 y 99 m respectivamente. Cuando las temperatura ambiente era más alta se observaron las vacas significativamente ($P < 0.01$) más cerca de la corriente. Los depósitos fecales dentro de la franja de 1 m de la corriente fueron similares ($P = 0.13$) en ambas épocas de apacentamiento. La calidad de forraje varió ($P < 0.01$) entre épocas, a inicios de verano el forraje tenía menos materia seca, mayor proteína cruda, menos fibra y una mayor tasa de desaparición in situ de la materia seca en comparación con el forraje de fines de verano. A inicios de verano el uso de la vegetación ribereña fue más bajo y el uso de la vegetación alejada del área ribereña fue mayor ($P < 0.05$) en comparación con la época de fines de verano. En resumen, la época de uso afectó la distribución del ganado en las áreas ribereñas, y es a fines de verano cuando se concentra el uso de la vegetación ribereña.

quality, and streambank degradation (Buckhouse and Gifford 1976, Thomas et al. 1979). Cattle are attracted to riparian areas by environmental and nutritional factors and may utilize riparian vegetation disproportionately more than adjacent uplands (Gillen et al. 1984, Howery et al. 1996).

Livestock grazing management in riparian areas is one of the most pervasive issues facing rangeland managers in the western

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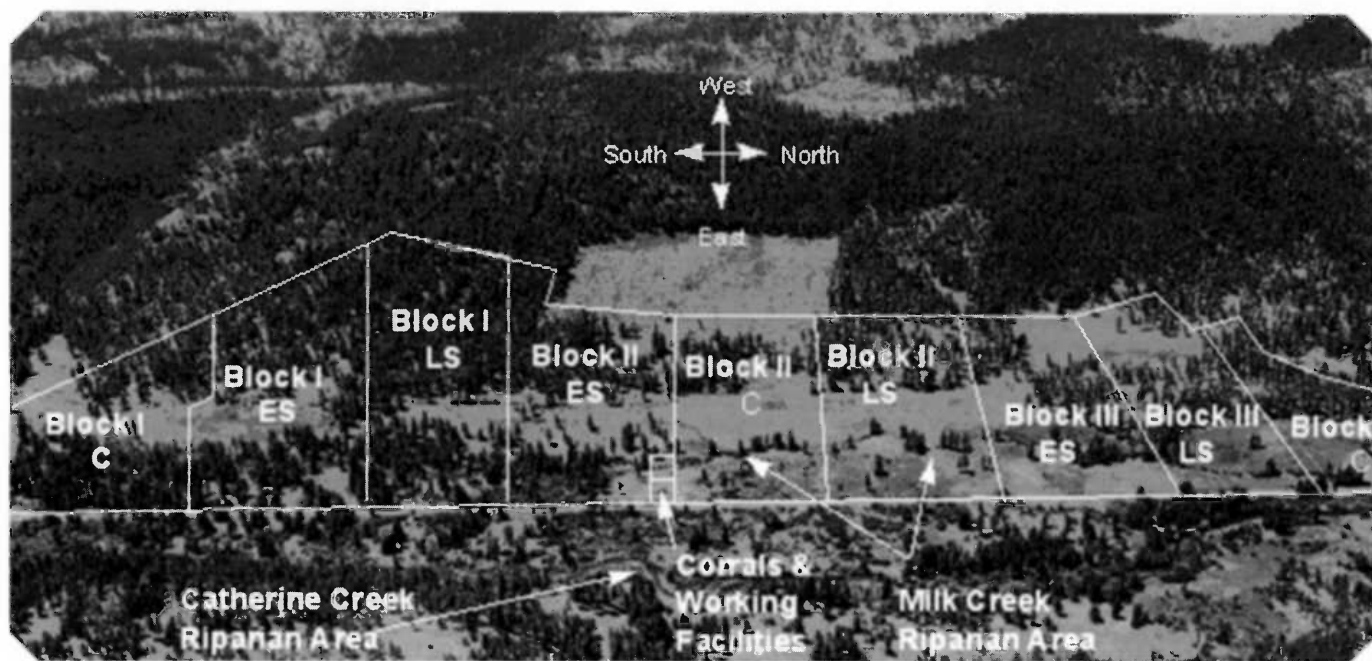


Fig. 1. Portion of Oregon State University's Hall Ranch utilized for the research project. Six pastures, 10 to 15 hectares in size were utilized in a replicated design evaluating 2 seasons of use over a 2-year study period. All pastures have riparian stream, riparian meadow, and adjacent uplands. Treatments included early summer grazing (ES), late summer grazing (LS), and a control (C). The three control pastures (one per block) were not grazed or used during this study.

U.S. (Leonard et al. 1997). Although riparian areas constitute only about 8% of the total public land acreage, and less than 1% of the public land in many of the more arid western states (USDI 1995), most grazing allotments contain some riparian acreage. Federal laws such as the Threatened and Endangered Species Act (1973), and the Federal Water Pollution Control Act (1972) are making it increasingly important for rangeland managers, to identify and implement grazing management strategies that maintain or improve the sustainability of riparian ecosystems. One such livestock management strategy may be grazing riparian areas in the spring when key forage species are vegetative, forage quality is high, and ambient air temperatures are low. Currently, the efficacy of this strategy for increasing the uniformity of grazing has not been quantitatively evaluated.

The objective of this research project was to provide a replicated, quantitative assessment of the effects of season of use (early versus late summer), on cattle grazing and vegetation utilization patterns within riparian areas and adjacent uplands in northeastern Oregon. Our hypothesis was that livestock grazing distribution and forage utilization patterns would be more uniform during early summer (Elmore and Kauffman 1994), and riparian areas would receive disproportionately more use than uplands during late summer (Gillen et al. 1985).

Materials and Methods

Location

This study was conducted on 109 ha of the Eastern Oregon Agricultural Research Center's Hall Ranch located in the foothills of the Wallowa Mountains in northeastern Oregon (latitude 45° 7' 48" N, longitude 117° 42' 32" W (Fig. 1)). Study site elevation is approximately 1,015-m, with annual precipitation averaging 350-mm. Most of the precipitation comes between October and June, which

results in dry summers and limited potential for vegetative re-growth during July through September.

The study site consisted of riparian meadows and adjacent uplands bordering Milk Creek, a tributary of Catherine Creek in the Grande Ronde River watershed. The site was cross-fenced with electric fence into nine, 10–15 ha pastures (Fig. 1). Each pasture contained about a 260-m reach of Milk Creek. Within each pasture, vegetation was classified into 4 vegetation types: gravel bar, riparian grass, riparian sedge/rush, and upland.

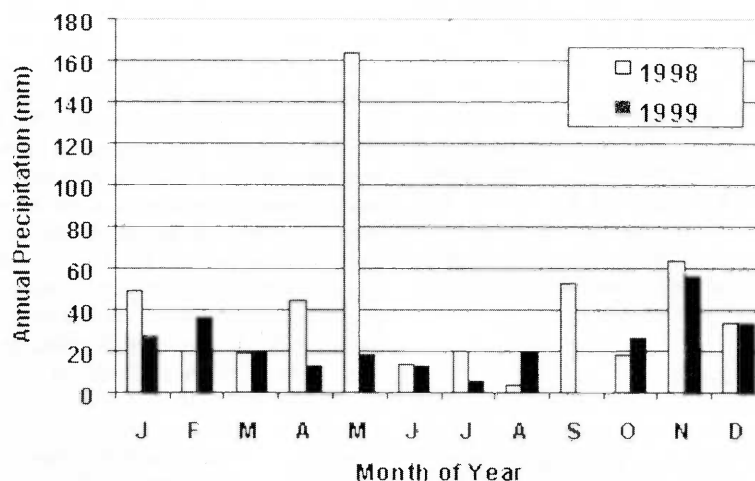


Fig. 2. Monthly precipitation during the study years of 1998 and 1999. Data were collected from the Eastern Oregon Agriculture Research Center Weather Station, Union, Ore.

Annual amounts of precipitation (Fig. 2) varied between years with 1998 receiving above normal precipitation, (500 mm), and 1999 receiving below normal precipitation, (264 mm).

Riparian Vegetation

Green line vegetation was that vegetation located immediately on the stream banks edge. Gravel bar vegetation types were located within the riparian area and appeared to be remnants of past stream channels. This vegetation type consisted of mostly cheatgrass (*Bromus tectorum* L.), and Canada bluegrass (*Poa comressa* L.).

Riparian vegetation types were located within the floodplain and currently, or (had) in the recent past, been influenced by water from Milk Creek. Riparian grass vegetation consisted of greater than 50 percent grass by weight (Porath et al. 2002). Riparian grass vegetation types consisted of Kentucky bluegrass (*Poa pratensis* L.), brome (*Bromus* spp.), meadow foxtail (*Alopecurus pratensis* L.), timothy (*Phleum pratense* L.), rushes (*Juncus* spp. L.), sedges (*Carex* spp. L.), and a variety of forbs. Riparian sedge/rush vegetation types were located within the riparian grass communities but were distinguished by greater than 50% sedges and (or) rushes by weight (Porath et al. 2002). The overstory of woody species bordering Milk Creek in the riparian area included hawthorn (*Crataegus douglasii* Lindl.), ponderosa pine (*Pinus ponderosa* Dougl.), snowberry (*Symphoricarpus albus* L.), black cottonwood (*Populus trichocarpa* T. & G.), and rose (*Rosa gymnocarpa* Nutt.).

Upland Vegetation

Upland vegetation types consisted of grasses including timothy, orchardgrass (*Dactylus glomerata* L.), needlegrass (*Stipa* spp. L.), brome, Idaho fescue (*Festuca idahoensis* Elmer), Kentucky bluegrass, pinegrass (*Calamagrostis rubescens* Buckl.) elk sedge (*Carex geyeri* Boott), a variety of forbs, and patches of shrubs including snowberry, spirea (*Spirea splendens* Baumann ex K. Koch), and ceanothus (*Ceanothus* spp. L.). Most of the upland sites had an overstory of ponderosa pine, though some areas were open, lacking a woody overstory.

Pasture Design

Nine pastures were stratified into 3 blocks based on vegetation type. Two treatments were randomly assigned to pastures within each block: 1) early summer grazing (mid-June to mid-July), and 2) late summer (mid-August to mid-September)

(Fig. 1). Each pasture within a block had similar proportions of the 4 vegetation types, with all cows having equal access to all portions of their assigned pasture.

Cattle

Fifty-two crossbred (Hereford x Angus) cow/calf pairs were randomly assigned to 1 of 3 blocks season of use⁻¹ year⁻¹. Cows used during the early summer trial were also used in the late summer grazing trial. In 1998, cows were all 2-year old primiparous heifers. In 1999, 49 cows were 2-year old primiparous heifers and 3 cows were 3 years old. All cows used in this study had previous exposure to similar grazing areas as yearling heifers. Cows averaged 420-kg at the beginning of the trial. Based on dry matter (DM) production estimates from previous years (Porath et al. 2002), pastures were stocked to achieve 50% relative herbaceous vegetation utilization (Frost et al. 1994) after 28-days of grazing, with resulting stocking density of 1.7 AU/ha.

Livestock Distribution and Behavior

Visual livestock observations and vibracorders were used to monitor hourly livestock distribution and grazing behavior patterns. Vibracorders were used to measure grazing times during each season of use and were placed on 6 randomly selected cows block⁻¹ observation period⁻¹ year⁻¹ for a total of 72 total vibracorder recordings. Vibracorder charts were read as minute's hour⁻¹ and hours day⁻¹ spent grazing during each season of use.

Visual observations during daylight hours (0600 to 1900 hours) were used to monitor cow location and activity throughout the day. Visual observations were collected during the second and third week of each season of use and were made hourly, for a total of 14 observations cow⁻¹ day⁻¹ pasture⁻¹. The number of daily observations averaged 252 early summer and 242 late summer in each pasture for a total of 23,744 individual livestock visual observations. Cow locations were recorded on aerial photos at each observation period by 3 observers, 1 observer block⁻¹. Large numbers were painted on both sides of each cow to facilitate individual cow identification. At each hourly observation, ambient air temperatures were recorded (n = 224). Livestock activities, (grazing, loafing/resting or drinking) were also recorded hourly during the visual observation period.

Vegetation Utilization and Stubble Height

Following procedures described by Pechanec and Pickard (1937), relative herbaceous vegetation utilization was measured at the end of each season of use, immediately following cattle removal. Vegetation utilization was ocularly estimated within 0.25-m² frames every 7.5-m beginning at Milk Creek in perpendicular directions on each of 6 equally spaced transects in each pasture, with a mean of 387 ocular utilization estimates collected per pasture. At each observation point a utilization class was assigned, (0 = 0 percent utilization, 1 = 1 to 25 percent utilization, 2 = 26 to 50 percent utilization, 3 = 51 to 75 percent utilization, and 4 = 76 to 100 percent utilization), remaining herbaceous stubble height measured and vegetation type recorded. The remaining herbaceous stubble height was measured by placing a ruler at the furthest edge of the 0.25 m² frame and measuring the height of the remaining forage to the nearest cm.

Given the complexity of measuring utilization (measuring what is no longer there), training exercises were conducted prior to each ocular utilization period with all 5 utilization classifications being equally represented during the training. Following a training class, each of 6 observers independently visually appraised ten, 0.25-m² clip plots, and assigned their estimate of utilization. These plots had previously been clipped and the removed vegetation weighed. After ocular estimates were taken the remaining standing vegetation was clipped to within 2-cm of the ground and weighed. The formula for determining actual utilization class was:

$$\text{Percent Utilization} = \frac{\text{initial clipped weight} \times 100}{(\text{initial clipped weight} + \text{final clipped weight})}$$

Observer estimates were then compared with actual utilization. Out of 156 total training estimates, only 1 was further than 1 utilization category from the actual. Observer bias was adjusted using the following regression equation which regressed estimated utilization against actual utilization: $Y = 0.77x + 0.42$ with $r^2 = 0.64$, and $P < 0.01$. The Y variable in the above equation is actual utilization and the X variable is estimated utilization. A utilization score of 1 corresponded to 13 percent utilization (halfway between 1 and 25 percent utilization) and a utilization score of 2 corresponded to 38%, 3 corresponded to 63% utilization, and 4 corresponded to 88% utilization. The regression equation

used to correct visual scores (0, 1, 2, 3, and 4) to estimated utilization percent was $Y = 22.6x - 4.8$ with $r^2 = 0.83$, with the Y variable being actual utilization score and the X variable being the estimated utilization score.

Fecal Deposits

Buckhouse and Gifford (1976) reported that a 1-month-old fecal deposit within 1-m of a stream significantly increased chances of impacting water quality following a high intensity simulated rainstorm, compared to fecal deposits beyond 1-m of a stream. It was easy to differentiate fresh from old feces because these pastures were grazed only during the 28-day trials each year. Based on this information, fresh fecal deposits located within 1-m of the stream's edge were counted on both sides of the stream in each pasture at the end of each grazing season.

Precipitation

Daily precipitation data were collected at the Eastern Oregon Agriculture Research Center's weather station (Union, Oregon) during the 2-year grazing study (Fig. 2).

Forage Nutrient Composition

At the end of the third week of each season of use, 20 randomly clipped plots were obtained from each grazed pasture. Ten, 0.25-m² plots were randomly collected from each riparian area and 10, 0.25-m² plots were randomly clipped from each upland area. Samples were dried at 60° C for 48 hours and composited according to vegetation type (riparian or upland) within each pasture. Composited samples were ground to pass a 1-mm screen in a Wiley mill and analyzed for DM, Kjeldahl nitrogen / crude protein (CP; AOAC 1990), acid detergent fiber (ADF; AOAC 1990 as modified by Komarek and Sirios 1993), neutral detergent fiber (NDF; Van Soest et al. 1991 as modified by Komarek 1993), lignin, and in situ dry matter disappearance (ISDMD).

Statistical Analysis

Time series data (time within day observations) were analyzed as a randomized complete block-repeated measures design using the GLM procedure of SAS (1990). Block was treated as the random variable in all GLM procedures, with pasture being the experimental unit and season of use and year being factors within the model. Main effects were delineated using season of use by block as the whole plot error

term. Time within day was considered the repeated variable. Interactions were tested using residual error (block interactions). Non-time series data (utilization, stubble height, fecal deposits, and precipitation) were analyzed as a randomized complete block design. This study was replicated over 2 years, 1998 and 1999. Treatment differences were delineated for all analysis using LSD procedures of SAS ($P < 0.05$). All percentage data were analyzed using the proc GLM procedures of SAS, and a normal probability plot was run for block, treatment and time and was determined to be normally distributed, thus no transformations were needed. In addition, ambient air temperature was regressed against livestock distance from the stream using standard linear regression techniques to describe the relationship of ambient air temperature to diurnal livestock distribution patterns.

Results and Discussion

Livestock Distribution and Behavior

Season of use affected livestock distribution patterns throughout the study. During early summer, cattle were consistently observed further from the stream at any given hour ($P < 0.01$) than during late summer, averaging 161 and 99-m respectively (Fig. 3). Cattle expressed diurnal distribution patterns in both early summer and late summer ($P < 0.01$; Fig. 3), with cattle being furthest away from the stream

in the early morning, and gradually moving closer to the riparian area as the day progressed.

Cows were observed closer to the stream when ambient air temperatures were higher (Figs. 3 and 4). Ambient air temperatures were highly correlated with livestock distances from the stream ($r^2 = 0.79$ and 0.90 early summer and late summer, respectively; $P < 0.01$). Ambient daytime air temperatures may have affected ($P < 0.01$) distribution patterns (Fig. 3) and grazing times (Fig. 5) of cows.

During early summer, cattle visited riparian areas during late morning hours, then either returned to the uplands, or remained around the riparian area during the heat of the day, later returning to the uplands around late-afternoon (Fig. 3). During late summer, cattle began the day away from the stream, but quickly moved closer to the riparian area during the morning hours, occupied the shady areas of the riparian area during the heat of the day, and gradually returned to the uplands around late afternoon (Fig. 3).

Vibracorder data revealed that season of use affected grazing activity of cattle ($P < 0.01$; Fig. 5). Cattle had distinct trimodal daily grazing patterns during both seasons of use, exhibiting definite peak grazing times during the morning, mid-day and evening. Although livestock grazing patterns exhibited a season of use x time of day interaction ($P < 0.01$), total daily grazing times did not differ between seasons ($P = 0.64$). Cattle grazed on average 584 minutes day⁻¹ during the early summer, and 574 minutes day⁻¹ during the late sum-

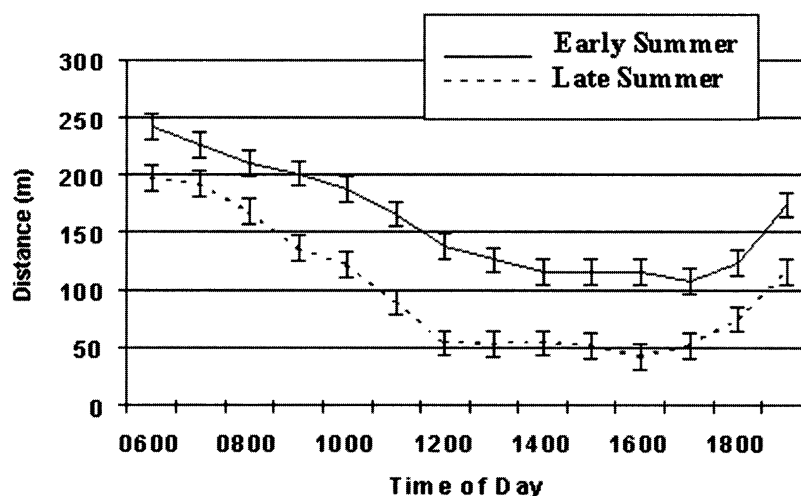


Fig. 3. Mean distance that cows were observed from the stream at hourly daylight intervals during early and late summer. Values are averaged over 1998 and 1999. Mean distances for early and late summer differed ($p < 0.01$) at all observed time periods. Bars on each value indicate standard errors. $N = 23,744$ cow observations.

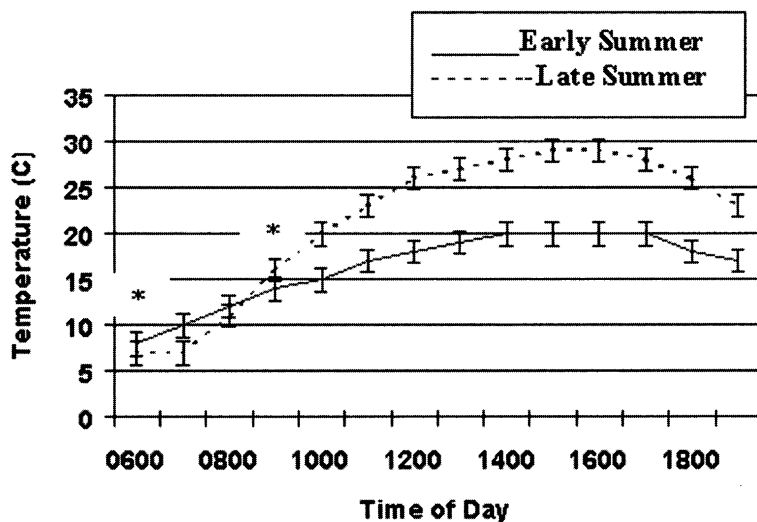


Fig. 4. Hourly ambient daylight temperatures during early and late summer. Values are averaged over 1998 and 1999. Values without an asterisk differ ($p < 0.01$). Bars indicate standard errors. $N = 224$ temperature recordings.

mer. However, cows grazed more ($P < 0.01$), from 0100-0300, 0700-0900, 1300-1400, and 1800-2000 hours during late summer than during early summer, and cows grazed less ($P < 0.01$) from 0400-0600, 1000-1200, and 1500-1600 hours during late summer than during early summer (Fig. 5). This seasonal difference in daily grazing activity is likely due to a difference in daylight hours coupled with a greater range of ambient air temperatures from morning until night in late summer.

Observational data showed that daylight cow activity, (grazing, loafing/resting, or

drinking), was not affected by season of use ($P > 0.05$). Grazing accounted for 65% of the time, loafing/resting accounted for 34% of the time, and drinking occupied only 1% of the daylight activities during both early and late summer grazing trials. Based on vibracorder data, cattle grazed approximately 40% of the entire day (24-hr period) (Fig. 5) during both early and late summer. Our vibracorder data parallels past vibracorder research by both Miner et al. (1992) and Sneva (1969) showing that very little grazing activity

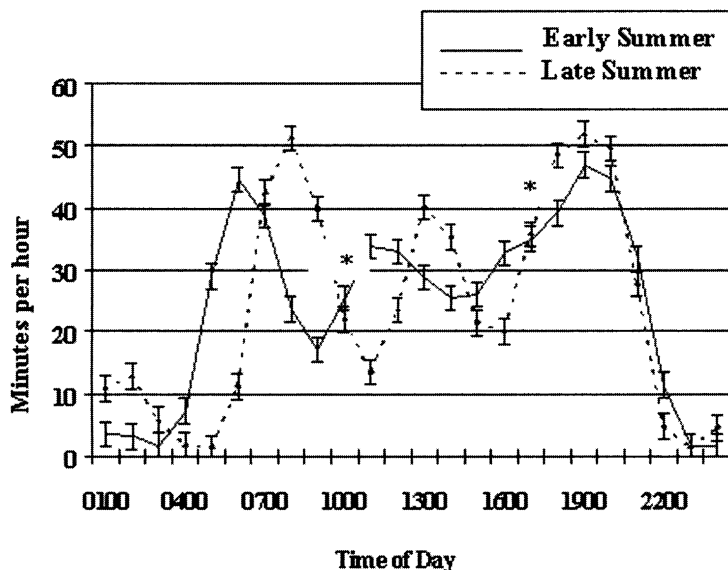


Fig. 5. Minutes per hour spent grazing during early and late summer. Values are averaged over 1998 and 1999. Sunrise for early and late summer occurred at 0500 and 0600 hours, respectively, with sunset occurring at 2100 and 1900 hours, respectively. Values without an asterisk differ ($P < 0.01$). Bars indicate standard errors. $N = 72$ vibracorder recordings.

occurs during the night. Our observations of livestock grazing patterns were very similar to previous work (Gillen et al. 1984, Howery et al. 1996, Porath et al. 2002). These researchers used the same or similar study sites and grazing seasons as our research.

The season of use \times time of day interaction was important ($P < 0.05$) for cattle use of various vegetation types (Fig. 6). In early summer, cattle spent the majority of their morning hours in upland vegetation types, gradually occupying riparian area vegetation types more frequently as the day progressed and hourly temperatures increased. During early summer, between the hours of 1230 until 1800 cattle spent nearly an equal proportion of time in upland and riparian vegetation types. Conversely, in late summer, cattle started out their day in upland vegetation types but rapidly moved into riparian vegetation types after 0800 hours. They spent the remainder of the day in the riparian vegetation types, gradually returning to upland vegetation types during the late evening hours.

Over 90% of the cow observations during late summer were in riparian areas from 1200 to 1700 hours. During early summer only 50 percent of observations were in riparian areas during the same time period (Fig. 6). Comparing the livestock observation data (Fig. 6) with the vibracorder data (Fig. 5) peak late summer mid-day grazing occurred from 1200 to 1400 hours, which was also the time of highest riparian area occupancy in late summer (Fig. 3). These data illustrate the potential for increased riparian vegetation utilization by cattle during the heat of the day in late summer.

Vegetation Utilization and Stubble Height

Vegetation utilization patterns differed between years (Table 1). During the 1998 early grazing season utilization levels in riparian and upland vegetation types averaged 31% and 37% use, respectively. Late summer utilization levels in riparian vegetation and upland vegetation averaged 42% and 34% use, respectively (Table 1). During the 1999 early grazing season utilization levels in riparian and upland vegetation types averaged 41% and 40% use, respectively. However, during the late summer grazing season riparian vegetation utilization was disproportionately higher 55% than upland vegetation utilization 34%. Thus, early summer grazing resulted in nearly equal utilization of upland and riparian vegetation types both years of the

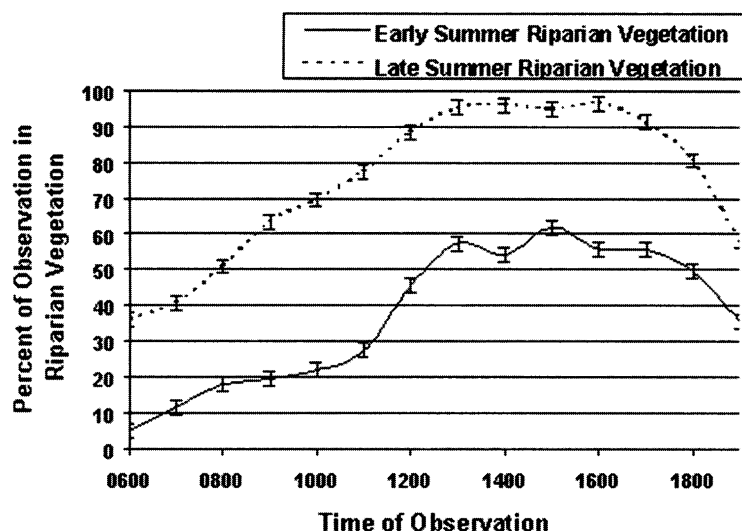


Fig. 6. Percent of livestock observations within riparian vegetation during early and late summer. Values are averaged over 1998 and 1999. All values within a time period differ at $p < 0.05$. Bars indicate the standard errors. $N = 23,744$ total observations.

study. This uniform use likely reflects more uniform livestock distribution during the early summer grazing period. During the late summer grazing period, the green line vegetation approached 60% use, compared to only 36% use during the early summer (Table 1), once again showing the increased potential for riparian area degradation in late summer.

Stubble height measurements differed between years ($P = 0.04$) and between seasons of use ($P = 0.01$), except for green line and gravel bar vegetation types ($P = 0.75$), but did not exhibit a season of use \times year interaction ($P = 0.81$), except for riparian grass ($P = 0.01$). Post grazing stubble height measurements closely followed our vegetation utilization estimates with increasing vegetation utilization

resulting in decreased stubble height. However, the magnitude of difference was less with the stubble height measurements, possibly due to the differing plant phenologies associated with early summer and late summer grazing seasons.

Forage Nutrient Composition and Quantity

Nutrient composition of available forage varied ($P < 0.01$; Table 2) between seasons of use with early summer forage having lower DM and fiber (ADF, NDF and lignin), and increased CP, and ISDMD compared with late summer forage. However, there was no difference ($P > 0.05$) between upland and riparian area forage composition within seasons. The lack of a difference in forage composition

between upland and riparian vegetation types could be due to random sampling. Free-ranging ungulates are more selective than can be simulated with randomly clipped samples (Van Dyne et al. 1980). The lack of a difference in forage composition does not preclude the potential for differences in actual cattle diets selected in riparian versus upland vegetation types.

As the grazing season progressed, ambient air temperatures increased and the herbaceous vegetation matured and senesced, leading to a decrease in forage quality and an increase in forage DM content. Past research has shown that vegetation quality and quantity play significant roles in determining distribution patterns of cattle. Marlow and Pogacnik (1986) reported differences in livestock distribution patterns due to physiological stage of vegetation, while Owens et al. (1991) listed grass quantity as a major influence of vegetation utilization. Forage quantity was similar ($P = 0.7$; Table 2) during early and late summer grazing seasons. Riparian areas had greater forage standing crop ($P < 0.05$) than uplands regardless of season (Table 2).

Water intake of a given class of cattle in a specific management regime is a function of dry matter intake and ambient air temperature (NRC 1996). Early summer ambient air temperatures averaged 16.4°C while late summer temperatures averaged 21.4°C . At these temperatures, a 450-kg lactating beef cow requires 55 and 64 liters of water daily in the early and late summer, respectively (NRC 1996). Assuming 2.5% of body weight intake and 40% forage DM (early summer), a 450-kg cow will consume 28-kg of forage. Of this 28-kg, 15.7-kg is water, providing 16.5 liters of required water day^{-1} , leaving 38.5 liters needed to meet the cow's daily water

Table 1. Influence of season of use on utilization and stubble height of upland and riparian vegetation measured immediately after cattle grazing during 1) early summer (mid-June to mid-July), and 2) late summer (mid-August to mid-September).

Utilization (%)	Vegetation Type	1998		1999		SE ¹	P-values		
		Early	Late	Early	Late		Year	Season	Season \times Year
Riparian Vegetation	Green Line	28	57	44	62	3.8	.01	.01	.05
	Gravel Bar	36	29	43	62	4.9	.01	.29	.01
	Grass	37	42	44	52	1.9	.01	.01	.16
	Sedge/Rush	22	38	33	44	2.5	.01	.01	.29
Upland Vegetation	Open	43	36	44	38	0.8	.02	.01	.54
	Covered	32	31	35	30	1.0	.12	.01	.03
Stubble Height (cm)									
Riparian Vegetation	Green Line	14	12	11	9	1.5	.04	.21	.81
	Gravel Bar	13	10	10	7	1.6	.01	.75	.09
	Grass	15	21	10	9	0.7	.01	.01	.01
	Sedge/Rush	33	26	21	17	2.1	.01	.01	.44
Upland Vegetation	Open	13	16	11	14	0.4	.01	.01	.49
	Covered	18	21	13	16	0.5	.01	.01	.77

¹SE = standard error ($n = 4,648$ total ocular utilization estimates).

Table 2. Effects of season of use and pasture vegetation classification on nutrient composition and quantity of forage averaged across 1998 and 1999.

Item	Early Summer		Late Summer		SE ⁴	P-values		
	Riparian	Upland	Riparian	Upland		Season	Vegetation	Season x Vegetation
Dry Matter %	42.9	40.7	68.2	70.3	3.57	.01	.97	.56
Neutral Detergent Fiber %	61.9	61.4	68.4	67.1	1.01	.01	.39	.74
Acid Detergent Fiber %	32.7	34.0	38.8	37.4	0.73	.01	.96	.11
Crude Protein %	8.2	7.4	4.5	4.2	0.22	.01	.06	.28
Lignin % ⁵	4.2	5.9	7.1	6.5	0.65	.04	.44	.13
ISDMD % ¹	49.1	50.4	42.4	42.9	0.85	.01	.35	.65
ISNDFD % ²	28.3	29.9	25.9	25.8	0.68	.01	.27	.25
Forage Quantity ³ (kg/ha)	1654	972	1726	1065	239	.74	.03	.97

Treatment= early summer (mid-June to mid-July), and late summer (mid-August to mid-September). Vegetation = vegetation site (riparian or upland). ¹ISDMD = In situ dry matter disappearance. ²ISNDFD = In situ neutral detergent fiber disappearance.

³Forage Quantity = random clipped plots mid way through grazing season (kg/ha). ⁴SE = standard error (n = 240 total clipped plots).

requirement. During late summer grazing with increased ambient air temperatures and increased forage DM, the same 450-kg lactating beef cow requires 64 liters of water (NRC 1996) and, due to higher forage DM (70%), the forage is providing only 4.7 liters, leaving 59.3 liters of water she must obtain from the stream or off-stream water sources. Therefore, cattle must utilize the stream for most of their daily-required water during late summer grazing. Additionally, declining forage quality during late summer can increase the amount of heat produced from microbial fermentation in the rumen, which may increase dependence on water for thermoregulation (NRC 1981).

Fecal Deposits

Fresh fecal deposits within 1-m of the stream were similar ($P = 0.13$) averaging 13 early summer and 28 late summer (Fig. 7). Because fecal deposits within 1-m of the stream's edge can negatively impact water quality (Buckhouse and Gifford 1976) pastures grazed in late summer may

have a higher potential of negatively impacting water quality than pastures grazed early summer. However, this may only be true if a high intensity rainstorm is experienced during grazing or up to 1 month post-grazing (Buckhouse and Gifford 1976).

Precipitation

The dramatic difference in annual precipitation could have a major impact on forage quality and quantity and possibly affect livestock distribution and vegetation utilization patterns. Timing of precipitation can also impact forage quality and quantity.

Management Implications

Early summer grazing of riparian areas altered cow-calf grazing distribution and forage utilization patterns in the foothill rangelands of the Wallowa Mountains compared to late summer grazing. During early summer, when forage quantity and quality were not limiting and ambient air temperatures were low, livestock distribu-

tion patterns were more evenly distributed and vegetation utilization patterns more uniform. During late summer, ambient air temperatures and forage DM increased, and livestock distance from the stream decreased. Early summer grazing of riparian areas may be less detrimental to riparian areas because of improved livestock distribution and more uniform vegetation use. Furthermore, by grazing the riparian areas early a manager is providing the potential for riparian vegetation regrowth (Elmore and Kauffman, 1994). During late summer grazing, management practices such as offstream water developments, herding cattle out of riparian areas during the heat of the day, and providing alternative shade sources may achieve more uniform cattle distribution and vegetation utilization patterns.

While these are potential management alternatives, managers must remain aware of the forces in a particular system that are driving livestock distribution patterns in a particular system and implement decisions accordingly. Rangelands and riparian areas are dynamic systems and are constantly changing, thus making management decisions a daily activity. This variability necessitates the need for adaptive management and monitoring aimed at meeting a variety of goals (e.g., environmental, ranch, and economic). Continued, focused research is needed to obtain a better understanding of the interactions between grazing animals and rangeland systems.

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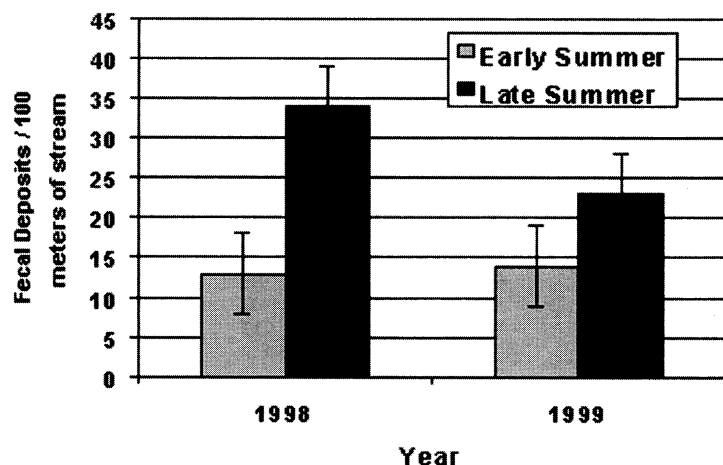


Fig. 7. Number of fresh fecal deposits within 1-m of stream in pastures grazed during early and late summer. Data did not differ within years ($P = 0.13$). Bars indicate standard errors. N = 673 total fecal deposits.

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Impacts of tracked vehicles on sediment from a desert soil

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Abstract

Off-road military vehicle traffic is a major consideration in the management of military lands. The objective of this study was to determine the impacts of military tracked M1A1 heavy combat tank vehicles on sediment loss from runoff, surface plant cover, and surface microtopography in a desert military training environment. A randomized block design was used which had 10 blocks with 4 plots (0.5 m²) in each block. Each block had randomly selected treatments that included an untreated control, 1 pass by a M1A1 tank under wet seasonal conditions, 3 passes by a M1A1 tank under wet seasonal conditions, 1 pass by a M1A1 tank under dry seasonal conditions, and 3 passes by a M1A1 tank under dry seasonal conditions. Data were analyzed using mean separation and stepwise regression techniques. Most sample periods showed that sediment losses from M1A1 tank treatments, single or triple passes under wet or dry seasonal conditions, did not differ statistically from natural sediment losses under nominal rainfall events. However, comparatively intense rainfall events often generated significantly ($P < 0.05$) greater sediment losses from the M1A1 tank triple pass treatments. Triple pass M1A1 tank impacts had detrimental effects that could last many years, particularly when disturbances were imposed under dry seasonal conditions. Seasonal drought for the area, occurring 2 out of 3 years during the study period, may have exacerbated the effects of triple pass M1A1 tank impacts. Analysis showed that grass cover, litter cover, and microtopographic variance were highly and negatively correlated ($R = -0.62$) with cumulative sediment loss. Depending on precipitation availability, a minimum of 3 years for most triple pass M1A1 tank impacts is suggested for suitable vegetation recovery and soil stability. It is recommended that site repetitious M1A1 tank training maneuvers should be conducted with particular attention to site recovery. Furthermore, the influence of climate, drought in particular, should be among the topics addressed by future military training land use models.

Key Words: military land, soil stability, site recovery, seasonal drought

Management of military lands has historically, and logically, prioritized weapons testing and combat readiness over soil and water conservation. However, attention to environmental concerns and the National Environmental Policy Act (NEPA) is becoming increasingly prevalent on military reservations. Off-

Resumen

El tráfico de vehículos militares fuera de los caminos (en campo traviesa) es una consideración importante en el manejo de los terrenos militares. El objetivo de este estudio fue determinar los impactos de los pesados tanques de combate M1A1 en las pérdidas de sedimento en el escurrimiento, en la cobertura vegetal de la superficie y en la microtopografía de un ambiente desértico de entrenamiento militar. Se usó un diseño de bloques completos al azar el cual tenía 10 bloques con 4 parcelas (0.5 m²) en cada bloque. Cada bloque tenía tratamientos asignados aleatoriamente que incluyeron un control sin tratamiento, 1 paso de tanque M1A1 bajo condiciones de estación húmeda, 3 pasos de M1A1 bajo condiciones de estación húmeda, 1 paso del tanque M1A1 en condiciones de estación seca y 3 pasos de M1A1 bajo condiciones de estación seca. Los datos fueron analizados usando técnicas de separación de medias y regresión. La mayoría de los periodos de muestreo mostraron que pérdidas de sedimento en los tratamientos del Tanque M1A1, uno o tres pasos, bajo condiciones de estación húmeda o seca, no difieren estadísticamente de las pérdidas naturales que ocurren en los eventos nominales de lluvia. Sin embargo, los eventos de lluvia intensa a menudo generaron una pérdida de sedimento significativamente mayor ($P < 0.05$) en los tratamientos de tres pasos de tanque M1A1. El paso triple de los tanques tuvo efectos detrimentales que pudieran durar muchos años, particularmente cuando los disturbios ocurrieron bajo condiciones de estación seca. La sequía estacional del área que ocurrió 2 de los 3 años del periodo de estudio pudo haber exacerbado los efectos del paso triple de los tanques M1A1. El análisis mostró que la cobertura de zacate y mantillo y la varianza microtopográfica estuvieron alta y negativamente correlacionados ($R = -0.62$) con la pérdida acumulativa de sedimento. Dependiendo de la disponibilidad de lluvia, se sugiere que se requiere un mínimo de 3 años para una recuperación adecuada de la vegetación y estabilidad del suelo después de un paso triple de tanques M1A1. Se recomienda que las maniobras de entrenamiento de los tanques M1A1 repetitivas en un sitio deben conducirse poniendo particular atención en la recuperación del sitio. Mas aun, la influencia del clima, en particular la sequía, debe ser uno de los temas que deben abordarse en modelos futuros de uso de la tierra para entrenamiento militar.

road military vehicle traffic is a major consideration in the management of military lands (Severinghaus et al. 1979, Johnson 1982, Goran et al. 1983, Braunack 1986, Shaw and Diersing 1990, Diersing et al. 1990). Although formalized research may not be necessary to establish that damage does occur as a result of

off-road vehicle traffic, quantified estimates of damage, specifically soil erosion, in response to variables such as soil type, precipitation, vegetation, soil surface microtopography, as well as kind and intensity of off-road vehicle traffic can provide a basis for managerial decisions. Military land managers are expected to maintain the natural resources, while military trainers are obligated to provide a realistic training experience (Diersing et al. 1990). A limited amount of information concerning off-road vehicle impacts is available from research on the effects of soil disturbance on the hydrological properties of agricultural (Van Doren 1959), forested lands (Moehring and Rawls 1970) and recreational lands (Eckert et al. 1979, Webb et al. 1983). However, information for site specific effects, military lands in particular, is slight. In 1974, Lathrop (1983) examined recovery since 1953 of Mojave Desert lands in California that had been impacted by military training from 1938 to 1942.

As the frequency and intensity of military training increases and the soil surface becomes further disturbed, the protective vegetation may be lost and soil erosion accelerated (Warren et al. 1991). If soil erosion is not monitored and management is not adjusted accordingly, extensive damage from gullying, sedimentation, and flooding may occur. This kind of damage is not only expensive to repair, but also diminishes the training realism and long-term use of military lands, as well as possibly jeopardizing the safety of soldiers and equipment. Military training exercises and associated off-road vehicle traffic are necessary to maintain combat readiness; therefore, attention to landscape training areas and associated soil erosion is necessary to implement effective and sustainable land management. The interrelationships between site soil and vegetation variables and the hydrologic impacts of tracked vehicle training exercises are often not considered by many military land managers.

The use of military tracked vehicles has been documented as particularly destructive of landscapes in military maneuvers (Goran et al. 1983, Braunack 1986, Shaw and Diersing 1990), primarily because military training exercises are generally not conducted with regard to landscape suitability (Diersing et al. 1990), but also because tracked vehicle track treads are inherently aggressive. Tracked vehicles are especially damaging to soil surfaces when the vehicle turns sharply (McKeys et al. 1980) because tracked vehicles require

the track tread associated with the direction the vehicle is turning to stop or slow considerably, while the opposing tread propels the vehicle in the desired direction. This results in a skidding effect of the stationary track tread on the soil surface that crushes and uproots vegetation and compacts the soil (Prose et al. 1987, Diersing et al. 1990). The collapsed pore structure of the soil slows water infiltration, increases runoff, and may result in poor soil aeration which can inhibit recovery of the vegetation. Fragile landscapes can be disrupted for decades by a single tracked vehicle pass (Prose and Metzger 1985, Wilshire 1991).

Materials and Methods

Site Description

The study was conducted during 1994, 1995, and 1996 on the New Mexico portion of the Fort Bliss Military Reservation, within the McGregor Guided Missile Range of the Tularosa Basin. This area is about 160 km west of Las Cruces, N. M., at latitude N 32° 11.515 and longitude W 105° 54.184. The site is characterized by rolling hills at 1,219 m elevation with a southeastern exposure and slopes range from 5 to 20%. The site contains Lozier series soils of the loamy-skeletal, carbonatic, thermic Lithic Calciorthid family. Typically, the surface layer is 18 cm thick. The substratum is very gravelly loam and very gravelly silty clay loam, generally 20 cm thick with a preponderance of lime. Unweathered limestone bedrock is at a depth of about 38 cm. This soil is strongly calcareous throughout and moderately alkaline. Permeability is moderate. Available water capacity is very low, but the soil receives extra water as run-on from the limestone outcrop. This run-on has accelerated erosion on parts of the area. The area is a desert grassland comprised primarily of black grama (*Bouteloua eriopoda* Torr.) and dropseeds (*Sporobolus* spp.) with scattered yucca (*Yucca* spp.) and creosote (*Larrea tridentata* Cav.). The area climate is typical of the Tularosa Basin, where high intensity, low frequency, convectional rainstorms deposit the majority of moisture in the summer months of July, August, and September. The average annual precipitation is 203 mm, and mean annual temperature ranges from 14 to 17° C. The freeze-free period averages 7 months (~219 days), from early April to early November. Because precipitation is gener-

ally low for the area, 80% of possible hours are occupied as sunshine, potential evapotranspiration usually approaches 2,540 mm year⁻¹, and relative humidity is typically no more than 65% in the early morning of the rainy season, rather dry soil moisture conditions persist (Derr 1981). Compounding the natural aridity of the area is strong wind, predominantly from the west or southwest in the spring. During the study, a seasonal drought characterized the basin climate with a preponderance of especially dry, windy conditions in April and May 1995 and 1996.

Treatments and Sampling

The study utilized a randomized block design with 2 areas chosen as replicates. The areas were chosen for similarity in slope (~5%). Each replicate area was randomly divided into several areas to be treated. Each area to be treated was called a pass by soil moisture condition plot. Pass referred to the number of vehicle passes across a plot, and soil moisture condition was either dry (late spring) or wet (late summer). Tank treatments were applied at the end of October 1994 (wet soil conditions), and tank treatments were applied at the end of March 1995 (dry soil conditions), i.e. 1 pass wet, 3 passes wet, 1 pass dry, and 3 passes dry. The military tracked vehicle used in this study was an M1A1 heavy combat tank. This tank weighs 58 metric tons (unarmed) and applies approximately 9,211 kg m⁻² of standing ground pressure on the soil surface. Application of the tank treatments and spatial randomization was conducted under the direction of the U.S. Army's Environmental Division at Fort Bliss.

On each pass by season treatment within a replicate, 4 runoff plots (0.5 x 1.0 m) were located. The plots were numbered 1 through 4 from the treatment area most downslope to the most upward, respectively. There were 8 plots per treatment resulting in 32 treated plots at the study site. Eight additional plots were installed, left untreated, and designated as control plots, resulting in a total of 40 plots. Plots were installed immediately after vehicle treatments and left for future evaluations (Eckert et al. 1979). Plots were constructed of sheet metal to form a 100 mm high border around the sides and top of the plot, and a runoff tray with a cover was placed on the downslope end of the plot. A hose was routed from the downslope end of the runoff tray to a sediment collection bucket buried outside the plot. Event rainfall was measured using a calibrated, Texas Electronics model 525 tipping-bucket rain

Sediment, surface microtopography, and surface vegetation cover data were subjected to statistical analysis to determine normality. The means of plot characteristics were compared with an analysis of variance and mean separation test (Least Significant Difference) at the 0.05, 0.10, and 0.20 levels of probability. Sediment loss was identified as a dependent variable, and soil surface microtopography and surface vegetation cover as independent variables. Stepwise regression was used to assess probable association of variables.

Figure 1 indicates weekly precipitation totals for 1994, 1995, and 1996 at the study site. Yearly totals were 192, 213, and 204 mm for 1994, 1995, and 1996, respectively. Although there is not much difference in the annual totals for all 3 years, there is considerable variation among years of those weeks where precipitation is concentrated. Weekly precipitation for 1994 indicated a comparatively even distribution of moisture, whereas 1995 and 1996 were characterized by especially wet periods late in summer and

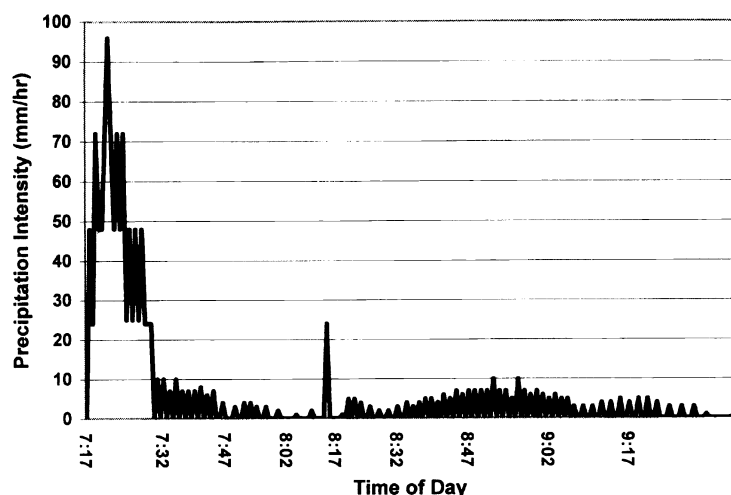


Fig. 2. Measured rainfall intensity for a select event of 2 hours and 34 min (morning of 30 June 1995) with a total rainfall of 17 mm and a maximum intensity of 96 mm/hr at the study site.

runoff as several years of average runoff (Osborn and Renard 1969). Figure 2 depicts a simple pluviograph for a storm event occurring in late June 1995 at the study site that was among the most intense rainfall events that occurred during the study period. The intensity, volume, and timing of these events created considerable potential to produce runoff and subsequent sediment transport. The absence of sunlight and subsequent lowering of radiant energy to the soil surface, as well as associated lower temperatures, would tend to minimize immediate evaporation (Penman 1948). These events were also significant because they immediately followed the spring drought period of 1995. However, large concentrations of precipitation are not unknown to this area. For example, nearby La Luz, N.M. received 165 mm on 29 June 1950 (Derr 1981).

Cumulative Sediment Loss

Sediment is the product of the erosion process, which is usually defined as the detachment and transport of soil material on the earth surface (Brooks et al. 1991). Sediment loss occurs coincident with and as a consequence of almost immediately to intense rainfall events (Smith and Olyphant 1994). The correlation between sediment yield and precipitation is improved if the seasonality of precipitation is considered (Cooke et al. 1993). Erosion rates tend to be higher in areas of seasonal rainfall such as northeast Queensland, Australia, where the erosive impacts of intense storms is increased because the vegetation is relatively sparse because of the annual dry season (Douglas 1967).

Cumulative sediment loss and site precipitation data were compiled for the wet

season treatments sampling periods of 5 November 1994 through 20 September 1996, and for the dry season treatments sampling periods of 23 June 1995 through 20 September 1996.

The wet season treatments cumulative sediment loss (Table 1) indicates 2 general leveling periods among all treatments. The first of these occurred from 25 August

1995 to 2 July 1996. The second occurred at the end of the sampling periods, from 28 August to 20 September 1996 and was dominated by the triple pass tank treatments at 12,970 kg ha⁻¹ total sediment. Total cumulative sediment for controls was slightly less at 11,347 kg ha⁻¹. Mean separation tests indicate that the difference between the cumulative total on 20 September 1996 for triple pass tank treatments and controls is not significant, even at the 0.20 level of probability. The most dramatic increase in sediment loss for wet season treatments and all respective sampling periods occurred on the 7 July 1995 sampling date. Control, single pass, and triple pass treatments experienced cumulative sediment loss increases of 180%, 153%, and 154%, respectively, during this period. Not surprisingly, these increases immediately follow the storm event discussed earlier (Fig. 2).

Dry season treatments' cumulative sediment loss (Table 2) indicated similar leveling periods as those of wet season losses, although the rate of erosion following dry season single and triple pass impacts was somewhat greater. The most substantial dry season treatments' total cumulative sediment losses at the end of the sam-

Table 1. Wet season treatments cumulative sediment loss and associated maximum daily precipitation.

Sample period	Total ppt. since last sample	Days with ppt.	Max. daily ppt.	Cumulative sediment loss**		
				Control	1 pass	3 pass
	(mm)	(No.)	(mm)	------(kg/ha)-----		
5/11/94	9.1*	1	9.1	330.3	344.3	514.8
25/11/94	26.1	7	11.6	401.3	369.6	582.6
16/12/94	19.7	4	10.6	460.3a	405.5a	711.6b
11/1/95	22.2	9	10.3	560.5a	513.5a	941.4b
17/2/95	27.7	10	9.3	716.0a	601.5a	1,147.4b
22/3/95	9.7	6	3.1	827.5a	714.3a	1,315.9b
23/5/95	1.5	6	0.6	955.3a	772.3a	1,440.1b
23/6/95	18.9	4	12.1	1,270.8a	1,392.5a	2,115.1b
29/6/95	15.4	3	9.7	1,682.8a	1,730.5a	2,512.9b
7/7/95	28.4	1	28.4	2,990.5ab	2,642.5a	3,863.1b
21/7/95	35.9	5	12.7	3,317.3ab	3,078.5a	4,099.6b
27/7/95	15.0	1	15.0	4,891.3	4,365.0	4,954.0
10/8/95	16.2	4	7.0	5,090.3	4,560.5	5,207.9
17/8/95	10.8	4	4.9	5,209.5	4,776.5	5,394.1
25/8/95	13.1	2	12.7	7,239.3	6,076.8	7,303.9
11/9/95	6.4	6	2.8	7,379.0	6,218.0	7,437.0
21/9/95	4.1	7	2.0	7,436.3	6,307.3	7,536.9
26/6/96	33.4	9	11.3	7,697.0	6,615.0	7,819.0
2/7/96	8.2	3	6.1	7,817.0	6,793.0	8,024.0
12/7/96	12.9	3	5.9	9,510.0	9,063.0	10,505.0
19/7/96	28.8	4	16.8	10,141.0	9,618.0	11,262.0
2/8/96	28.0	5	13.8	10,351.0	10,119.0	11,818.0
28/8/96	46.9	11	12.6	11,185.0	10,589.0	12,798.0
4/9/96	7.0	3	4.8	11,318.0	10,658.0	12,927.0
20/9/96	15.5	4	14.7	11,347.0	10,681.0	12,970.0

*Precipitation received through 10 days prior to the first sample period.

**Means followed by the same letter within a sample period are not significantly different at the 10% level of probability; absence of letters indicates no significant differences.

Table 2. Dry season treatments cumulative sediment loss and associated maximum daily precipitation.

Sample period	Total ppt. since last sample	Days with ppt.	Max. daily ppt.	Cumulative sediment loss**		
				Control	1 pass	3 pass
	(mm)	(No.)	(mm)	----- (kg/ha) -----		
5/11/94	18.9*	4	12.1	315.5a	458.0ab	581.2b
29/6/95	15.4	9.7	727.5a	1,116.2b	1429.2c	
7/7/95	28.4	1	28.4	2,035.3a	2,115.9a	3,390.7b
21/7/95	35.9	5	12.7	2,362.1a	2,703.7a	3,856.2b
27/7/95	15.0	1	15.0	3,936.0a	3,987.0ab	5,026.3b
10/8/95	16.2	4	7.0	4,135.0	4,142.2	5,247.5
17/8/95	10.8	4	4.9	4,254.3a	4,327.0a	5,496.8b
25/8/95	13.1	2	12.7	6,284.0	5,504.1	6,652.8
11/9/95	6.4	6	2.8	6,423.8	5,638.6	6,832.0
21/9/95	4.1	7	2.0	6,481.0	5,732.4	6,936.5
26/6/96	33.4	9	11.3	6,742.0	5,966.0	7,374.0
2/7/96	8.2	3	6.1	6,862.0	6,218.0	7,722.0
12/7/96	12.9	3	5.9	8,555.0a	8,464.0a	13,971.0b
19/7/96	28.8	4	16.8	9,186.0a	9,227.0a	14,583.0b
2/8/96	28.0	5	13.8	9,396.0a	9,716.0a	15,147.0b
28/8/96	46.9	11	12.6	10,230.0a	10,332.0a	15,980.0b
4/9/96	7.0	3	4.8	10,363.0a	10,609.0a	16,173.0b
20/9/96	15.5	4	14.7	10,392.0a	10,661.0a	16,264.0b

*Precipitation received through 10 days prior to the first sample period..

**Means followed by the same letter within a sample period are not significantly different at the 10% level of probability; absence of letters indicates no significant differences.

pling periods were associated with triple pass tank treatments at 16,264 kg ha⁻¹. Control and single pass treatment total cumulative losses were essentially identical and statistically similar at 10,392 and 10,661 kg ha⁻¹, respectively, even at the 0.20 level of probability. Cumulative sediment losses for triple pass tank treatments were significantly greater ($P < 0.05$) than control or single pass treatments from 12 July 1996 through the final 20 September 1996 sampling period. Other researchers have reported similar findings under dry conditions. For example, Wilcox and Wood (1986) found that sediment loss was greater in dry areas, regardless of slope.

Like wet season results, the most dramatic increase in sediment loss for dry season treatments occurred on the 7 July 1995 sampling date. Control, single pass, and triple pass treatments experienced cumulative sediment loss increases of 280%, 190%, and 240%, respectively, during this period. The control (no disturbance) response to the exceptional storm events in late June 1995 (Fig. 2) was greater than single or triple pass treatments, regardless of season. This suggests that timing and intensity of precipitation, as well as antecedent soil moisture conditions, may have had a greater influence on the Lozier soil series and associated sediment loss at this site than the impact of 1 or 3 pass M1A1 tank disturbances. However, as stated by Parsons et al. (1994), there may be no specific temporal

pattern to the soil detachment process controlling sediment loss in runoff, thereby suggesting that different temporal patterns of sediment loss can be found even from the same location on different occasions. In contrast, Hairsine and Rose (1992) reported that sediment loss can fluctuate with time between an upper transport limit reflecting the ability of runoff to carry sediment, and a lower source limit that depends on the soil surface strength or resistance to removal of soil by runoff. Therefore, it seems plausible that even a single pass by an M1A1 tank, an infantry foot soldier, or a naturally occurring grazing herbivore would all have some deflation impact on the soil surface and thereby lower the soil surface strength or resistance to removal of soil by runoff, but the impacts are probably temporary.

Derr (1981) estimated that a Lozier soil series in this area can sustain an average maximum rate of 2,242 kg ha⁻¹ yr⁻¹ of sediment loss without reducing environmental quality. Measured losses for control treatments (no disturbance) during the study period averaged 7,192 kg ha⁻¹ yr⁻¹. Measured losses for wet season treatments during the study period averaged 6,085 and 7,437 kg ha⁻¹ yr⁻¹ for single and triple pass treatments, respectively. Measured losses for dry season treatments during the study period averaged 6,056 and 8,053 kg ha⁻¹ yr⁻¹ for single and triple pass treatments, respectively. The average annual

sediment losses from control treatments during the study period were 3.2 times greater than the tolerance estimate (T-value) provided by Derr (1981). Assuming that Derr's estimate was even remotely accurate, then further consideration should be given to the earlier suggestion that timing and intensity of precipitation, as well as antecedent soil moisture conditions, may have far greater implications on sediment loss in the Lozier soil series at this site than the impact of 1 or 3 pass M1A1 tank disturbances. However, T-value provided by Derr (1981) in the soil survey for the study site is among a family of estimates generally criticized as being somewhat arbitrary, reflecting societal and political views rather than science (McCormack et al. 1979). For example, Wight and Siddoway (1981) stated that T-values for rangelands may be a concept with only an idealistic application.

Although observance of seasonal drought and variable precipitation during the study period may provide some merit in accepting the reported levels of sediment loss, particularly in the absence of disturbance, it should be noted that precipitation has historically varied greatly from year to year and from month to month in the study area. For example, Derr (1981) reported that at nearby Orogrande, N.M., 573 mm of precipitation fell in 1905 and 75 mm fell in 1934. At nearby Tularosa, N.M., 249 mm fell in September 1941 and none in September 1918. The consideration of variable climates' contribution to soil erosion is certainly not new. Langbein and Schumm (1958) suggest that the variation in sediment yield with climate can be explained by the balancing of 2 opposing forces, each related to precipitation. The erosive influence of precipitation increases with its amount through its direct impact in eroding soil and in generating runoff with further capacity for erosion and transportation. Opposing this influence is the effect of vegetation, which tends to increase in surface area cover with increasing annual precipitation.

Surface Vegetation Cover

Plant cover is an important variable in water distribution on rangelands for 3 primary reasons. First, plants intercept raindrops, thereby reducing surface sealing and soil detachment by raindrops (Wood et al. 1998). Second, plant stems and litter increase surface roughness and hydraulic resistance, decreasing surface runoff velocity (Wood et al. 1994). Third, plant roots bind soil and diminish soil erodibility (Wischmeier and Smith 1978, Lee

1980, Branson et al. 1981, Thompson and James 1985, Abrahams et al. 1988, Johnson and Gordon 1988, Brooks et al. 1991, Thurow 1991, Satterlund and Adams 1992). In amenable contrast, however, Rogers and Schumm (1991) suggest that plant cover influences on runoff and sediment loss may be both positive and negative. In their view, vegetation results in the disruption of overland flow, and flow across a surface can be both concentrated, as well as deflected and dispersed by individual vegetation obstructions. Deflection reduces velocity, which reduces the erosive ability of flow, whereas concentration of flow increases velocity and depth which causes quicker initiation of erosion and deeper scour of rills on surfaces with low ground cover. Mean surface vegetation cover is reported as a percentage of the components grass, forb, shrub, litter, total plant, rock, and bare ground of the total plot area at each sample date for each treatment.

Grass cover is considered among the most effective agents in promoting soil stability because the fine, adventitious grass root tissues cover an extensive subsurface area relative to the area of the grass crown and tend to secure soil particles (Wischmeier and Smith 1978). Measurement of grass cover revealed low percentages (Table 3). The 4 November 1995 sample period produced the lowest cover values for all treatments, coinciding with little or no precipitation. Vegetation cover is a particularly useful measurement tool for perennial species as it responds more acutely to seasonal climatic fluctuation (particularly drought) than density measurements (Bonham 1989). Despite the recorded seasonal aridity among all sample periods, the control plots produced appreciable mean grass cover. Table 3 indicates that all other treatment means are significantly less ($P > 0.20$) than control means under wet and dry season condition treatments at every sampling period. The triple pass tank (dry) treatments produced less mean grass cover ($P > 0.20$) than single pass (dry) treatments at every sampling period. The final sample period revealed mean control grass cover at 21% (dry) and 21% (wet) and single pass tank (wet) and single pass tank (dry) treatments at 13 and 13%, respectively, each not significantly different from the control at the 0.05 level of probability.

As a percentage of plot area, mean forb cover was comparatively scarce ranging from 0 to just over 3 % (Table 4). Tall, slender stems tend to make forbs less effective in preventing sediment loss

Table 3. Mean grass cover at several sampling periods and significant differences at several levels of probability with wet and dry season treatments.

Treatment	Mean	Level of probability		
	(%)*	0.05	0.10	0.20
Date: 28/3/95				
Control	14.50	a	a	a
Tank 1 Pass Dry	8.52	b	b	b
Tank 3 Pass Dry	2.08	c	c	c
Date: 4/11/95				
Control	10.21a	a	a	
Tank 1 Pass Dry	4.91	b	b	b
Tank 3 Pass Dry	1.70	b	b	c
Date: 26/10/9				
Contro	21.02	a	a	a
Tank 1 Pass Dry	13.46	ab	b	b
Tank 3 Pass Dr	6.64	b	b	c
Date: 28/3/95				
Control	14.41	a	a	a
Tank 1Pass Wet	8.71	b	b	b
Tank 3 Pass Wet	3.59	c	c	c
Date: 4/11/95				
Control	10.21	a	a	a
Tank 1 Pass Wet	2.26	b	b	b
Tank 1 Pass Wet	3.21	b	b	b
Date: 26/10/96				
Control	21.05	a	a	a
Tank 1 Pass Wet	13.44	ab	b	b
Tank 1 Pass Wet	7.59	b	b	c

*Means followed by the same letter within a sample date and probability level are not significantly different.

Table 4. Mean forb cover at several sampling periods and significant differences at several levels of probability with wet and dry season treatments.

Treatment	Mean	Level of probability		
	(%)*	<u>0.05</u>	<u>0.10</u>	<u>0.20</u>
Date: 28/3/95				
Control	0	-	-	-
Tank 1 Pass Dry	0	-	-	-
Tank 3 Pass Dry	0	-	-	-
Date: 4/11/95				
Control	0.75	a	a	a
Tank 1 Pass Dry	0.94	a	a	a
Tank 3 Pass Dry	1.70	a	a	a
Date: 26/10/96				
Control	0.19	a	a	a
Tank 1 Pass Dry	0.75	a	a	a
Tank 3 Pass Dry	0.75	a	a	a
Date: 28/3/95				
Control	0	-	-	-
Tank 1 Pass Wet	0	-	-	-
Tank 3 Pass Wet	0	-	-	-
Date: 4/11/95				
Control	0.75	a	a	b
Tank 1 Pass Wet	2.65	a	a	ab
Tank 3 Pass Wet	2.84	a	a	a
Date: 26/10/96				
Control	0.19	b	b	b
Tank 1 Pass Wet	3.02	a	a	a
Tank 3 Pass Wet	2	a	a	a

*Means followed by the same letter within a sample date and probability level are not significantly different.

Table 5. Mean shrub cover at several sampling periods and significant differences at several levels of probability with wet and dry season treatments.

Treatment	Mean (%)*	Level of probability		
		0.05	0.10	0.20
Date: 28/3/95				
Control 0	-	-	-	-
Tank 1 Pass Dry	0	-	-	-
Tank 3 Pass Dry	0	-	-	-
Date: 4/11/95				
Control 0	-	-	-	-
Tank 1 Pass Dry	0	-	-	-
Tank 3 Pass Dry	0	-	-	-
Date: 26/10/96				
Control 0	-	-	-	-
Tank 1 Pass Dry	0	-	-	-
Tank 3 Pass Dry	0	-	-	-
Date: 28/03/95				
Control 0	b	b	b	
Tank 1 Pass Wet	0	b	b	a
Tank 3 Pass Wet	0.88	a	a	a
Date: 4/11/95				
Control 0	-	-	-	-
Tank 1 Pass Wet	0	-	-	-
Tank 3 Pass Wet	0	-	-	-
Date: 26/10/96				
Control 0	a	b	b	
Tank 1 Pass Wet	0	a	b	b
Tank 3 Pass Wet	0.75	a	a	a

*Means followed by the same letter within a sample date and probability level are not significantly different.

through raindrop interception, as well as poor soil stabilization due to less extensive root development. Forbs were generally only seen during the study period as occupying tank impacts associated with the study. Since many of the forbs in the study area are annuals, dependence upon yearly germination of seed is vital for survival. Forbs are largely opportunistic, frequently taking root in soil conditions conducive to growth. Such conditions are often disturbed areas, like the tank treatments of this study. With the exception of control plots compared with wet season results at the 4 November 1995 and 26 October 1996 sample dates, no significant differences ($P > 0.20$) of mean forb cover were found between any treatments or sampling periods. Mean forb cover was highest on single pass tank (wet) treatments of 3.02% at the final, 26 October 1996 sample period.

Mean shrub cover was lower (<1% for all treatments) than forb cover (Table 5). The highest shrub cover was observed at the first sampling, 28 March 1995, and occurred on the triple pass tank (wet) treatments at a mean of 0.88%. Interestingly, this same treatment hosted no shrub occurrence on the second sampling period, but appeared again at a mean of 0.75% on the final, 26 October 1996 sample period. This sporadic behavior is likely a result of the nature of the shrub, or

half-shrub in this case, broom snakeweed (*Gutierrezia sarothrae* Shinnery). Snakeweed is a perennial half-shrub that

commonly undergoes cyclic fluctuations in population densities due to seasonal climatic variation (Vallentine 1974). There were no significant differences (0.20 probability) among the respective means of basal shrub covers at any sampling period among dry season treatments, but control (wet) season treatment cover was less ($P > 0.20$) than triple pass tank impacts on 28 March 1995, as well as on 26 October 1996.

Litter cover was the most abundant plant-related property on the surface of all treatments. Though not immediately useful from the standpoint of a soil-binding agent, litter cover does help protect the soil surface from the erosive forces of raindrop energy through interception. Table 6 shows results were quite variable among treatments and between sampling periods. The 4 November 1995 sampling period, however, illustrates general agreement among treatments. At this period, all treatment means, with the exception of triple pass tank (dry), exhibited no significant differences at the 0.20 level of probability. Other results of mean litter cover are less clear, most likely due to the influence of wind at the site between sampling periods. Surface organic material is commonly dry and lightweight, and vegetal portions are readily moved by the forces of wind. Many desert rangeland plants rely

Table 6. Mean litter cover at several sampling periods and significant differences at several levels of probability with wet and dry season treatments.

Treatment	Mean (%)*	Level of probability		
		0.05	0.10	0.20
Date: 28/3/95				
Control	32.20	b	b	b
Tank 1 Pass Dry	43.37	a	a	a
Tank 3 Pass Dry	21.21	c	c	c
Date: 4/11/95				
Control	33.71	a	a	a
Tank 1 Pass Dry	32.96	a	a	a
Tank 3 Pass Dry	15.15	b	b	b
Date: 26/10/96				
Control	28.40	a	a	a
Tank 1 Pass Dry	30.49	a	a	a
Tank 3 Pass Dry	25.79	a	a	a
Date: 28/03/95				
Control	32.20	a	a	b
Tank 1 Pass Wet	46.21	a	a	a
Tank 3 Pass Wet	37.50	a	a	a
Date: 4/11/95				
Control	33.71	a	a	a
Tank 1 Pass Wet	33.90	a	a	a
Tank 3 Pass Wet	3.35	a	a	a
Date: 26/10/96				
Control	27.40b	b	b	
Tank 1 Pass Wet	45.44	a	a	a
Tank 3 Pass Wet	32.68	b	b	b

*Means followed by the same letter within a sample date and probability level are not significantly different.

Table 7. Mean total plant cover at several sampling periods and significant differences at several levels of probability with wet and dry season treatments.

Treatment	Mean	Level of probability		
	(%)*	0.05	0.10	0.20
Date: 28/3/95				
Control	46.61	a	a	a
Tank 1 Pass Dry	51.89a	a	a	
Tank 3 Pass Dry	23.29	b	b	b
Date: 4/11/95				
Control	44.68	a	a	a
Tank 1 Pass Dry	38.81	a	a	a
Tank 3 Pass Dry	18.56	b	b	b
Date: 26/10/96				
Control	49.61	a	a	a
Tank 1 Pass Dry	44.70	ab	a	a
Tank 3 Pass Dry	33.14	b	b	b
Date: 28/3/95				
Control	46.61	a	a	a
Tank 1 Pass Wet	54.92	a	a	b
Tank 3 Pass Wet	41.09	a	a	a
Date: 4/11/95				
Control	44.05	a	a	a
Tank 1 Pass Wet	38.81	a	a	a
Tank 3 Pass Wet	38.39	a	a	a
Date: 26/10/96				
Control	49.61	ab	b	b
Tank 1 Pass Wet	61.90	a	a	a
Tank 3 Pass Wet	43.01	b	b	b

*Means followed by the same letter within a sample date and probability level are not significantly different.

on wind to aid in the transport and distribution of seed. The final sample period, 26 October 1996, exhibited greater litter cover (45%) for single pass tank (wet) treatments than for ($P < 0.05$) other treatments. This is probably a result of forb colonization and is useful from the standpoints of retaining soil moisture and building soil organic matter.

The culmination of surface vegetation is reported as total plant cover (Table 7). This measure is simply the addition of the individual mean grass, forb, shrub, and litter components previously determined. As expected, the control means remained fairly consistent between sampling periods, ranging from a low of 45% on 4 November 1995 to a high of 50% on 26 October 1996. The triple pass tank (dry) treatments consecutively and significantly produced less ($P > 0.20$) total plant cover than all other treatments at every sampling period. Single pass tank (wet) treatments yielded appreciable plant cover at all sampling periods and was significantly the highest ($P < 0.20$) of all periods on 26 October 1996 at 62%. The foremost contributing component of total plant cover for all treatments was litter. Therefore, some of the variation that occurred among treatments and between sampling periods may be explained by the same confounding influence of wind described for mean

litter cover values. While litter is a property of vegetation, and it is certainly beneficial in curtailing sediment dislocation, lit-

Table 8. Mean rock cover at several sampling periods and significant differences at several levels of probability with wet and dry season treatments.

Treatment	Mean	Level of probability		
	(%)*	0.05	0.10	0.20
Date: 28/3/95				
Control	15.91	b	b	b
Tank 1 Pass Dry	11.93	b	b	b
Tank 3 Pass Dry	22.92	a	a	a
Date: 4/11/95				
Control	21.02	a	ab	ab
Tank 1 Pass Dry	16.29	a	b	b
Tank 3 Pass Dry	24.24	a	a	a
Date: 26/10/96				
Control	13.45	a	a	a
Tank 1 Pass Dry	16.09	a	a	a
Tank 3 Pass Dry	15.16	a	a	a
Date: 28/3/95				
Control	15.91	a	aa	
Tank 1 Pass Wet	17.23	a	a	a
Tank 3 Pass Wet	16.10	a	a	a
Date: 4/11/95				
Control	21.02	a	a	a
Tank 1 Pass Wet	20.27	a	a	a
Tank 3 Pass Wet	14.20	a	a	a
Date: 26/10/96				
Control	13.47	a	a	
Tank 1 Pass Wet	12.69	a	a	a
Tank 3 Pass Wet	16.46	a	a	a

*Means followed by the same letter within a sample date and probability level are not significantly different.

ter should probably not be considered as prominent as established vegetation for soil stabilization media.

Rock cover is also an important surface feature of desert landscapes because it exerts exceptional control on surface stability. Rock cover commonly acts as a barrier to processes impacting the surface, and in this sense can be seen as a substitute in aridity for otherwise sparse vegetation. Table 8 shows, with the exception of the final sampling period, that triple pass tank (dry) treatments exhibited the most mean rock cover. These treatments represented the most disturbed areas in terms of sediment loss and total plant denudation. However, because of this disturbance, it appears that coarse particles remained on the surface after finer materials had been dislodged by raindrop erosion and removed by runoff. The remaining coarse particles account for much of the measured rock cover. Triple pass tank (dry) treatments were highest on the 4 November 1995 sampling period at 24%, though not significantly ($P > 0.20$) greater than controls.

Bare ground is essentially the antithesis among soil erosion preventative agents. Unfortunately, bare ground contributed a substantial percentage of the total plot area among all treatments among sampling periods (Table 9). Not surprising, the

Table 9. Mean bare ground at several sampling periods and significant differences at several levels of probability with wet and dry season treatments.

Treatment		Mean	Level of probability		
		(%)*	0.05	0.10	0.20
Date:	28/3/95				
Control		37.50	b	b	b
Tank 1 Pass Dry		36.17	b	b	b
Tank 3 Pass Dry		53.79	a	a	a
Date:	4/11/95				
Control		34.28	b	c	c
Tank 1 Pass Dry		44.89	b	b	b
Tank 3 Pass Dry		57.20	a	a	a
Date:	26/10/96				
Control		41.10	a	a	a
Tank 1 Pass Dry		41.29	a	a	a
Tank 3 Pass Dry		44.70	a	a	a
Date:	28/3/95				
Control		37.50	ab	ab	a
Tank 1 Pass Wet		27.44	b	b	b
Tank 3 Pass Wet		42.80	a	a	a
Date:	4/11/95				
Control		34.28	a	b	b
Tank 1 Pass Wet		40.91	a	ab	ab
Tank 3 Pass Wet		46.97	a	a	a
Date:	26/10/96				
Control		41.11	a	a	a
Tank 1 Pass Wet		25.40	a	a	a
Tank 3 Pass Wet		38.65	a	a	a

*Means followed by the same letter within a sample date and probability level are not significantly different.

triple pass tank (dry) treatments maintained the highest mean bare ground percentages within each sampling period consecutively at 54, 57, and 45 %, and were significantly higher ($P < 0.20$) on the 28 March 1995 and 4 November 1995 periods. Bare ground quite readily forms impermeable soil surface crusts on desert landscapes. These crusts are formed when wet soil aggregates are first broken down by raindrop impact and finer materials are washed into surface pores, reducing their volume. After aggregate destruction, raindrop impact causes compaction of the surface and produces a thin coating which is largely impermeable. The compaction is a function of the size and terminal velocity of raindrops. The surface sealing reduces infiltration rate, thus encouraging runoff. No significant differences among bare ground treatment (wet) means were found at the 0.05 level of probability between 4 November 1995 and 26 October 1996 sampling periods, and no differences (0.20 probability) were found among wet or dry season treatment means at the final, 26 October 1996 period.

Surface Microtopography

Surface roughness, microrelief, or microtopography is defined as a measure of variation in surface elevation (Huang and Bradford 1992). Surface microtopog-

raphy is considered an important variable since greater surface undulations tend to increase hydraulic resistance, slow surface

flow, and allow more time for infiltration (Eldridge 1991, Wood and Eldridge 1993). This variable was reported as mean surface microtopographic variance (Table 10) among 4 plots per treatment and 2 repetitions between sampling periods (Kincaid and Williams 1966). Variance was calculated from 66 individual points measured with the point frame on each plot for each treatment and repetition. The control treatments, as expected, tended to have higher mean variance, though most results were quite variable. The general trend of most treatments was comparatively high mean variance on the first, 28 March 1995 sample period, and consecutively lower means through the final, October 1996 period. One possible explanation for this behavior is that the very intense precipitation events that occurred in the summer months prior to each of the last 2 sampling periods facilitated soil surface crusting. Such impermeable crusts would most likely exhibit more uniform surfaces because the intense rainfall events necessary to create the crusts would tend to break-apart and disperse surface soil aggregates, resulting in a smoother surface. Single pass tank (wet) treatment variance means were consistently lower than other treatments at all sampling periods. No difference was found at the 0.20 level of probability among all treatments for the dry season,

Table 10. Mean surface microtopographic variance at several sampling periods and significant differences at several levels of probability with wet and dry season treatments.

Treatment		Mean	Level of probability		
		(cm)*	0.05	0.10	0.20
Date:	28/3/95				
Control		1.6125	a	a	a
Tank 1 Pass Wet		0.6825	b	b	b
Tank 3 Pass Wet		0.9075	b	b	b
Date:	4/11/95				
Control		0.6062	a	a	a
Tank 1 Pass Wet		0.2100	b	b	b
Tank 3 Pass Wet		0.5012	ab	a	a
Date:	26/10/96				
Control		0.3712	a	a	ab
Tank 1 Pass Wet		0.2538	a	a	b
Tank 3 Pass Wet		0.6412	a	a	a
Date:	28/3/95				
Control		1.6125	a	a	a
Tank 1 Pass Dry		0.9337	b	b	b
Tank 3 Pass Dry		0.7300	b	b	b
Date:	4/11/95				
Control		0.6062	a	a	a
Tank 1 Pass Dry		0.5175	a	a	a
Tank 3 Pass Dry		0.4862	a	a	a
Date:	26/10/96				
Control		0.3712	a	a	a
Tank 1 Pass Dry		0.2888	a	a	a
Tank 3 Pass Dry		0.2250	a	a	a

*Means followed by the same letter within a sample date and probability level are not significantly different.

Table 11. Correlation analysis (N = 40) for wet season treatments for each surface property measured with cumulative sediment loss being the dependent variable.

Independent variables	R*	F**	P***
Grass cover	-0.34	5.12	0.029
Forb cover	-0.02	0.01	0.912
Shrub cover	-0.05	0.09	0.764
Litter cover	-0.36	5.69	0.022
Total plant cover	-0.52	14.32	0.001
Rock cover	-0.23	2.04	0.161
Bare cover	-0.36	5.70	0.022
Microtopography	-0.48	11.58	0.022
Grass cover + Litter cover	-0.53	7.35	0.022
Grass cover + Litter cover + Microtopography	-0.62	7.45	0.001
Bare ground + Microtopography	-0.56	8.09	0.001
Grass cover + Litter cover + Microtopography + Rock cover	-0.62	5.46	0.002

*Multiple correlation coefficient (R)

** Variance ratio (F)

*** Level of probability (P)

on the second, 4 November 1995 and third, 26 October 1996 sampling periods.

Correlation Analysis

Cumulative sediment loss was identified as the dependent variable. Grass, forb, shrub, litter, total plant, rock, and bare ground cover, as well as microtopographic variance, were identified as independent variables.

Table 11 presents correlation coefficients for treatments under wet seasonal conditions. The most negatively and strongly correlated individual variable was total plant cover at $R = -0.52$, $F = 14.32$, at the 0.001 level of probability. As anticipated, higher values of total plant cover are associated with lower values of cumulative sediment loss. The most negatively and strongly correlated group of variables was grass cover, litter cover, and microtopographic variance. This combination pro-

duced an $R = -0.62$, $F = 7.45$, at the 0.001 level of probability.

Correlation coefficients were slightly lower for treatments under dry seasonal conditions (Table 12). Similar to wet season treatments' analysis, the most negatively and strongly correlated individual variable under dry conditions was total plant cover at $R = -0.44$, $F = 5.34$, at the 0.031 level of probability. The most negatively and strongly correlated group of variables was grass cover, litter cover, and rock cover at $R = -0.48$, $F = 2.68$, at the 0.14 level of probability.

Conclusions

The results from this study acknowledge the impact of military tracked vehicles in a desert rangeland environment. However,

the extent to which multiple pass disturbances are responsible for accelerated sediment loss in this study environment may not be altogether obvious, particularly where the effects of drought are concerned. Antecedent soil moisture conditions, as well as timing and intensity of precipitation, are widely recognized variables that play a profound role in governing the erosion process (Branson et al. 1981). To this end, it would not necessarily be correct to eliminate tracked vehicle training activities in the presence of drought, nor would it necessarily be correct in the presence of generally wet soil conditions. Rather, training activities should be scheduled with regard to landscape suitability and capacity to sustain disturbance, and should also be conducted with attention to site recovery. Individual installations may be able to implement site vehicle "carrying capacities," in which case these results should be helpful. Scheduling should reflect necessary recovery periods and sites should be monitored for progress. Although area soil surveys are an excellent source of information, reliance on soil loss tolerance estimates, "T-values" in particular, should be used with caution.

Despite the desire for stringent control of land management, it is very important to consider the inherent variability and unpredictable nature of climate and microclimate in rangeland systems. While some research is being conducted in this area (Ham et al. 1995, Polley et al. 1997), continued efforts are needed to better understand and describe the delineations between variable climate and land uses, and the associated impacts on the hydrologic cycle. The system variability creates the need for adaptive, proactive management. Such an approach endeavors to achieve environmental goals while maintaining the efficiency, longevity, and integrity of the land use operation in question. Watershed scale impacts need to be the subject of additional research.

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Table 12. Correlation analysis (N = 40) for dry season treatments for each surface property measured with cumulative sediment loss being the dependent variable.

Independent variables	R*	F**	P***
Grass cover	-0.33	2.74	0.112
Forb cover	-0.04	0.04	0.837
Shrub cover	0	0	0
Litter cover	-0.33	2.61	0.121
Total plant cover	-0.44	5.34	0.031
Rock cover	-0.38	3.74	0.066
Bare cover	-0.17	0.68	0.417
Microtopography	-0.1	0.22	0.644
Grass cover + Litter cover	-0.45	2.68	0.092
Grass cover + Litter cover + Rock Cover	-0.48	2.05	0.014
Total plant + Rock cover	-0.47	3.3	0.07

*Multiple correlation coefficient (R)

** Variance ratio (F)

*** Level of probability (P)

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Acute toxic plant estimation in grazing sheep ingesta and feces

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Abstract

'Romerillo' (*Baccharis coridifolia* DC), 'duraznillo negro' (*Cestrum parqui* L'Hérit.), and 'sunchillo' (*Wedelia glauca* (Ort.) Hoff.) are highly toxic species producing important economic losses of livestock in Argentina. This study assessed the accuracy and precision in the estimation of the percentage and the mass of these species in the ingesta and feces of sheep experimentally poisoned. This study also evaluated whether the quantified percentage and the calculated mass of each toxic species in the rumen+reticulum, the easiest region to sample, are good estimates of their relative consumption. Results indicate that if species fragment density is quantified, and the percentages of non recognized fragments of the toxic species in their in vitro digestion residues are accounted for (attributing some proportion of the unidentified fragment pool to the target species), estimations are accurate, but their precision differ among species. For a 3 sheep sample, the average mass estimated by microhistological analysis represented 92.3 ± 5.8 (romerillo), 96.5 ± 17.3 (duraznillo negro), and $92.0 \pm 12.5\%$ (sunchillo) ($P < 0.10$) of the actual amount of each species consumed. The percentages of the toxic species in the total ingesta plus feces produced since the intoxication did not differ ($P > 0.05$) from those in the rumen+reticulum. For the evaluated species, the microhistological analysis of the rumen+reticulum not only confirmed the ingestion of the toxic species, but also adequately estimated the percentage in which they were ingested.

Resumen

Romerillo' (*Baccharis coridifolia* DC), 'duraznillo negro' (*Cestrum parqui* L'Hérit.), y 'sunchillo' (*Wedelia glauca* (Ort.) Hoff.) son especies de alta toxicidad que causan importantes pérdidas económicas en la producción ganadera de Argentina. Este estudio evalúa la exactitud y la precisión de la estimación por microanálisis del porcentaje y de la masa de cada una de estas especies presente en la ingesta y en las heces de ovejas intoxicadas experimentalmente. Además, analiza si los porcentajes de las especies tóxicas cuantificados en el rumen+reticulum, la región más fácil de muestrear, son buenos estimadores de su consumo relativo. Los resultados indican que si la cuantificación se realiza registrando la densidad de los fragmentos de las diferentes especies, y si los porcentajes de las especies tóxicas son corregidos de acuerdo al porcentaje de fragmentos no reconocidos en los residuos de digestiones in vitro, las estimaciones son exactas, y que su precisión varía según la especie tóxica. Con una muestra de tres animales, los porcentajes estimados por microanálisis representaron 92.3 ± 5.8 (romerillo), 96.5 ± 17.3 (duraznillo negro), y $92.0 \pm 12.5\%$ (sunchillo) ($P < 0.10$) de la cantidad suministrada en la intoxicación. Los porcentajes de las especies tóxicas en la ingesta y heces no difirieron ($P > 0.05$) de los de rumen+retículo. Para las especies evaluadas, el microanálisis del rumen+retículo no sólo permite confirmar su ingestión, sino que además estima adecuadamente el porcentaje en el que fueron ingeridas.

Key Words: Microhistological technique, accuracy, precision, *Baccharis coridifolia*, *Cestrum parqui*, *Wedelia glauca*

The heterogeneity of ecological conditions in the Argentinean Pampas favors the growth of many valuable plant species in terms of their use as forages. These different conditions also provide optimal opportunities for the growth of a large number of poisonous plants, which yearly cause the death or severe sickness of all kinds of livestock through acute or chronic poisoning. Three of these species are romerillo (*Baccharis coridifolia* DC),

duraznillo negro (*Cestrum parqui* L'Hérit.), and sunchillo (*Wedelia glauca* (Ort.) Hoff.). These species have different growth forms; duraznillo negro and romerillo are shrubs, and sunchillo is a forb. Duraznillo negro and sunchillo are usually found in areas of disturbed and fertile soils; romerillo grows in hillsides, where soils are shallow. Methods for the detection of the toxic substances in the remains of dead animals are far beyond the analytical instrumentation availability of local diagnostic laboratories. Therefore, other diagnostic methods are necessary.

In sheep fed 'annual ryegrass' (*Lolium multiflorum* Lam.)–oat (*Avena sativa* L.) hay and orally administered duraznillo negro, sunchillo or romerillo in water suspensions, microhistological analysis of the epidermal fragments in the ingesta shows that distribution of these toxic species fragments is not uniform in the digestive tract (Yagueddú et al. 1998). Therefore the percentage of a toxic species estimated in 1 of the regions of the digestive tract is not necessarily a good estimate of the percentage in

This study was carried out at the Diet Botanical Composition Laboratory at the Unidad Integrada Balcarce (FCA, UNMdP – EEA Balcarce, INTA). The authors are grateful to Marina Dosanto and María Salomón (INTA) for their technical assistance, and to Dr. M. Ralphs for his insightful comments and suggestions on drafts of this manuscript. This study was financially supported by the Agencia Nacional de Promoción Científica y Tecnológica de Argentina, CONICET and the UNMdP.

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which it was ingested. Moreover, in our field conditions, vegetation heterogeneity makes fragment recognition of the toxic species substantially more difficult than in the simpler experimental situation of the toxic species fed with a basal hay diet.

When a farmer or a veterinarian brings to the Diet Botanical Composition Laboratory a sample from the digestive content of an animal found dead in the field, he does not only want to know which toxic species the animal ate, but also the amount ingested, or at least the percentage in which it was consumed. Accordingly, the objectives of this study were: (1) to assess the accuracy and precision of microhistological estimations of the actual amounts of the 3 mentioned poisonous species present in the ingesta of experimentally intoxicated sheep grazing a multi-species vegetation, and (2) to determine if the quantified percentages of the toxic species in the rumen+reticulum and in the feces, the most common sampling points, are good estimators of their consumption.

Materials and Methods

The study was conducted at the Estación Experimental Agropecuaria Balcarce, Instituto Nacional de Tecnología Agropecuaria, Balcarce, Buenos Aires province, Argentina (37°45'S, 58°18'W), and consisted of 2 trials. In trial 1 we experimentally poisoned 3 sheep with each toxic species, estimated the dried weight of each digestive tract region and that of the feces, and sampled their contents for microhistological quantification of the percentages of the different species in the diet. In trial 2 each toxic species was evaluated for the percentage of recognizable fragments before and after digestion. The percentage of recognizable fragments after digestion was used as a correction factor to account for the unrecognizable fragments. Finally, with the information obtained from both trials, we calculated the mass of the toxic species in the ingesta and feces, and evaluated the accuracy and precision of the microhistological estimations.

Trial 1 (Intoxication Trial):

In November 1996, nine Corriedale ewes grazed during 8 days in a 2 ha paddock of a naturalized pasture made up by 23 species, dominated by 'tall wheatgrass' (*Thinopyrum ponticum* (Podp.) Barkw. & D.R. Dewey), 'pasto sedilla' (*Vulpia dermatensis* (All.) Gola), and perennial and annual ryegrass (*Lolium perenne* L. and

L. multiflorum Lam., respectively). There were 10 other minor grasses in the pasture. Although there were 8 species of forbs (which represented approximately 10% of the total biomass), only 'oreja de ratón' (*Dichondra mycrocalyx* (Hall.) Fabris) represented more than 2% of the available forage. The cool season grasses were in bloom. Biomass availability was estimated by cutting ten, 0.10 m² randomly distributed frames.

Plants of the 3 mentioned poisonous species were collected from different farms where cases of intoxication had previously occurred. The collected plant material consisted of young shoots and fully expanded leaves. At the time of harvest, romerillo plants were at the vegetative stage, and those of duraznillo negro and sunchillo were in bloom. We estimated the dry matter percentage of each toxic species (24 hours, 60° C) to calculate the amount of fresh plant material to be administered to the experimental animals. The dry matter percentages were 19.6, 20.0 and 27.0% for sunchillo, duraznillo negro and romerillo, respectively.

Each toxic species was randomly assigned to a group of 3 sheep. The average animal weight of each group was: 44.8 ± 5.0, 42.0 ± 2.6 and 47.3 ± 1.5 kg for duraznillo negro, romerillo and sunchillo, respectively. Sheep were brought in from the pasture, housed in separate pens, and dosed via esophageal tube as described by Yagueddú et al. (1998). We intoxicated the sheep with the lethal doses of fresh sunchillo (1.5 g DM kg⁻¹ LW; Platonow and López 1978), and romerillo (1.0 g DM kg⁻¹ LW; T. López and G. Pinilla, unpublished data). However, due to the large volume of plant material required for the duraznillo negro lethal dose (10.0 g DM kg⁻¹ LW; López et al. 1978), one fourth of the lethal dose was used. Administered doses were: duraznillo negro 112.2 ± 13.1, romerillo 42.0 ± 2.6, and sunchillo 71.0 ± 2.3 g DM. After dosing, water was offered ad libitum. Twenty-four hours later all sheep poisoned with romerillo and sunchillo had died, and those poisoned with duraznillo negro showed the signs of poisoning usually produced by non-lethal doses of this species. These sheep were sacrificed by electric shock.

Upon necropsy the entire content of the digestive tract regions (except rumen+reticulum), and the total amount of feces collected in each pen were individually processed for microhistological quantification as described by Yagueddú et al. (1998). Because of its large size, the manipulation of the rumen+reticulum con-

tent is cumbersome, so the quantification of the botanical composition of this region was performed on a sample composed of 15 randomly taken sub-samples of 50 g DM each. The remaining mass of the rumen+reticulum was also dried and weighed, to establish the total net weight of the digestive content of this region. Samples were individually washed with tap water over a 200 mesh screen to remove soluble endogenous substances which can coagulate when samples are dried, dried (60° C, 24 hours), weighed, and ground to pass a 1 mm screen (16 mesh) for microhistological species fragment quantification according to Sparks and Malechek (1968). Samples prepared for microhistological quantification were individually soaked 30 to 60 seconds in full strength household bleach to clear the material as suggested by Holechek et al. (1982), and washed over a 200 mesh sieve to remove the bleach and very small fragments. Small aliquots of each sample were evenly spread and mounted on 5 microscope slides using gelatine:glycerine (1:7). One of the basic assumptions of the microhistological technique outlined by Sparks and Malechek (1968) is that a 1 to 1 relationship exists between relative density of identifiable fragments ground to a uniform size and percentage of dry weight of the species in the samples. Accordingly, fragment density of the different species was counted in 100 microscopic fields as an estimation of its relative dry weight. The density of unidentifiable grasses and forbs was also recorded. In our study all the determinations were made by a 15 year experienced observer, who regularly checks her accuracy with hand compounded mixes, as recommended by Holechek and Gross (1982).

Trial 2 (Digestion Trial):

Epidermis is the only vegetal tissue whose fragments have taxonomic value and are not degraded by digestion. However, not all the epidermal fragments have cytological features that allow their identification to species level. Furthermore, digestion can reduce the percentage of the identifiable fragments (Leislle et al. 1983, Samuel and Howard 1983, Holechek and Valdez 1985). We needed an accurate estimation of the number of fragments of the toxic species in the ingesta and in the feces (recognized plus non-recognized). We also wanted to know the percentage of non-recognized fragments in the digestion residues of the toxic species that could be attributed to the lack of cytological features with taxonomic value or to the diges-

tion effect. So, we analyzed the percentage of recognizable fragments before and after in vitro digestion in three, 200 g DM samples of each toxic species collected simultaneously with the plant material used in the intoxication trial. Samples were dried for 24 hours at 60° C, ground in a Willey mill with a 1 mm sieve screen, and divided in 2 subsamples for analysis of the percentage of recognizable fragments before and after digestion. In vitro digestibility was determined by a modified Tilley and Terry (1963) procedure, reducing incubation time with rumen microbes from 48 to 24 hours, and omitting the incubation with pepsin. We stopped incubation at 24 hours because the poisonous species considered in this study cause death within this period. Rumen inoculum was obtained from a steer fed on a lucerne hay maintenance diet. After 24 hours of microbial digestion, the subsample residues were recovered by filtration, and were dried. Finally, digested and undigested samples were soaked in domestic bleach to remove plant pigments. Five slides were prepared for each sample, the numbers of recognizable and unrecognizable fragments in 20 microscope fields per slide were registered, and results were expressed as percentage of recognizable fragments before and after digestion.

Differences among species in digestibility, and in percentages of fragments recognized before and after digestion, as well as the effect of digestion on each species fragment recognition (estimated by the difference in the percentages of fragment recognized before and after digestion), were analyzed by ANOVA. Differences among means were determined by the Tukey test.

Calculation of the toxic species mass

The mass of each toxic species in the ingesta and in the feces of each sheep was estimated by accounting for both the percentage of recognizable fragments and the effect of digestion on them in 5 steps. In step 1, we calculated the corrected number of fragments (recognizable plus non recognizable) of each toxic species in each region of the digestive tract and in the feces as follows: Corrected number of fragments_i = (number of recognizable fragments_i / % recognized fragments_i after digestion) x 100, where i represents the different digestive regions or the feces. We corrected the number of fragments estimated by microanalysis assuming that the percentage of the toxic species we could not recognize was in the pool of fragments of forbs not identifiable to species level. In step 2, the remaining

fragments in this forb pool were proportionally distributed among the non-toxic forb species of the diets according to the proportion of recognizable fragments. In a similar way, the fragments of grasses not recognized to species level were proportionally distributed into the grass species in the diet. In step 3, the corrected numbers of fragments quantified in the diet of each sheep were directly expressed as corrected percentages. In step 4, we estimated the total mass (g DM) of each toxic species in each region of the gastro-intestinal tract or in the feces(i), using the following equation: Mass_i = net dry weight_i x corrected percentage_i / 100. Finally, in step 5, the mass of all the digestive regions and the feces was added to evaluate the total mass of the toxic species and compare it to the amount administered.

Accuracy and precision

For each toxic species, we evaluated the accuracy of the corrected microanalysis by t test analyzing whether the estimated mass in the total ingesta plus the feces differed from the administered amount, and the precision by the confidence interval (90%) around the mean of the 3 sheep. Next we determined by t-test whether the percentage and the mass of each toxic species in the rumen+reticulum differed from those in the total ingesta plus feces. Furthermore, we compared the mass in the rumen+reticulum with the administered mass. We made the same test in the feces, but only for the percentages. These tests were performed with the corrected percentages (for digestion and unrecognizable fragments) and also with the uncorrected percentages.

Results and Discussion

Forage availability of the paddock grazed by the sheep before the intoxications was 3335 kg DM ha⁻¹. All the sheep consumed varied diets, consisting of 16 to 20 species. The average percentages of the

main species in the diets were ryegrass (11.6%), 'Bermudagrass' (*Cynodon dactylon* (L.) Pers.) (10.9%), tall wheatgrass (10.6%), 'tall fescue' (*Festuca arundinacea* Schreb.) (10.3%), pasto sedilla (9.6%) and 'pasto miel' (*Paspalum dilatatum* Poir) (8.2%).

Dry matter digestibility differed among species, being highest in sunchillo, intermediate in duraznillo negro and lowest in romerillo (Table 1). Digestion did not affect the recognition of the fragments of duraznillo negro and sunchillo ($P > 0.05$) but strongly reduced the recognition in romerillo ($P < 0.05$). In this species, digestion caused a separation of the epidermis from the lower tissues, increasing the proportion of the non recognized fragments.

The corrected percentages of the poisonous species in the different regions of the digestive tract ranged from 0 to 15.0% for romerillo, 13.1 to 22.7% for duraznillo negro, and 9.2 to 17.6% for sunchillo (Table 2). The highest percentages of romerillo and sunchillo were in the rumen+reticulum, and that of duraznillo negro in the omasum+abomasum. The net dry weight of the rumen+reticulum was 75.5, 83.8 and 87.5% of the total mass (digesta+feces) for the sheep intoxicated with duraznillo negro, romerillo and sunchillo, respectively. In our study, sheep intoxicated with duraznillo negro received only one fourth of the lethal dose, so they were still alive after 24 hours of the ingestion. This longer digestion time may account for the lower percentage of ingesta in the rumen+reticulum.

The average concentration of duraznillo negro and sunchillo in the feces were 17.0 ± 4.2 and 10.2 ± 5.8%, respectively. We could not find fragments of romerillo in the feces of any of the 3 sheep intoxicated with this species (Table 2). The distribution of the fragments of duraznillo negro and sunchillo throughout the digestive tract and in the feces was fairly uniform, but the fragments of romerillo tended to concentrate in the rumen+reticulum.

Table 1. Average ($\bar{x} \pm SD$) dry matter digestibility, and digestion effect on fragment recognition by microhistological analysis in 3 poisonous plant species that produce acute intoxication (n = 3).

Species	Dry Matter Digestibility	Recognizable Fragments (%)	
		Before Digestion	After Digestion
Duraznillo negro	69.4 ± 0.80b	74.3 ± 7.0bA	73.2 ± 1.5cA
Romerillo	67.5 ± 0.70c	57.5 ± 7.1aA	31.0 ± 5.0aB
Sunchillo	73.0 ± 0.84a	54.7 ± 4.5aA	51.5 ± 3.0bA

^{abc}For each variable, means with different low letters differ among species ($P < 0.05$).

^{AB}For each species, the average percentages of recognizable fragments with different capital letters differ before and after digestion ($P < 0.05$).

Table 2. Average ($\bar{x} \pm \text{SD}$) net dry weight (g DM) of the ingesta and the feces of sheep experimentally poisoned with 3 toxic species, the percentage of these toxic species quantified by microanalysis, their calculated DM mass (g DM), and the percentage of the toxic species administered represented by the amount estimated by microanalysis (% recovered). CI = confidence interval.

	Ingesta									Total	Administered (g)	Recovered (%)	90% CI
	Rumen + Reticulum	Omasum + Abomasum	Duodenum	Jejunum	Ileum	Cecum	Colon	Rectum	Feces				
Duraznillo negro													
Net dry weight (g)	421.5 ± 40.3	7.6 ± 5.3	0.0	6.8 ± 1.0	0.0	15.3 ± 1.8	14.0 ± 9.0	8.3 ± 2.5	84.7 ± 61.2	558.2 ± 67.9			
% toxic species corrected (*)	20.2 ± 2.3	22.7 ± 3.5	---	16.2 ± 3.3	---	13.1 ± 2.9	18.1 ± 4.7	17.8 ± 4.3	17.0 ± 4.2	19.4 ± 2.3 ⁺			
uncorrected	14.8 ± 1.7	16.6 ± 2.6		11.9 ± 2.4		9.6 ± 2.1	13.2 ± 3.4	13.0 ± 3.1	12.4 ± 3.1	14.2 ± 1.7			
Calculated DM mass (g) of toxic species (*)	85.1 ± 1.2	1.7 ± 0.9	---	1.1 ± 0.2	---	2.0 ± 0.4	2.5 ± 1.3	1.5 ± 0.5	14.4 ± 7.7	108.3 ± 8.3	112.2 ± 13.1	96.5 ± 17.3	± 16.4%
Romerillo													
Net dry weight (g)	250.0 ± 11.0	14.3 ± 4.5	0.0	4.2 ± 5.2	0.0	3.3 ± 4.0	8.3 ± 10.2	5.3 ± 6.8	13.0 ± 6.0	298.4 ± 13.6			
% toxic species corrected (*)	15.0 ± 1.1	4.2 ± 3.0	---	7.2 ± 7.8	---	2.4 ± 1.2	2.4 ± 2.8	0.0	0.0	12.9 ± 1.0 ⁺			
uncorrected	4.7 ± 0.3	1.3 ± 0.9		2.2 ± 2.4		0.7 ± 0.4	0.7 ± 0.9			4.0 ± 0.3			
Calculated DM mass (g) of toxic species (*)	37.5 ± 3.0	0.6 ± 0.4	--	0.3 ± 0.3	---	0.1 ± 0.1	0.2 ± 0.2	0.0	0.0	38.7 ± 3.0	42.0 ± 2.6	92.2 ± 5.8	± 5.6%
Sunchillo													
Net dry weight (g)	341.1 ± 92.6	11.0 ± 1.1	0.0	0.0	0.0	5.6 ± 3.2	12.5 ± 5.5	3.9 ± 1.8	16.0 ± 3.3	390.0 ± 99.4			
% toxic species corrected (*)	17.6 ± 2.9	9.2 ± 6.5	---	--	---	11.6 ± 7.0	12.0 ± 6.1	15.1 ± 9.1	10.2 ± 5.8	16.7 ± 2.4 ⁺			
uncorrected	9.1 ± 1.5	4.7 ± 3.3				6.0 ± 3.6	6.2 ± 3.1	7.8 ± 4.7	5.3 ± 3.0	8.6 ± 1.2			
Calculated DM mass (g) of toxic species (*)	60.0 ± 11.1	1.0 ± 0.8	---	---	---	0.6 ± 0.2	1.5 ± 0.3	0.6 ± 0.5	1.6 ± 1.3	65.3 ± 10.1	71.0 ± 2.3	92.0 ± 12.5	± 11.9%

(*) Corrected by the percentage of non recognizable fragments in digestion residues.

(+) Calculated as: (total DM mass of the toxic species x 100) / (total digesta + feces dry weight) . These percentages do not differ from those in rumen+reticulum.

The calculated total mass of each toxic species in the ingesta and feces was accurate (Table 2). The total mass represented 96.5 \pm 17.3, 92.2 \pm 5.8 and 92.0 \pm 12.5% of the amount administered of duraznillo negro, romerillo and sunchillo, respectively, and these percentages did not differ from 100% ($P > 0.05$). Romerillo mass was estimated with the highest precision. The 90% confidence intervals were narrowest for romerillo (5.6%), intermediate for sunchillo (11.9%), and broadest for duraznillo negro (16.4%).

When estimations were made correcting the percentage of recognizable fragments in the digestion residues, the estimated percentages of the toxic species in rumen+reticulum did not differ ($P > 0.05$) from those estimated in the total ingesta plus the feces. Moreover, for romerillo and sunchillo, the calculated mass of each toxic species in the rumen+reticulum did not differ from either for those calculated for the total ingesta plus feces, or the administered amounts ($P > 0.05$). However it did differ for duraznillo negro ($P < 0.05$).

When corrections were not carried out, the estimations were not good for any of the species. Percentage and mass estimations without correction for rumen+reticulum were 14.8 \pm 1.7, 4.7 \pm 0.3, 9.1 \pm 1.5%, and 62.3 \pm 0.8, 11.7 \pm 0.9, 30.5 \pm 5.7g for duraznillo negro, romerillo and sunchillo, respectively. Differences between corrected and uncorrected values reflect the magnitudes of the lack of fragment recognition in digestion residues. They clearly show the digesta microhistological analysis is not accurate for either the percentage nor the mass of duraznillo negro, romerillo and sunchillo, unless the effect of digestion is taken into account.

The percentages of duraznillo negro and sunchillo estimated in feces did not differ from the total when they were corrected ($P > 0.05$) but they did differ when they were not ($P < 0.05$). Correction by digestion requires that when an animal is found dead in the field, samples of the suspicious poisonous plant species should be collected and an in vitro digestion performed to quantify the percentage of fragments rec-

ognized in the digestion residues.

The distribution of the fragments of duraznillo negro and sunchillo throughout the digestive tract and in the feces was fairly uniform, but the fragments of romerillo tended to concentrate in the rumen+reticulum. Passage rate of the plant particles generally increases as particle size decreases and particle density increases. Romerillo was the species with the lowest digestibility, so its particles could have been denser than those of the other 2 species. Digestion not only affects fragment identification but also in some forb and shrub species can cause their complete destruction (Holechek and Valdez 1985). In our study the fact that the estimated mass of each toxic species did not differ from the administered suggests that digestion did not totally destroy any of the fragments or that the amount of fragments totally destroyed was minimum.


Both the accuracy and precision of the microhistological technique have been broadly evaluated in different ecological systems. Holechek et al. (1984) presented

a extensive discussion on these attributes when samples come from feces or from esophageal or ruminal fistulas. It is commonly accepted that the microanalysis only provides an appropriate qualitative description of the botanical composition of range herbivores diets (Holechek et al. 1984, Holechek and Valdez 1985). However, our results indicate that correcting by the percentage of fragment recognition after digestion, and quantifying mass according to fragment density, the microanalysis of the rumen+reticulum content is an accurate estimate of the percentage in which the toxic species considered in this study were ingested.

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Ungulate herbivory on buckbrush in an Arizona ponderosa pine forest

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Abstract

Monitoring processes that affect plant population dynamics and determine community structure is central in forest restoration ecology. To study effects of mule deer (*Odocoileus hemionus*) and elk (*Cervus elaphus*) on buckbrush (*Ceanothus fendleri* Gray), we built exclosures around 90 plant-centered plots in 3 ponderosa pine (*Pinus ponderosa* Laws.) forest restoration management units and compared vegetative and flowering characteristics with unprotected plots for 2 years. On unprotected plots, 69% of the current-year branches were browsed during the first year and 44% were browsed the second year. There was no difference in number of aerial stems or current-year branches in the first year, yet stems on protected plots were longer (24.1 cm; $P < 0.01$) and retained more than 4 times the current-year biomass (1.4 g stem⁻¹; $P < 0.01$) than those on unprotected plots (12.9 cm and 0.3 g stem⁻¹, respectively). Stem number, length and diameter, number of current-year branches, and current-year biomass on protected plots were all greater ($P < 0.01$) than on unprotected plots in the second year. Stems on protected plots had significantly higher ($P < 0.01$) length-diameter ratios and had fewer current-year branches per unit length ($P < 0.05$) than unprotected stems. Flowering stems were found on significantly ($P < 0.05$) more protected plots (55%) than unprotected plots (8%) in the second year. Effects of ungulate herbivores on buckbrush size, stem recruitment, morphology, and flowering represent important constraints to early understory development and restoration in this Southwest ponderosa pine forest.

Key Words: ecological restoration, *Ceanothus fendleri*, stem morphology, flower production, *Cervus elaphus*, *Odocoileus hemionus*

It is widely recognized that large mammalian herbivores, through selective grazing and physical disturbance to sites, often play key roles in ecosystems and affect community composition, structure, and development as well as various ecological processes (Anderson and Loucks 1979, Naiman 1988, Augustine and McNaughton 1998). Under episodic or light herbivory, browsed plants may compensate for tissue loss by increasing production of

Resumen

El monitoreo de procesos que afectan las dinámicas de las poblaciones de plantas y determinan la estructura de la comunidad es un punto central en ecología de restauración de bosques. Para estudiar los efectos del "Mule deer" (*Odocoileus hemionus*) y el "Alce" (*Cervus elaphus*) sobre el "Buckbrush" (*Ceanothus fendleri* Gray), construimos exclusiones alrededor de 90 parcelas con plantas en el centro ubicadas en 3 unidades de manejo de restauración de "Pino ponderosa" (*Pinus ponderosa* Laws.), y en 2 años comparamos las características vegetativas y de floración con parcelas sin excluir. En las parcelas sin protección el 69% de las ramas nuevas producidas en el año fueron consumidas y el 44% consumidas en el segundo año. No hubo diferencias en el número de tallos aéreos o ramas nuevas producidas en el primer año, pero los tallos en las parcelas protegidas fueron mas largos (24.1 cm; $P < 0.01$) y conservaron 4 veces más biomasa nueva (1.4 g tallo⁻¹; $P < 0.01$) que las plantas en las parcelas sin protección (12.9 cm y 0.3 g tallo⁻¹, respectivamente). En el segundo año el número de tallos, longitud y diámetro, número de ramas nuevas y la biomasa nueva fueron mayores en las parcelas protegidas que en las no protegidas. Los tallos en las parcelas protegidas tuvieron una relación longitud-diámetro significativamente mayor ($P < 0.01$) y tuvieron menos ramas nuevas por unidad de longitud ($P < 0.05$) que los tallos sin protección. En el segundo año, se encontró una proporción significativamente mayor de parcelas protegidas (55%; $P < 0.05$) con tallos florales en comparación con las no protegidas (8%). Los efectos de los herbívoros ungulados en el tamaño, dinámica de tallos, morfología y floración del "Buckbrush" representa un importante restricción para el desarrollo inicial y restauración las capas bajas de la estructura de este bosque de "Ponderosa pine" del suroeste.

biomass or reproductive structures (Paige and Whitham 1987, Rosenthal and Kotanen 1994, Augustine and McNaughton 1998, Throop and Fay 1999). Intense herbivory can lead to decreased stature and reproductive output, regeneration failure, and population decline (Strohmeyer and Maschinski 1996, Kay 1997, Augustine and Frelich 1998, Augustine and McNaughton 1998, Suzuki et al. 1999, Opperman and Merenlender 2000). Through direct competition with other herbivores and indirect "knock-on" effects, large herbivores can affect population dynamics and distribution of other members of the food web (Baines et al. 1994, Rooney 2001, Stewart 2001). The array of potential ecosystem-level consequences makes assessment and monitoring of herbivore impacts particularly important for ecological restoration programs.

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An extraordinary increase in tree density over the last century has led to critical conservation problems in ponderosa pine (*Pinus ponderosa* Laws.) ecosystems of the southwestern United States (Arnold 1950, Covington and Moore 1994a, 1994b, Kolb et al. 1994, Biondi 1996, Savage et al. 1996, Fulé et al. 1997, Mast et al. 1999). Among other effects, dense forest conditions have reduced forage abundance and habitat quality for wildlife that rely on understory vegetation (Covington and Moore 1994a). In concert with forest structural changes, Rocky Mountain elk (*Cervus elaphus nelsoni*) were introduced to the region in the early 1900s to replace the extirpated Merriam's elk (*C. e. merriami*). Numbers of elk have increased over the last 100 years to around 30,000 animals in Arizona and 40,000–50,000 animals in New Mexico (Truett 1996). Although restoration treatments such as thinning small diameter trees and reintroducing low-intensity surface fires have been suggested to restore ecological structure and function to these forests (Kolb et al. 1994, Covington et al. 1997, Moore et al. 1999), research on the impacts of herbivory on plant species' response to restoration thinning is presently lacking.

Buckbrush (*Ceanothus fendleri* Gray), is a semi-evergreen, nitrogen-fixing shrub common in ponderosa pine forest understories of the Southwest (Story 1974, Conard et al. 1985). As a shrub species in primarily herbaceous communities, buckbrush populations can provide structural heterogeneity in forest understories and enhance ecological diversity. Although buckbrush has been reported as an important browse plant for mule deer (*Odocoileus hemionus*), and other animals including elk apparently consume its leaves, stems, fruit, and seeds (Urness et al. 1975, Epple 1995, Allen 1996, Huffman 2002), effects of herbivory on buckbrush growth and reproduction have not been studied. Information concerning intensity of wild ungulate herbivory and its effects on important understory species can help land managers interpret trends in community development and better understand processes constraining restoration of ecosystems. Our objectives in this study were to: 1) quantify the effects of large ungulate herbivory on buckbrush vegetative characteristics such as size, production, and morphology; and 2) examine herbivory effects on buckbrush potential reproduction.

Methods

Study Site

We conducted our study from 1999–2000 on the Fort Valley Experimental Forest (35° 16' N, 111° 41' W) in Coconino County approximately 10 km northwest of Flagstaff, Ariz. The area receives around 52 cm of precipitation annually with a distinct dry period in May and June. Precipitation falls in late summer as rain from monsoonal thunderstorms and in winter as snow. The study area was located from 2,225 to 2,380 m above mean sea level. Aspect was generally southern and the topography was gentle with average slopes of approximately 5–10%. Soils are classified as Brolliar clay loams (fine, smectitic, mesic Typic Argiustolls) developed on tertiary basalt parent material and are moderately well drained (Unpublished report, Meurisse).

Overstory vegetation was nearly pure ponderosa pine less than 120-years-old with scattered old-growth trees. Common understory species included grasses Arizona fescue (*Festuca arizonica* Vasey), mountain muhly (*Muhlenbergia montana* (Nutt.) A.S. Hitchc.), bottlebrush squirreltail (*Elymus elymoides* (Raf.) Swezey) and pine dropseed (*Blepharoneuron tricholepis* (Torr.) Nash); forbs lupine (*Lupinus* spp.), fleabane (*Erigeron* spp.), buckwheat (*Eriogonum* spp.), yarrow (*Achillea millifolium* L.), and pussytoes (*Antennaria* spp.); and shrubs buckbrush and woods rose (*Rosa woodsii* Lindl.). Large mammalian herbivores present on the site included mule deer and elk. Cattle were excluded from the study site.

Experimental Design

In late winter 1998, tree thinning was initiated on 9 units of 14–16 hectares each on the study site. The thinning from below reduced tree density by 80% to approximately 111–210 trees per hectare, which were grouped around the spatial locations of presettlement tree structures (see Covington et al. 1997 for restoration guidelines). We selected 3 of these units for our study, each separated by at least 1 kilometer.

In early spring 1999, we located 60 buckbrush clonal assemblages in each of the 3 units (180 total). The plots were randomized into either protected or unprotected treatments. Circular plots, 1 m², were established around 1 or more existing stems and contained 1–25 buckbrush stems. Buckbrush is rhizomatous and can expand vegetatively (Vose and White 1987). Sprouting also occurs from a pronounced root crown (Huffman pers. obs.).

Thus, it is not known whether 1 or many clones produced the aerial stems we sampled. Stem assemblages selected were spatially discrete and generally covered an area less than 2 m². Hereafter, we refer to stem assemblages within plots as “plants”. Herbivore exclosures 4 m² in area and 1.4 m in height were constructed around plots receiving the protection treatment. Mesh size used for fencing exclosures was 5 x 10 cm. This allowed entry of small mammalian and invertebrate herbivores but excluded large ungulates.

In each of the 2 study years, we collected data on flower production and vegetative characteristics. In June of each year, we examined stems in all plots for production of inflorescences. For stems producing flowers or flower buds, we measured total stem length and basal diameter. We classified stems into 4 relative age groups according to stem base characteristics as follows: Class-1) first-year stems, not suberized, generally supple, gray-green pubescence at stem base; Class-2) bright green, not suberized, previous year's growth of lateral branches present, generally lacked pubescence; Class-3) similar to Class-2 with bark developing in patches at stem base; Class-4) stem bases dark brown to black, fully suberized, bark often furrowed. Although we have observed buckbrush plants on long-term plots at other sites develop similar characteristics over time (Moore pers. obs.), we were not able to confirm actual ages through ring counts or meristem scars. We also counted number of inflorescences on flowering stems. In September, measurements collected for flowering stems were taken for all stems on the plots. Additionally, the number of current-year branches was counted, average length of current-year branches was estimated, and longest current-year branch was measured.

For all stems, biomass, and leaf area (LA) of current-year branches were estimated using predictive relationships developed from separate sampling in the study units. Forty-five to 50 current-year stems were collected from clonal assemblages outside the experimental plots. For biomass determination, current-year stems (n = 50) were measured for length, oven-dried (70° C for 48 hours), and weighed to the nearest 0.01 g. For leaf area (LA) determination, current-year stems (n = 45) were measured for length and leaves were removed and analyzed for 1-sided LA by a video projection system (AgVision™). The equation to predict current-branch biomass was: Ln Biomass = -4.919 + 1.395(Ln Branch Length) (r² = 0.94, P <

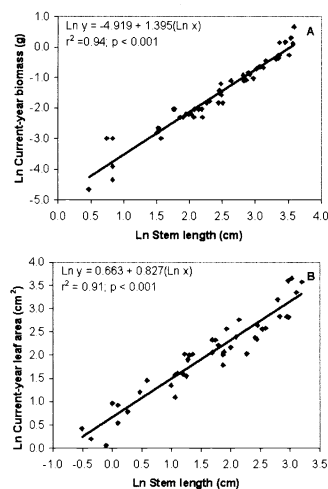


Fig. 1. Relationships used to estimate biomass (A) and leaf area (B) of current-year branches on *Ceanothus fendleri* plants.

0.001) (Fig. 1a). The equation to predict current-branch LA was: $\text{Ln LA} = 0.663 + 0.827(\text{Ln Branch Length})$ ($r^2 = 0.91$, $P < 0.001$) (Fig. 1b).

Data Analyses

One-way analysis of variance (ANOVA) was used to test for effects of protection on vegetative characteristics of buckbrush plants within study years (1999 and 2000). Overstory unit was included in the ANOVA model as a blocking factor. Paired t-tests were used to test ($P < 0.10$) between-year differences in vegetative parameters within treatment (protected and unprotected) groups. Data for individual stems (i.e., length, number of current-year branches, length of current-year branches, biomass and leaf area per stem) were averaged at the plot level and analyses were performed on these values.

Additionally, stem diameter, current year biomass, and current-year leaf area were summed at the plot level and analyzed for treatment differences. Morphological characteristics tested were stem height-diameter ratio and branchiness. Branchiness was calculated as the number of current-year branches divided by stem length. Data met distribution and variance assumptions for ANOVA tests and were not transformed. In April 2000, 24 of the plots were burned as part of another experiment. These plots were excluded from analysis in year 2000.

A Mantel-Haenszel test was used to compare ($P < 0.05$) proportions of unprotected and protected plots with flower-producing stems. Mann-Whitney nonparametric tests were used to analyze ($P < 0.05$) differences in stem and current-branch number between treatments.

Results

Plant Size and Current-Year Biomass

Analysis of pretreatment data indicated no difference in stem length or number of stems between treatments. Stem length averaged 7.6 cm (SE = 0.30) and number of stems per plot averaged 4.9 (SE = 0.31).

By the end of the first growing season (1999), 69% of the current-year branches on unprotected plots had been browsed. Two percent of the new branches inside exclosures had terminal buds removed apparently by invertebrates. We did not observe signs of small rodent herbivory inside exclosures although mesh size permitted rodent access. Herbivory on unprotected plants appeared consistent with

browsing from large ungulates; current-year branches were nipped roughly, often near their bases, and we did not find discarded shoots or leaves that might suggest herbivory by rodents (Bullock 1991, Balgooyen and Waller 1995). In addition, deer and elk were frequently observed on the study site and their tracks and scat were noted near experimental plots.

One growing season after installing the herbivore exclosures, plant size was significantly different between protected and unprotected treatments. Stem and current-year branch lengths of protected plants were from 1.9 to 2.8-fold greater than those of unprotected plants (Table 1). Average stem diameter was also greater for protected plants than unprotected plants. Differences in current-year branch lengths between protected and unprotected plots translated directly to differences in biomass and leaf area (Table 1). Individual stems on protected plots retained more current-year biomass by a factor of 4.7, and leaf area by a factor of 2.5, compared to stems on unprotected plots. No difference was found in average number of stems on plots or the number of new branches produced by stems on protected and unprotected plots in 1999. All stems produced an average of 5.3 (SE = 0.2) new branches during the first growing season.

In 2000, growing season precipitation (20.4 cm; March–September) was about 66% of the 91-year average (31.0 cm; Western Regional Climate Center 2000) and both protected and unprotected buckbrush plants showed varying degrees of stem dieback. Forty-four percent of current-year branches were browsed on unprotected plots. Average total stem length on protected plots increased ($P = 0.05$) slightly from the previous year and

Table 1. Means (and standard errors) of buckbrush vegetative characteristics on plots protected from large herbivores and on unprotected plots in 1999 and 2000.

Variable	1999		2000	
	Protected	Unprotected	Protected	Unprotected
Stems				
Number	8.1 (1.0)	6.9 (0.6)	9.1 (1.2)*	5.4 (0.5)
Length (cm)	24.1 (0.8)** [†]	12.9 (0.7)	25.9 (1.0)**	11.2 (0.8)
Diameter (mm)	3.5 (0.1) [†]	3.1 (0.1)	4.1 (0.2)*	3.5 (0.1)
Current-Year Branches				
Number	5.3 (0.3)	5.3 (0.3)	15.3 (1.5)**	7.1 (0.6)
Length (cm)	13.1 (0.4)**	4.7 (0.4)	5.8 (0.4)**	2.5 (0.2)
Longest (cm)	19.5 (0.6)**	7.7 (0.5)	9.7 (0.6)**	4.5 (0.4)
Biomass (g)	1.4 (0.1)**	0.3 (<0.1)	1.6 (0.5)**	0.2(<0.1)
Leaf Area (cm ²)	83.9 (6.3)**	33.5 (3.3)	129.7 (26.1)**	27.1 (3.2)
Plot				
Sum Diameter (mm m ⁻²)	24.5 (3.0)*	18.5 (1.5)	30.4 (3.4)**	17.1 (1.5)
Sum Current-Year Biomass (g m ⁻²)	8.1 (0.9)**	1.7 (0.2)	8.7 (1.7)**	0.7 (<0.1)
Sum Current-Year Leaf Area (cm ² m ⁻²)	492.0 (55.0)**	177.5 (16.3)	739.1 (95.1)**	109.5 (9.7)

[†]Symbols indicate significant difference between treatments within years ([†] $P < 0.10$; * $P < 0.05$; ** $P < 0.01$)

was significantly greater than that of unprotected plots, which decreased ($P = 0.06$) (Table 1). Similarly, average stem diameter was greater on protected plots than unprotected plots. Although current-year branch lengths on both protected and unprotected plots decreased ($P < 0.001$ for both treatments) in 2000 from 1999 values, number of current-year branches increased ($P < 0.001$ and $P = 0.003$ for protected and unprotected plots, respectively). Average number of current-year branches produced by stems on protected plots nearly tripled from 1999 and was significantly greater than the number produced by stems on unprotected plots (Table 1). Both average length and length of the longest current-year branch were greater on protected plots than unprotected plots by a factor of 2 or greater. Individual stems on protected plots comprised significantly more current-year biomass than stems on unprotected plots by a factor of 8 (Table 1). Large differences also existed between protected and unprotected stems for current-year leaf area.

Average number of stems did not change significantly ($P = 0.31$) from 1999 to 2000 on protected plots, but decreased on unprotected plots ($P = 0.002$). More stems of larger average diameter led to significantly greater sum stem diameter (sum of all stems on a plot) on protected plots in 2000 (Table 1). Similarly, sum current-year biomass on protected plots in 2000 did not change from 1999 ($P = 0.81$), whereas biomass decreased significantly ($P < 0.001$) on unprotected plots. In 2000, current-year biomass summed on protected plots was greater than that on unprotected plots by a factor of 12 (Table 1). Similar patterns existed between protected and unprotected plots for sum current-year leaf area (Table 1). Sum leaf area significantly increased ($P = 0.014$) from 1999 to 2000 on protected plots but decreased ($P < 0.001$) on unprotected plots.

Stem Morphology

Herbivory of current-year branches on buckbrush stems led to noticeable differences in stem morphology. Stem height-diameter ratios were significantly greater for plants on protected plots than for those

on unprotected plots (Table 2). Stems within herbivore exclosures typically appeared long and drooping whereas stems exposed to herbivores were most often short and stubby in appearance. Although protected plants produced more current-year branches than unprotected plants in 2000, the number of branches relative to stem length was significantly greater for stems on unprotected plants in both 1999 and 2000 (Table 2).

Flower Production

In June 1999, three months after exclosures were established, no difference in flower production was found between protected and unprotected buckbrush plots. Stems produced flowers on just 2 of 180 total plots (1.1% overall).

In June 2000, flowering stems were found in a significantly greater proportion of protected plots (55%) than unprotected plots (8%). On average, 22% ($SE = 3.6$) of stems on protected plots produced flowers whereas 0.8% ($SE = 0.4$) of stems produced flowers on unprotected plots. In protected plots, up to 11 (maximum) stems produced flowers whereas no more than 1 stem flowered in any unprotected plot.

Stems (all pooled) that produced flowers tended to be larger and apparently older individuals (Fig. 2). No stems under 20 cm in length produced flowers and 85% of the flowering stems were greater than 30 cm in length. Similarly, 82% of the flowering stems were greater than 4 mm in diameter. No current-year stems flowered and more than 90% of the flowering stems had suberized bases (age classes 3 and 4). The mean number of inflorescences (panicles) produced per flowering stem was 7.3. Inflorescences were comprised of many individual flowers although these were not counted. An average of 2 branches per stem flowered; the maximum number of flowering branches was 9 per stem.

Discussion

Mule deer and Rocky Mountain elk appeared to be the primary large herbivores of buckbrush and caused significant reduction of current-year biomass in both

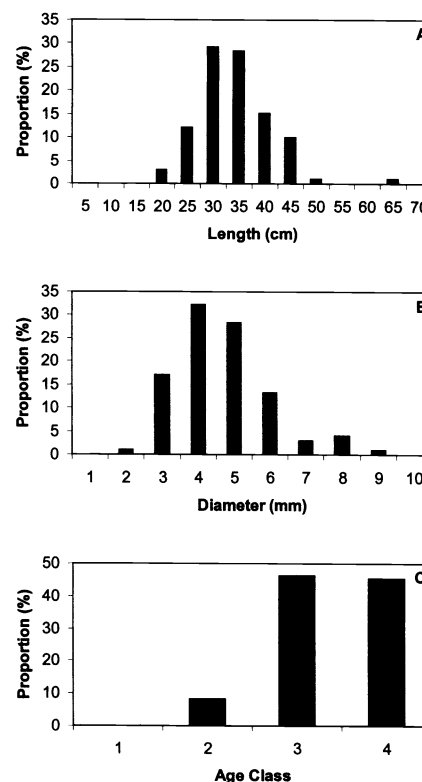


Fig. 2. Proportion of *Ceanothus fendleri* stems that produced flowers by length (A), diameter (B), and age class (C).

study years. Plants that were not protected from large herbivores had small, branchy stems, decreased aerial stem survival, and limited flowering compared with protected plants. Reduced flowering and stem survival could in turn lead to declines in local buckbrush abundance, affect community successional dynamics, and have indirect effects on other ecosystem components (Baines et al. 1994, Augustine and Frelich 1998). It is clear that herbivory by deer and elk is limiting development of understory structure. We did not examine interactions of herbivory and low-intensity fire, although prescribed burning is an important component of Southwest ponderosa pine restoration programs (Covington et al. 1997). Fire often leads to increases in vegetative and sexual regeneration through sprout production and seed germination, however, it can also increase palatability of

Table 2. Means (and standard errors) of morphological characteristics of buckbrush stems on protected and unprotected plots.

Variable	1999		2000	
	Protected	Unprotected	Protected	Unprotected
Height-Diameter Ratio (cm cm^{-1})	73.5 (1.9)** ¹	42.3 (1.8)	68.3 (2.1)**	32.6 (1.8)
Branchiness ² (N cm^{-1})	0.2 (<0.1)**	0.4 (<0.1)	0.5 (<0.1)*	0.7 (<0.1)

¹Symbols indicate significant difference between treatments within years (* $P < 0.05$; ** $P < 0.01$).

²Branchiness = Number Current-year Branches \div Stem Length

plant tissues and create conditions that attract herbivores (Whelan 1995). Our results indicate that deer and elk herbivory after forest thinning should be considered an important constraint to the ecological restoration of these ecosystems.

Intensity of deer and elk herbivory on buckbrush and other species varies with season, site conditions, and ungulate population characteristics (Reynolds 1962, Patton 1974, Urness et al. 1975, Furniss et al. 1978, Allen 1996, Throop and Fay 1999). For example, Urness et al. (1975) found that buckbrush comprised up to 6.9% of mule deer summer diet and was a consistently important browse species throughout the year at Beaver Creek, a site located around 55 km south of ours. Other woody species preferred by mule deer at Beaver Creek were Gambel oak (*Quercus gambelii* Nutt.), mountain mahogany (*Cercocarpus breviflorus* Gray), and Utah serviceberry (*Amelanchier utahensis* Koehne). These species are not commonly found on our study site and thus preference for buckbrush may be greater at Fort Valley than that reported by Urness et al. (1975). Allen (1996) noted severe browsing of buckbrush 15 years after an extensive wildfire in New Mexico and related intensity of herbivory to a dramatic elk population increase. Patton (1974) found that mule deer use increased in ponderosa pine forests after overstory thinning. Thus, deer and elk may have been attracted to the open conditions created by forest thinning treatments in our study.

Under conditions that stimulate flower production or enhance plant growth, herbivory may positively contribute to ecological restoration goals by providing resource richness and abundance for various organisms in the food web and enhancing ecosystem function (Jackson et al. 1995). Paige and Whitham (1987) reported increased flower production after experimental clipping as well as natural herbivory by deer and elk for a northern Arizona forb, scarlet gilia (*Ipomopsis aggregata* (Pursh) V. Grant). Similarly, Throop and Fay (1999) found that browsed New Jersey tea (*Ceanothus herbaceus* Raf. var. *pubescens* (T. & G.) Shinnery) produced a greater number of inflorescences than unbrowsed plants on a tallgrass prairie site. In contrast, Stein et al. (1992) noted that elk completely consumed arroyo willow (*Salix lasiolepis* Benth.) resprouts after experimental burning in northern Arizona. Similarly, Strohmeier and Maschinski (1996) reported both wild and domestic herbivores reduced total shoot length and number of

branches of Arizona willow (*Salix arizonica* Dorn). Intense deer and elk herbivory can limit production of flowers, seeds, and vegetative regeneration of various plant species in other western ecosystems (DeByle 1985, Dunlap 1988, Mitchell and Freeman 1993, Hoffman and Wambolt 1996, Kay 1997, Opperman and Merenlender 2000). In our study, buckbrush flowers were observed on less than 10% of the unprotected plots. Limiting flower production may affect populations of species dependent on the reproductive structures of buckbrush (Huffman 2002). This suggests that ungulate herbivory can affect diversity and composition of invertebrate communities through direct competition for resources and "knock-on" effects occurring from changes in microclimate or predator-prey relationships (Baines et al. 1994, Rambo and Faeth 1999, Rooney 2001, Stewart 2001).

Further research is needed to explore the roles of wild ungulate herbivory in conservation and ecological restoration of Southwest ponderosa pine ecosystems. Current understanding of presettlement conditions—attributes that provide baselines to guide ecological restoration—is greatest for overstory characteristics and fire regimes (Covington and Moore 1994a, Covington et al. 1997, Fulé et al. 1997, Mast et al. 1999). Little is known regarding presettlement population dynamics and spatial distribution of large herbivores or the range of historical variability for their effects in Southwest forest ecosystems. On some landscapes, including that of our study area, elk are thought to be more abundant and distributed more evenly than they were for possibly the last 800 years (Allen 1996, Truett 1996, Kay 1997). Indeed, ungulate herbivory in combination with forest structural changes appears to be exacerbating conservation problems in these ecosystems. For ecological restoration activities that seek to reestablish ecosystem integrity and function, it is important to understand evolutionary environments of native species and emulate historical conditions of landscape-scale processes that include herbivory by large, wild ungulates.

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Perennial grass abundance along a grazing gradient in Mendoza, Argentina

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Abstract

The study analyzed the basal area and density of perennial grasses along a cattle grazing intensity gradient away from a water development. Several mechanisms explaining combinations of changes in basal area and density with increasing grazing intensity were proposed. There was a curve-linear gradient of decreasing utilization of grasses at greater distances from water, and that gradient declined at greater distances from water. Basal diameter and density of 8 grasses were recorded at 11 distances from water ranged from 0.1 to 4.6 km within 16, 1-m² plots for each distance. Circular basal area for each species was derived from its mean basal diameter. Plant density was estimated counting each tussock for bunchgrasses and each tiller as an individual for the 1 rhizomatous grass. The abundance of basal area and density to the gradient of distance from water was analyzed for grasses grouped according to their selectivity by cattle (undesirable, preferred, desirable, and secondary preference) and for the major preferred grass, *Chloris castilloniana* Lillo & Parodi and the 2 undesirable grasses, *Aristida inversa* Haeck. and *A. mendocina* Phil. Distance from water was regressed separately on basal area and on density for each selectivity group and each individual species. Basal area of total, undesirable, and desirable grasses increased up to intermediate distances from water and decreased at sites farther from water. Basal area of both the preferred grasses combined and the major preferred species increased linearly with distance from water. Basal area of *A. inversa* showed the same trend as the undesirable grasses while basal area of *A. mendocina* showed no definite pattern with increasing grazing intensity. Basal area of secondary preference species showed no definite pattern with distance from water. Density of total and desirable grasses increased up to intermediate distances from water and decreased at sites farther from water. Density of preferred species combined and the major preferred grass increased linearly with distance from water. Density of the 2 undesirable grasses and the secondary preference grass showed no definite trend with increasing grazing intensity. The combined patterns of basal area and density across the grazing intensity gradient suggest that the expression of recruitment, mortality, and plant growth (or shrinkage) in relation to grazing intensity varies among species and at different levels of grazing intensity. However, controlled experiments are needed to decipher the relative contributions of grazing intensity, neighboring species composition, or vegetation patterns existing before the establishment of the livestock water in the patterns of abundance.

Key Words: distance from water, basal area, plant density

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Resumen

El estudio analizó el área basal y la densidad de las gramíneas perennes a lo largo de un gradiente de intensidad de pastoreo por bovinos a partir del punto de provisión de agua. Se propusieron varios mecanismos para explicar las combinaciones de cambios en área basal y densidad con el incremento de la intensidad de pastoreo. Se verificó un gradiente de utilización decreciente de los pastos a mayores distancias desde la aguada que respondió a una función curvilínea; dicho gradiente declinó a mayores distancias desde la aguada. Se midieron el diámetro basal y la densidad de 8 gramíneas en 11 distancias desde la aguada (0,1 a 4,6 km), en 16 parcelas de 1 m² en cada distancia. El área basal circular para cada especie se derivó de su diámetro basal medio. La densidad de plantas se estimó contando cada mata de las gramíneas amacolladas y cada vástago de la gramínea rizomatosa como un individuo. La abundancia de área basal y densidad en función del gradiente de distancia desde la aguada se analizó para las gramíneas agrupadas de acuerdo a su selectividad por los bovinos (indeseables, preferidas, deseables y de preferencia secundaria), para la gramínea preferida más importante, *Chloris castilloniana* Lillo & Parodi, y para las 2 gramíneas indeseables, *Aristida inversa* Haeck y *A. mendocina*. Se estimaron regresiones entre área basal y distancia desde la aguada y entre densidad y distancia desde la aguada para cada grupo de gramíneas y para cada una de las tres especies individuales. El área basal del total de gramíneas y de las especies indeseables y deseables se incrementó hasta distancias intermedias desde la aguada y decreció a distancias más alejadas. El área basal de las especies preferidas combinadas y de la especie preferida más importante se incrementó linealmente con la distancia desde la aguada. El área basal de *Aristida inversa* mostró la misma tendencia que el conjunto de las especies indeseables, mientras que el área basal de *A. mendocina* no mostró un patrón definido con la distancia desde la aguada. El área basal de la gramínea de preferencia secundaria no mostró una tendencia definida con la distancia desde la aguada. La densidad del total de especies y de las gramíneas deseables se incrementó hasta distancias intermedias desde la aguada y decreció a distancias más alejadas. La densidad de las especies preferidas combinadas y la de la especie preferida principal aumentó linealmente con la distancia desde la aguada. La densidad de las 2 especies indeseables y la de la especie de preferencia secundaria no mostraron una tendencia definida con el gradiente de intensidad de pastoreo. Los patrones combinados de área basal y densidad a través del gradiente de intensidad de pastoreo sugieren que la manifestación de reclutamiento de individuos, mortalidad y crecimiento de plantas (o encogimiento) en relación con la intensidad de pastoreo varía entre especies y a diferentes niveles de intensidad de pastoreo. Sin embargo, se requieren experimentos controlados para descifrar las contribuciones relativas a los patrones de abundancia de factores tales como la intensidad de pastoreo, la composición de las especies vecinas o los patrones de vegetación existentes antes del establecimiento de la aguada.

In arid regions, artificial watering points are the most common water sources for livestock. Location of water has an important effect on stock movements and livestock in turn will affect the abundance and diversity of forage species within paddocks (Stuth 1991). Regular movement of animals from forage to water produces a gradient of decreasing intensity of grazing and trampling from the vicinity of watering points to sites far from water (Lange 1969, Walker and Heitschmidt 1986, Andrew 1988, James et al. 1999). On the other hand, the extent of the impact of watering points on grass biomass appears to be related to rainfall in previous year (Guevara et al. 2001).

Major vegetation changes along the gradient occurs particularly in perennial grasses which are virtually eliminated or replaced by unpalatable and/or short-lived grasses, shrubs, and poisonous plants in zones close to water (Adámoli et al. 1990, Beeskow et al. 1995, Fusco et al. 1995, Saba et al. 1995). In a previous study (Guevara et al. 2001), we showed that response of grass abundance, in terms of above-ground biomass, to a grazing gradient further from water was predicted by the degree at which grasses were selected by cattle. However, in Mongolia, the abundance of biomass and cover along a gradient of grazing intensity varied along an aridity gradient, where declines in biomass and cover occurred with increased grazing intensity in mesic areas, but in arid areas the abundances were related to inter-annual precipitation rather than grazing intensity (Fernandez-Gimenez and Allen-Diaz 1999). Angell and McClaran (2001) noted a general absence of grass density response to a grazing intensity gradient up to 500 m from water over 28 years. Whereas, Fuhlendorf et al. (2001) noted some inverse relationships between grass density and individual plant basal areas as grazing intensity increased. This latter study illustrates the benefits of combining measures of density (number of plants) and cover (plant size) to interpret the mechanisms of vegetation response to different levels of grazing intensity. When taken alone, each measure can only provide 3 general responses: increase, decrease or neutral. However, in combination, there are 9 possible patterns of plant response, and the interpretation of possible mechanisms driving these responses is considerably richer (Table 1). For example, when only a positive change in cover and density occur simultaneously, then the interpretation will focus on mechanisms that stimulate both increases in plant size

and plant number. In contrast, only a less focused interpretation would occur if only cover was measured.

Our objectives are to compare the abundance of different species exposed to increasing levels of grazing intensity, and to compare these patterns of abundance when measured as plant cover and density.

Materials and Methods

Study area

This study was conducted at El Divisadero Cattle and Range Experiment Station (33° 45' S, 67° 41' W, elev. 520 m), in the north central Mendoza plain, mid-west Argentina. Daily mean minimum and maximum temperatures annually range from -0.9 to 16.0° C, and 14.9 to 32.4° C, respectively. Mean annual rainfall for 1987–98 was 303.4 mm (SD = 96.6) with nearly 85% occurring during the growing season (October–March). Soils are Torripsamments with greater silt content in interdunal depressions.

The vegetation is an open xerophytic savanna and shrubland of *Prosopis flexuosa* DC. (algarrobo dulce). Warm-season grasses dominate the herbaceous vegetation. These species include: *Aristida inversa* Haek. (flechilla), *Aristida mendocina* Phil. (flechilla crespá), *Chloris castilloniana* Lillo & Parodi (falso plumerito), *Digitaria californica* (Benth.) Henr. (pasto algodón), *Panicum urvilleanum* Kunth (tupe), *Pappophorum philippianum* Roseng. (pasto blanco), *Setaria leucopila* (Scrib. & Merr.) Schum. (cola de zorro), and *Sporobolus cryptandrus* (Torr.) A. Gray (gramilla cuarentona). *Panicum urvilleanum* is a rhizomatous species and the others are tussock grasses.

The grazing history of the range is not well known until 1980 when the Experiment Station was established. The grazing by livestock appears to begin after

1910 (Guevara et al. 2001). During the 1930's the range was heavily grazed (11 ha AU⁻¹) mainly by cattle. Because the range was not fenced, the estimation of this stocking rate assumed that livestock used all the range. Data obtained in 1976 (Guevara et al. 1981) showed that stocking rate had been reduced from 11 to 15 ha AU⁻¹. In 1980 the range was fenced and livestock was removed. A 4-pasture (1,150 ha each), 1-herd grazing rotation system was installed in 5,000 ha of the range in 1990. The grazing system design involving paddocks radiating from a central watering point. A cow-calf operation with Angus and Criollo Argentino breeds was introduced at this time. The stocking rate ranged from about 40 ha AU⁻¹ in 1990–91 to 25 ha AU⁻¹ from 1995 onwards. The latter corresponds to a conservative rate based on 30% use of forage by weight and the dependable annual rains, i.e. those having 80% probability of occurrence (Guevara et al. 1997). Removal of livestock during 10 years (1980–90) may have ameliorated the previous impact of grazing intensity on perennial grasses. In fact, above-ground biomass of grasses grouped according to their selectivity by cattle showed no definite pattern with distance from water in 1991–92 (Guevara et al. 2001).

Sampling, calculations and statistical analyses

A homogeneous paddock, in terms of soil, vegetation, and topography, was selected to sample vegetation along a transect originating from the watering point. Individual basal diameter to the nearest 1 mm and density of each perennial grass were recorded at increasing distances (0.1, 0.4, 0.7, 1.0, 1.3, 1.65, 1.875, 2.5, 3.25, 3.95, and 4.6 km) from water within 16, 1-m² plots for each distance. Plots were arrayed at fixed distances (30 m) along a transect placed perpendicular to the main gradient.

Table 1. Mechanisms that can create the spatial differences in the abundance of grass basal area and density along the grazing intensity gradient.

		Differences in density with increasing grazing intensity		
		Positive (A)	Neutral (B)	Negative (C)
Differences in basal area with increasing grazing intensity	Positive (I)	more plants	bigger plants	bigger and fewer plants
	Neutral (II)	smaller and more plants	same number and size of plants	larger and fewer plants
	Negative (III)	smaller and more plants	smaller plants	smaller and fewer plants

The gradient of decreasing grazing intensity with distance from water was verified by an analysis of utilization based on the percent ungrazed method (Roach 1950). All plant species were measured at each distance. Observed utilization in 2001–2002 (a wet period) ranged from 50.4% at 0.1 km from water to 18.6% at 4.6 km from water. Utilization decreases with increasing distance from water according to the curve-linear function (Fig. 1).

Basal diameter was taken as the average of the longest diameter and the greatest perpendicular to the first. The circular basal area for each individual grass species ($\text{mm}^2 \text{ plant}^{-1}$) was derived from this average basal diameter. For plant density (plants m^{-2}) estimation, each tussock and each tiller was counted as an individual for the bunchgrasses and the rhizomatous grass, respectively. Therefore, density equals number of tillers for the 1 desirable species, *Panicum urvilleanum*, because it is rhizomatous.

To analyze the pattern of abundance of grass basal area and density in relation to the gradient of grazing intensity, the species were grouped according to their selectivity by cattle after Guevara et al. (1996) as: preferred (*Chloris castilloniana*, *Digitaria californica*, *Pappophorum philippianum* and *Sporobolus cryptandrus*), desirable (*Panicum urvilleanum*), secondary preference (*Setaria leucopila*), and undesirable (*Aristida inversa* and *A. mendocina*). Mean basal area and mean density were calculated for each grass selectivity group at each distance. The relationship of basal area and density to the gradient from water was also analyzed for the major preferred grass, *Chloris castilloniana* whose contribution to preferred grass basal area and density was 74 and 64%, respectively, and for the 2 undesirable grasses (*Aristida inversa* and *A. mendocina*).

Distance from water was regressed separately on basal area and on density for each selectivity group and each individual grass species. Least squares method was used for obtaining estimates of parameters in linear and non-linear regression models.

Results and Discussion

Relationship between basal area and distance from water

Contribution of species to total basal area was: undesirable species, 72%; preferred species, 16%; secondary preference species, 9%; and desirable species, 3%.

Basal area was significantly related to distance from water for total (Fig. 2A), undesirable (Fig. 2B), preferred (Fig. 2C), and desirable (Fig. 2D) grasses. On the contrary, basal area of secondary preference species showed no definite pattern with distance from water (Fig. 2E). Basal area of total, undesirable, and desirable grasses increased up to about 1.9, 1.9, and 2.5 km from water, respectively, and decreased at sites farther from water (Fig. 2). These distances nearly coincide with a noticeable decrease in observed grass utilization levels between 1.3 and 1.9 km from water (Fig. 1). Conversely, basal area of preferred grasses increased linearly with increasing distance from water. As it was mentioned above, undesirable species were the most important contributors to total basal area of grasses and, thus, it appears that the abundance of total grasses is driven largely by the abundance of undesirable grasses.

The analysis of basal area abundance for individual grass species indicated that basal area was significantly related to distance from water for *Chloris castilloniana* (Fig. 3A) and *Aristida inversa* (Fig. 3B). Conversely, basal area of *Aristida mendocina* showed no definite pattern with distance from water (Fig. 3C).

Because basal area proved to be a good predictor of biomass for the grasses included in the present study (Guevara et al. 2002), in our previous study (Guevara et al. 2001) biomass of undesirable and preferred species showed the same pattern as basal area with distance from water. Furthermore, biomass distribution of secondary preference species showed a definite pattern with distance from water (Guevara et al. 2001).

Relationship between grass density and distance from water

Density was significantly related to distance from water for total (Fig. 4A), preferred (Fig. 4C) and desirable grasses (Fig. 4D). Measured density of total and desirable grasses increased up to about 1.9 and 2.5 km from water, respectively, and decreased at sites farther from water. As occurred with basal area, these distances nearly coincide with a noticeable decrease in observed grass utilization levels between 1.3 and 1.9 km from water (Fig. 1). The density of total grasses appears to be driven largely by the abundance of the desirable grass whose density contributed 72% to total grass density. Contribution of the other grasses to total density was: undesirable, 14%; preferred, 9%; and secondary preference, 5%. Undesirable (Fig. 4B) and secondary preference (Fig. 4E) grasses showed no definite pattern with distance from water. Density was significantly related to distance from water for *Chloris castilloniana* (Fig. 5A) but density of *Aristida inversa* (Fig. 5B) and *A. mendocina* (Fig. 5C) showed no definite trend with distance from water.

The positive relationship between distance to water and density of preferred species and the absence of any relationship for secondary preference species are similar relationships reported for the distribution of biomass for these species (Guevara et al. 2001).

Integration of trends in basal area and density along the grazing intensity gradient

The response of grass basal area and density to changes in grazing intensity can

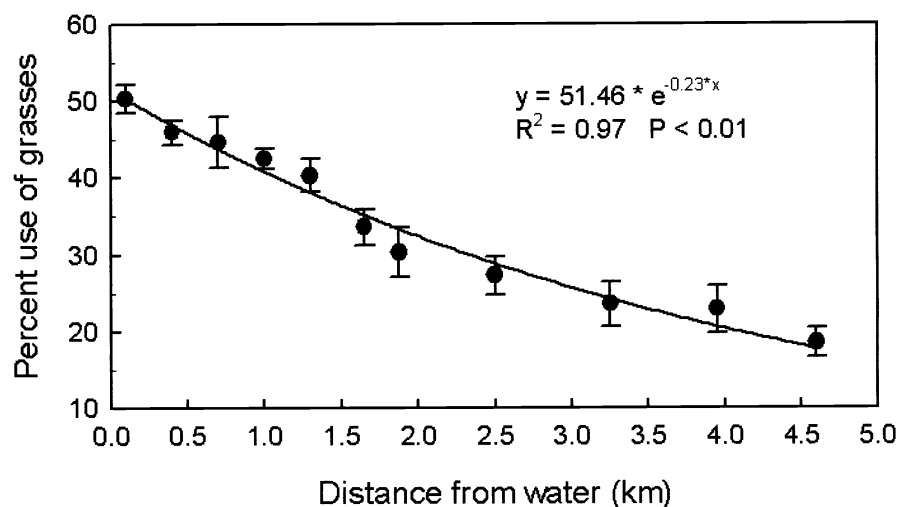


Fig. 1. Utilization of grasses as determined by the distance from water on a Mendoza plain rangeland. Vertical bars are one SE of the mean.

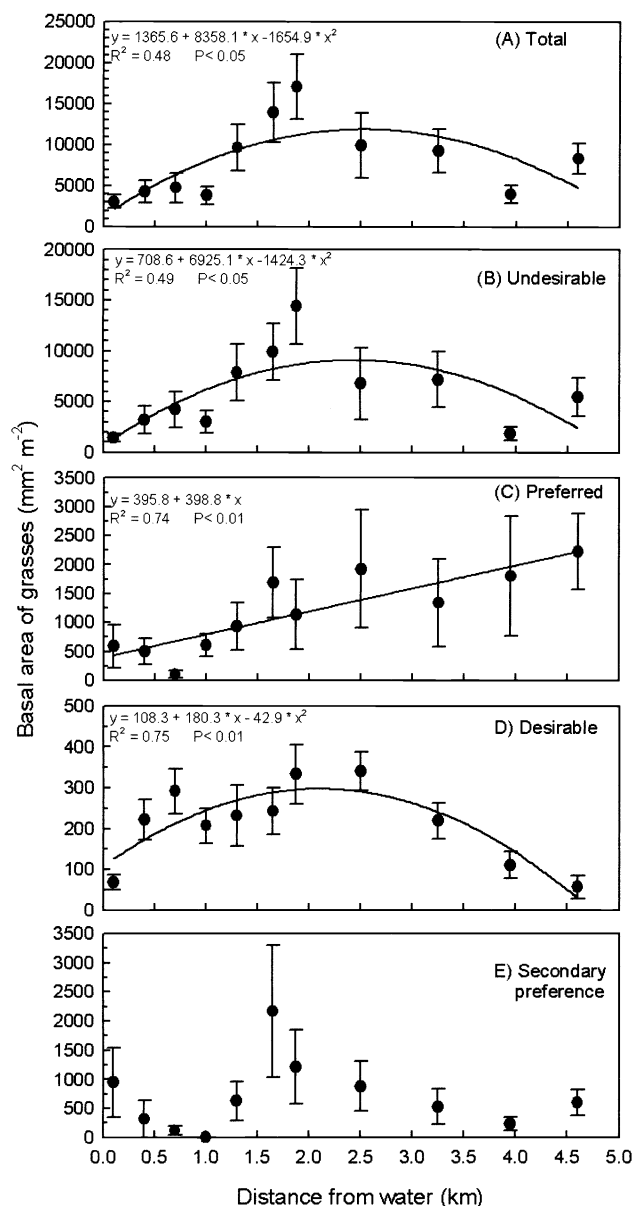


Fig. 2. Relationship between mean basal area for total grasses and grass species grouped according to their selectivity by cattle and distance from water on a Mendoza plain rangeland. Vertical bars are one SE of the mean.

be dependent on the level of grazing: whether from lowest to intermediate intensity or from intermediate to highest intensity. For total and desirable grasses, both basal area and density increased from sites farthest from water to those located at intermediate distances from water. The recruitment of tillers for the desirable grass and individuals for tussock grasses is suggested as the mechanism creating this pattern (Table 1, cell I A). On the contrary, tiller or plant mortality could be the mechanism creating the pattern observed in basal area and density at sites of the gradient located between those intermedi-

ate distances from water and zones close to water (Table 1, cell III C).

For the preferred grasses combined and particularly for *Chloris castilloniana*, plant mortality appears to be the mechanism causing the responses of basal area and density with increasing grazing intensity (Table 1, cell III C).

One interpretation for the increased basal area and neutral plant density for undesirable plants between the lowest grazing intensity locations and the intermediate intensity locations (between 4.6 and 1.9 km from water) is compensatory growth following defoliation (Table 1, cell

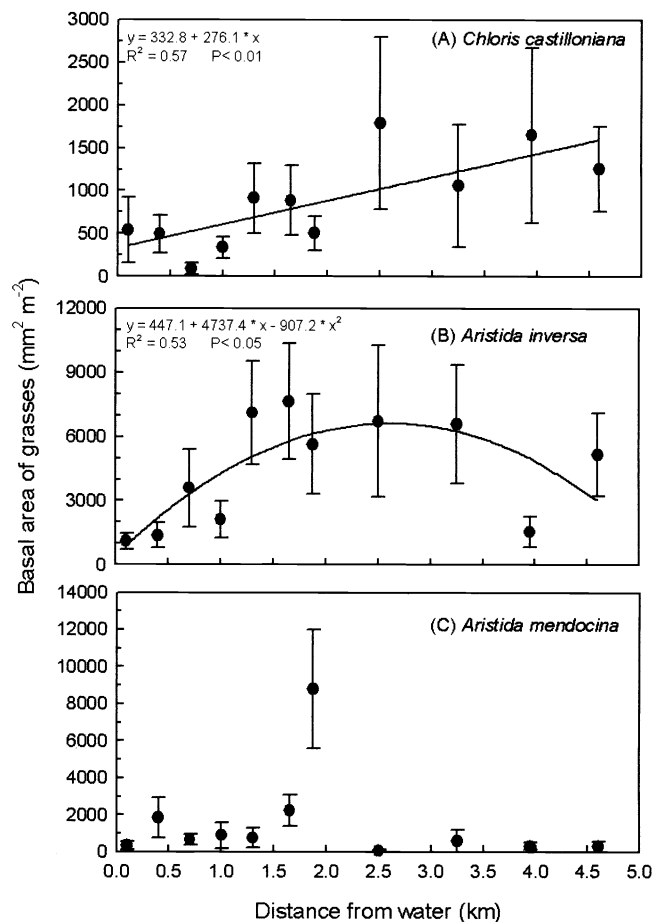


Fig. 3. Relationship between mean basal area for individual grass species and distance from water on a Mendoza plain rangeland. Vertical bars are one SE of the mean.

I B). Mechanisms such as the light quality, determined by canopy density, that reaches intercalary meristems (Deregibus et al. 1983), assimilate allocation, and hormone and water balance, among others (see McNaughton 1979, 1983 and references therein) may be responsible for this process. However, it is possible that these responses are a function of competitive relations with neighboring species that occur in differing amounts between these distances from water. On the other hand, mortality of tillers could be the mechanism creating the pattern observed at sites located between the intermediate distances

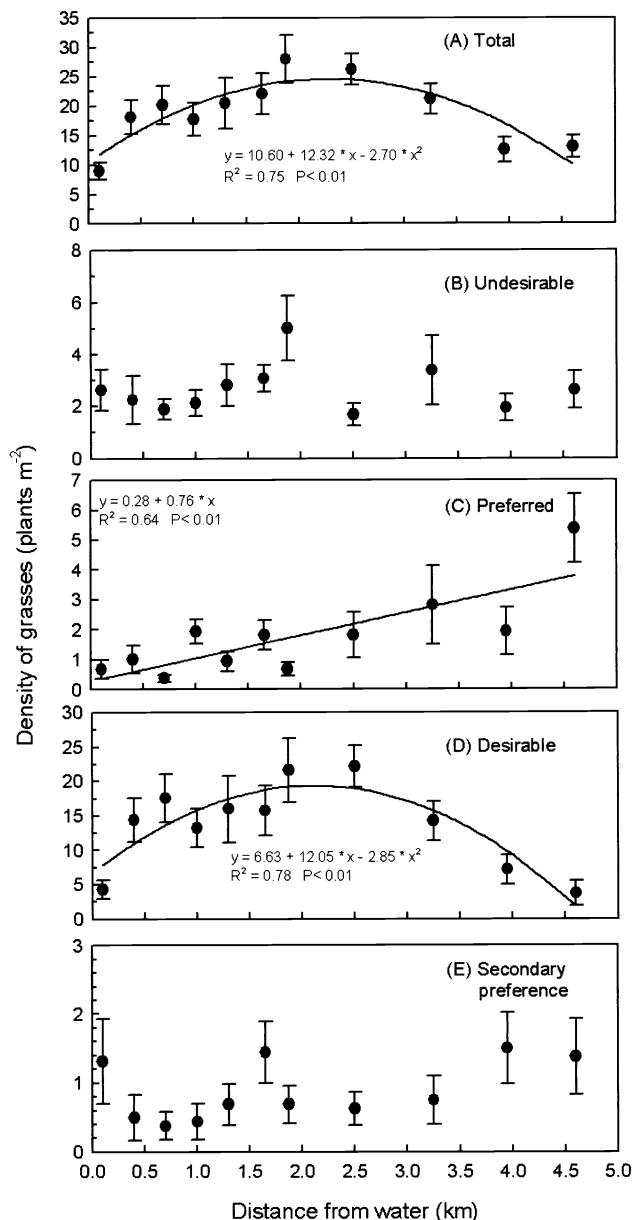


Fig. 4. Relationship between mean density for total grasses and grass species grouped according to their selectivity by cattle and distance from water on a Mendoza plain rangeland. Vertical bars are one SE of the mean.

from water and those located at the vicinity of watering points (Table 1, cell III B).

The abundance of basal area and density of *Aristida inversa* were similar to those for the class of undesirable grasses and consequently, the mechanisms mentioned for these species are applicable to this grass. This result can be explained by the significant contribution of *A. inversa* (74%) to basal area of undesirable species. Conversely, *Aristida mendocina* and the secondary preference grass appear not to be affected by grazing intensity along the gradient from water.

Based on the measure of plant basal areas, the undesirable and desirable species could be considered increasers in the classification proposed by Dyksterhuis (1949). However, based on the measure of plant density, the undesirable species would not fit that scheme because it would be unresponsive to grazing intensity. In Australian shrublands (James et al. 1999) and in the Chihuahuan desert (Fusco et al. 1995), *Aristida* spp. are considered increasers based on the measure of plant density and biomass, respectively. Based on both area and density measures, pre-

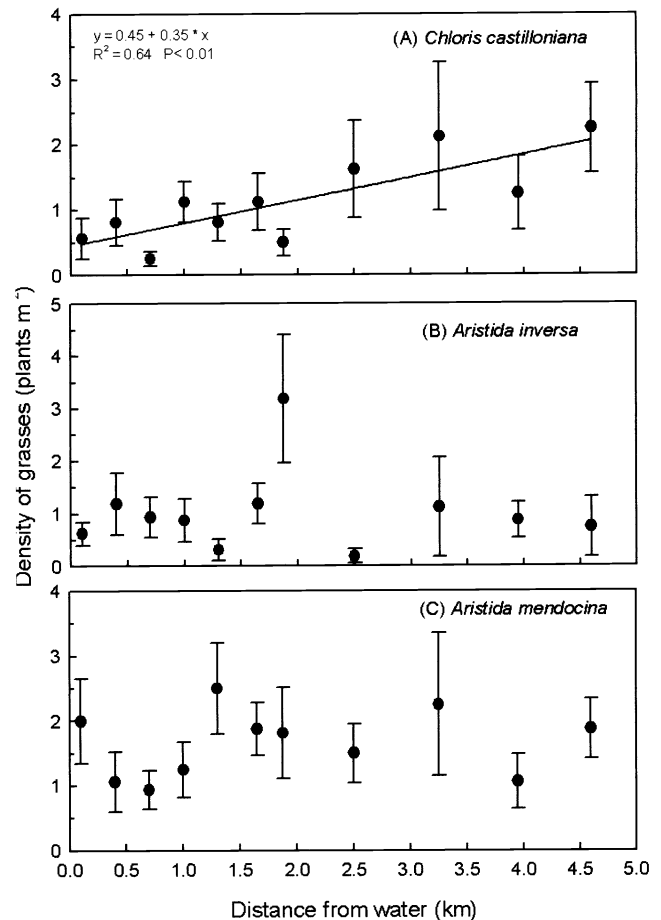


Fig. 5. Relationship between mean density for individual grass species and distance from water on a Mendoza plain rangeland. Vertical bars are one SE of the mean.

ferred species are clearly decreasers in the Dyksterhuis scheme. Similarly, in the Chihuahuan desert (Fusco et al. 1995) and Patagonia (Beeskow et al. 1995, Saba et al. 1995) patterns of declining abundance of the most preferred grasses by cattle around watering points were the most pronounced.

Mechanisms such as plant or tiller recruitment, plant or tiller mortality, and changes in plant size appear to be the mechanisms that create the observed patterns in basal area and density of perennial grasses along a grazing intensity gradient.

The type and number of mechanisms creating the observed patterns depended on the grass selectivity group or individual grass species considered. Although the interpretation of mechanisms and possible processes driving these patterns of species abundance along the grazing intensity gradient are made richer by the combined measurement of density and basal area, in this case they do not provide evidence to judge the relative importance of utilization, the abundance of neighboring species, or the persistence of vegetation patterns established under different grazing practices. For example, was the increased size of *Aristida inversa* between 4.6 and 2.5 km from water a function of compensatory growth following moderate utilization, the decline in the abundance of neighboring preferred species, or an artifact of vegetation patterns existing before the establishment of the livestock water? Future experimentation that eliminates these confounding variables or the repeated measurement of these areas will help decipher the relative roles of utilization and neighbors in creating these patterns of species abundance along this grazing intensity gradient.

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Oxalate and tannins assessment in *Atriplex halimus* L. and *A. nummularia* L.

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Abstract

The study was conducted at 3 locations in the arid region of Jordan to assess the seasonal changes of oxalate and tannins in *Atriplex halimus* L. and *A. nummularia* L. plants commonly used for revegetation of degraded rangelands. During spring and fall seasons, 20 shrubs of each species were selected randomly at each location, 20 similar twigs per shrub were clipped and analyzed for oxalate and tannins. *Atriplex halimus* contained higher levels of oxalate (7.00%) compared with *A. nummularia* plants (6.20%) ($P < 0.001$). Oxalate levels averaged 8.29 and 4.92% in spring and fall season, respectively. Plants of *A. halimus* accumulated more oxalate in spring than those of *A. nummularia*. Clipping had no effect on oxalate concentration. The seedlings of *A. nummularia* contained more oxalate than old plants whereas old shrubs of *A. halimus* contained more oxalate than the young seedlings. The browse of *A. halimus* contained more condensed and hydrolyzable tannins (1.05% and 0.67%, $P < 0.0001$) than *A. nummularia* (0.80% and 0.39%, $P < 0.0001$), respectively. Clipping had no effect on the levels of tannic phenols, condensed and hydrolyzable tannins. Young plants of the 2 species had higher levels of condensed tannins compared to older plants. However, seedlings of *A. nummularia* contained significantly higher levels of condensed tannins compared to *A. halimus* seedlings (1.57% and 1.47%, respectively). *Atriplex halimus* synthesized more oxalate, tannic phenols, condensed and hydrolyzable tannins than *A. nummularia*. These secondary metabolites may explain the low palatability of *Atriplex halimus* compared to *A. nummularia*.

Key Words: *Atriplex halimus*, *Atriplex nummularia*, tannins, oxalate, clipping, arid region

Rangelands in Jordan cover 90% of the total surface area of the country. Serious declines in productivity have occurred over extensive areas of these lands. This decline takes the form of depletion of high value fodder species and their replacement by plants that are less productive, less palatable, and less nutritious than the original plants they replaced (Abu-Zanat 1995). Artificial revegetation may be a tool for rehabilitation of these degraded rangelands. Because of drought and scarcity of precipi-

Resumen

El estudio se condujo en 3 localidades de la región árida de Jordania para evaluar los cambios estacionales del los oxalatos y taninos en *Atriplex halimus* L. y *A. nummularia* L., plantas comúnmente utilizadas para revegetar áreas de pastizal degradadas. Durante primavera y otoño en cada localidad se seleccionaron aleatoriamente 20 arbustos de cada especie y se cortaron 20 ramas similares por arbusto y fueron analizadas para determinar el contenido de oxalatos y taninos. *El Atriplex halimus* presentó más altos niveles de oxalatos (7.00%) que el *A. nummularia* (6.20%) ($P < 0.001$). Los niveles de oxalatos promediaron 8.29 y 4.92% en primavera y otoño respectivamente. En primavera, las plantas de *A. halimus* acumularon mas oxalatos que las de *A. nummularia*. El corte no tuvo efecto en la concentración de oxalatos. Las plántulas de *A. nummularia* contenían mas oxalatos que las plantas viejas mientras que los arbustos viejos de *A. halimus* presentaron a mas oxalatos que las plántulas. El forraje ramoneable de *A. halimus* contenía mas taninos condensados e hidrolizables (1.05 % y 0.67%, $P < 0.0001$) que *A. nummularia* (0.80% y 0.39%, $P < 0.0001$). El corte no tuvo efecto en los niveles de fenoles tánicos y taninos condensados e hidrolizables. Las plantas jóvenes de las dos especies tuvieron niveles mas altos de taninos condensados que las plantas viejas. Sin embargo, las plántulas de *A. nummularia* contenían niveles significativamente mas altos de taninos condensados que las plántulas de *A. halimus* (1.57% y 1.47%, respectivamente). *Atriplex halimus* sintetizó mas oxalatos, fenoles tánicos, taninos condensados e hidrolizables que *A. nummularia*. Estos metabolitos secundarios pueden explicar la baja gustocidad del *Atriplex halimus* comparado con el *A. nummularia*.

tation, fodder shrubs are preferred to herbaceous species for rangeland revegetation. In Jordan, the common fodder shrubs that are used for revegetation are *Atriplex halimus* L. and *A. nummularia* L. *Atriplex halimus* is native to Jordan and represents 60 to 70% of saltbush plantations in the Middle East region (LeHouerou 1994) whereas, *Atriplex nummularia* is an introduced species from Australia. However, they contain secondary chemical compounds, which may restrict grazing by herbivores. The type, level and activity of these chemical compounds depend on the age of plants as well as growing conditions (Cheeke 1995).

Atriplex species accumulate oxalates (James 1977, Libert and Franceschi 1987) up to 4–16% DM (Barry and Blaney 1987). Both soil salinity and moisture can alter the level of oxalate in the plant. Plants growing in saline soil need oxalates for osmoregulation of Na, K and Cl ions (Cymbaluk et al. 1986). Under high

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soil moisture, *Atriplex halimus* plants were reported to accumulate higher levels of oxalate in leaves and twigs (Ellern et al. 1974). Plants containing 10% oxalate or more are considered toxic and should not be grazed (James 1977).

Tannins, on the other hand, are a chemically diverse group of water-soluble phenols, which bind proteins to form insoluble complexes (Hagerman et al. 1992). The level of tannins in the plant is not constant. Factors within the plant and the external environment influence the variability of tannin levels. Within a given species the proportion of tannins may change with plant maturity and/or climatic stress (Singleton 1981). Factors that may increase tannin level in plants are low soil fertility, drought and high temperature. Tannins inhibit cellulolytic and proteolytic enzymes and decrease the production of volatile fatty acids, microbial DNA and RNA in the rumen. Feeding tannins to ruminant animals in large amounts have produced negative effects on the animal, inducing low feed palatability, inhibited digestion, and may cause systematic animal poisoning (Singleton 1981, Kumar and Singh 1984).

The objectives of this study were to: 1) assess the seasonal levels of oxalate and tannins in *Atriplex halimus* and *A. nummularia* in the arid region of Jordan, and 2) compare the effect of clipping versus no clipping on the level of tannins and oxalate in the browse of the 2 species.

Materials and Methods

Experimental Sites

The study was conducted at 3 locations: Khanasry (36° 03' 05" E, 32° 26' 4" N), Muwaqqar (36° 13' 30" E, 31° 46' 40" N) and Khalideyah (36° 17' 42" E, 32° 10' 36" N) research stations. These locations are classified in Jordan as arid lands with annual rainfall of 100–200 mm. Rainfall is basically irregular, sporadic, and poorly distributed. Maximum and minimum temperatures ranged between 11–35° C and 2–17° C, respectively with a relative humidity of 57%, which ranged between 86% in winter and 40% in summer. The soil is mainly silt-clay with a pH between 6.7–8.1.

Plant Material

In 1985, seeds of *Atriplex halimus* were collected from Jordan and seeds of *Atriplex nummularia* were introduced from Australia. All plant collections were propagated at the Khalideyah Nursery,

Mafraq Governorate, which is the only source of all saltbush plantations existing at the experimental sites and range reserves in Jordan. In October 1996, seedlings of *A. halimus* and *A. nummularia* (9 months old) were transplanted in contour furrows at the 3 experimental sites. Old shrubs (5–10 years) of both species existed at all the sites.

Sampling

Browse from seedlings and old plants of *A. halimus* and *A. nummularia* was collected during May (spring season) and November (fall season) in 1997. At each location, 20 shrubs of each species and age class were selected randomly and tagged with plastic wires at the main stem. Twenty identical twigs (1 cm in diameter, 10–15 cm long) from each shrub were selected randomly from all sides of the shrub and clipped. The samples from each shrub were placed into plastic bags for weight determination and chemical analysis. In November 1997, regrowth of twigs previously clipped in May were re-clipped to determine the effect of clipping (a simulation of grazing) on the content of tannins and oxalate.

Chemical Analysis

Since the equipment for freeze drying is not available, the samples were dried using an air-circulating oven at 25° C for 48 hours according to Makker et al. (1988) and dry weights were recorded. The low drying temperature was selected to prevent the degradation of tannins by excessive heating (Makker et al. 1988). Waterman and Mole (1994) preferred that the drying temperature should be higher than 40° C to avoid oxidation by the still active enzymes and lower than 60° C to avoid heat damage and polymerization. The partially dried samples were ground to 0.2-mm mesh size and stored in plastic bags into a refrigerator at 3 ± 1° C for later chemical analysis. The dry matter of browse was determined by placing the residues of samples in an oven and dried at 100 ± 5° C for 48 hours.

Oxalate content was determined according to the procedure of the AOAC (1990). A sample weighing 1.5 g was treated with HCL (6 M), boiled for 30 minutes and the solution was filtered into a 100 ml volumetric flask. The solution was treated with 5 ml of tungstophosphoric acid reagent, after filtration the pH of the solution was adjusted to 4–4.5 using NH₄OH and acetate buffer. Test tubes were centrifuged at 1700 rpm for 15 minutes and the oxalate crystals were redissolved by 5 ml

of H₂SO₄ (10 %) and titrated with KMnO₄ (0.01 M). All types of oxalates existing in the plant material were converted to oxalic acid, precipitated and titrated with KMnO₄.

Tannins were determined according to Makker and Goodchild (1996). Tannins were extracted from the sample (100 mg) using 10 ml of 70% ultra-pure acetone, immersed into an ice-cold sonicator and exposed to ultra-sonic for 15 minutes, transferred into a test tube and centrifuged at 3000 rpm for 20 minutes. The supernatant was separated and stored at 3° C. The dye Folin-Ciocalteu was added to 0.5 ml of the extract and absorbance of the dye-phenolics complex was measured at 725 nm wavelength. The amount of total phenols as tannic acid equivalent was determined from a calibration curve (10–60 mg tannic acid/ liter). Tannins were precipitated using polyvinyl pyrrolidones and 1.0 ml of the tannins extract was centrifuged at 3000 rpm for 15 minutes and the supernatant containing only simple non-tannic phenols was collected. The dye Folin-Ciocalteu was added to 0.5 ml of the supernatant and absorbance of the dye-phenolics complex was measured at 725 nm wavelength. Tannic phenols were calculated as the difference between total phenols and non-tannic phenols. Condensed tannins were determined by mixing the tannic extract with butanol-HCL reagent and ferric ammonium sulfate in a screw cap test tube. The test tube was heated in a water bath (97–100° C) for 60 minutes, cooled and absorbance was measured at 550 nm wavelength. Hydrolyzable tannins were calculated as the difference between tannic phenols and condensed tannins. Duplicates of each sample were analyzed for the confirmation of results. All results were expressed on a dry matter basis.

The least square analysis of variance was performed on data using the SAS General Linear Models (GLM) procedure for a randomized complete block design (SAS 1988). The first analysis compared experimental sites, shrub species, season and the appropriate interactions. The second analysis compared shrub species, age (seedlings versus old plants) and the appropriate interactions. The third analysis compared the effect of previous clipping on these components in secondary growth tissue and included experimental sites, shrub species, time of clipping and the appropriate interactions. Variables considered in the statistical analysis were oxalates, total phenols, non-tannic phenols, tannic phenols, condensed and

hydrolyzable tannins. A protected LSD test was used to compare means.

Results and Discussion

Oxalate

Shrub Species

Oxalate content differed between *Atriplex halimus* and *A. nummularia* (Table 1). Regardless of location or season, *A. halimus* contained significantly ($P < 0.001$) higher levels of oxalate (7.01%) compared with *A. nummularia* (6.20%). The oxalate content in the 2 shrub species ranged between 4.17% and 10.67% and averaged 6.5%. The oxalate values reported in this study are within the range of values (4-1%) reported in various studies reviewed by Barry and Blaney (1987). A significant ($P < 0.0001$) location x shrub species interaction in oxalate content resulted from high levels of oxalates in *A. halimus* (7.84%) and low levels of oxalates in *A. nummularia* (5.97%) at the Khalideyah site. The soils of this site are characterized by high salt content.

Season

Seasonal variations greatly affected the level of oxalate in *A. halimus* and *A. nummularia*. The 2 saltbush species contained much higher levels of oxalate during spring (8.96% and 7.62%) compared to fall season (5.06% and 4.78%) for *A. halimus* and *A. nummularia*, respectively. Moisture stress during the fall season may have reduced oxalate levels, or mature tissue synthesized less oxalate (Ellern et al. 1974). During the fall season, there was no significant difference in oxalate content between the two-saltbush species, whereas, in the spring, plants of *A. halimus* accumulated more oxalate than *A. nummularia* (Table 1). There was a significant ($P < 0.0001$) location x season interaction in oxalates content due to variations in soil salinity among the experimental sites.

Table 1. Seasonal changes in oxalate levels¹ in *Atriplex halimus* and *Atriplex nummularia* plants growing at 3 locations in the arid region of Jordan.

Location	Spring		Fall	
	<i>A. halimus</i>	<i>A. nummularia</i>	<i>A. halimus</i>	<i>A. nummularia</i>
	----- (%) -----			
Khanasry	8.53 ± 0.20b ²	7.80 ± 0.18c	5.35 ± 0.18d	5.37 ± 0.18d
Muwaqqar	7.67 ± 0.20c	7.29 ± 0.18c	4.83 ± 0.18de	4.80 ± 0.16e
Khalideyah	10.67 ± 0.18a	7.77 ± 0.20c	5.00 ± 0.16de	4.17 ± 0.18f
Species mean ³	8.96a	7.62b	5.06c	4.78c
Season mean ³	8.29a		4.92b	

¹Least square means as % on dry matter basis ± standar error.

²Means within columns and rows followed by the same letter are not significantly different at the 0.05 level of probability.

³Means within a row followed by the same letter are not significantly different at the 0.05 level of probability.

Table 2. Seasonal changes in levels¹ of total phenolic compounds, non-tannic phenols, tannic phenols, condensed tannins and hydrolyzable tannins in *Atriplex halimus* and *Atriplex nummularia* plants growing at 3 locations in the arid region of Jordan.

Location	Spring		Fall	
	<i>A. halimus</i>	<i>A. nummularia</i>	<i>A. halimus</i>	<i>A. nummularia</i>
	----- (%) -----			
Total phenols				
Khanasry	1.98ab ²	1.22c	1.10c	1.09c
Muwaqqar	2.15a	1.69b	1.48bc	2.04a
Khalideyah	2.28a	1.43bc	2.28a	0.71d
Location mean ³	2.14a	1.45b	1.62b	1.28bc
Season mean ³	1.79a		1.45b	
Non-tannic phenols				
Khanasry	0.14c	0.28a	0.13c	0.05d
Muwaqqar	0.12c	0.21b	0.07cd	0.14c
Khalideyah	0.23b	0.25b	0.22b	0.09c
Location mean ³	0.16b	0.25a	0.14c	0.09d
Season mean ³	0.21a		0.12b	
Tannic phenols				
Khanasry	1.84a	0.95c	0.97c	1.03c
Muwaqqar	2.02a	1.48b	1.40b	1.91a
Khalideyah	2.03a	1.18bc	2.05a	0.61d
Location mean ³	1.97a	1.20c	1.47b	1.18c
Season mean ³	1.58a		1.33b	
Condensed tannins				
Khanasry	1.57a	0.74e	0.63e	0.68e
Muwaqqar	1.08c	1.15c	0.85d	0.72e
Khalideyah	1.25b	1.05c	0.89d	0.44f
Location mean ³	1.30a	0.98b	0.79c	0.61d
Season mean ³	1.14a		0.70b	
Hydrolyzable tannins				
Khanasry	0.27cd	0.21d	0.33cd	0.36cd
Muwaqqar	0.95ab	0.32cd	0.54c	1.18a
Khalideyah	0.78bc	0.13d	1.16a	0.17d
Location mean ³	0.67a	0.22b	0.68a	0.57a
Season mean ³	0.44b		0.62a	

¹Least square means as % on dry matter basis. Standard errors of least square means are 0.11, 0.01, 0.11, 0.03 and 0.11 for total phenols, non-tannic phenols, tannic phenols, condensed tannins and hydrolyzable tannins, respectively.

²Means within columns and rows for each parameter followed by the same letter are not significantly different at the 0.05 level of probability.

Clipping

Clipping had no effect on the oxalate concentrations of saltbush plants, 4.99% in unclipped twigs versus 4.80% in regrowth. Clipping was confined to some twigs and not for the whole shrub. This lenient clipping was not severe enough to induce substantial differences in oxalate synthesis of saltbush plants.

Shrub Age

A significant interaction ($P < 0.001$) existed between shrub species and age. Seedlings of *A. nummularia* contained more oxalate than old plants (9.65% and 7.63%, $P > 0.0001$), whereas old shrubs of *A. halimus* (10.69%) contained more oxalate than the young seedlings (8.8%) ($P < 0.0001$). Young seedlings of *A. nummularia* contained more oxalate (9.65 %) than the seedlings of *A. halimus* (8.83%) ($P < 0.005$). During early stages of growth, there is a rapid rise in oxalate content followed by a decline in oxalate level as the plant matures (Davis 1981, Hodgkinson 1977).

Tannins

Shrub Species

Atriplex halimus contained more total phenols (1.88% vs 1.36%), tannic phenols (1.72% vs 1.19%), condensed tannins (1.0% vs 0.80%) and hydrolyzable tannins (0.6% vs 0.3%) than *A. nummularia* ($P < 0.0001$) (Table 2). Levels of tannic phe-

nols in the 2 saltbush species varied between 0.61% to 2.05% and averaged 1.46%. These values are much higher than those reported by Davis (1981) for various saltbush species in different countries (0.32% to 0.9%). Variation in levels of tannins among saltbush plants and even within the same species could be attributed to differences in soil and climatic conditions of the sites (Barry and Blaney 1987). Difference in plant ability to synthesize tannins is well-documented (Mangan 1988, Davis 1981). These higher levels of tannins in the tissues of *A. halimus* may explain its low palatability compared to the browse of *A. nummularia*.

The type of tannins is more important than the quantity of tannic phenols regarding the nutrition of animals. The hydrolyzable tannins have adverse effects on health and nutrition of animals compared to condensed tannins which mainly reduce the palatability of feeds. Plants of *A. halimus* contained more condensed and hydrolyzable tannins (1.05 and 0.67%) than those of *A. nummularia* (0.89 and 0.39%). The ratio of hydrolyzable to condensed tannins was 0.64 in *A. halimus* compared to 0.49 in *A. nummularia* plants. A significant ($P < 0.0001$) shrub species by location interaction in condensed tannins resulted from high content of condensed tannins in *A. halimus* (1.07%) and low levels in *A. nummularia* (0.75%) at the Khalideyah site. A similar pattern of shrub species by location interaction ($P < 0.0001$) was also noted for hydrolyzable tannins which peaked to 0.97% in *A. halimus* and dropped to the lowest levels (0.15%) in *A. nummularia* plants.

Season

In spring, saltbush plants contained higher levels of tannic phenols and condensed tannins (1.58% and 1.14%) compared to fall levels (1.33% and 0.70%, respectively) ($P < 0.001$). These results did not agree with the findings of Davis (1981), who observed no significant differences in the levels of tannin phenols in *A. halimus* plants compared to *A. nummularia* in spring and fall seasons.

The temporal variation in tannic phenols resulted from the variation of environmental factors prevailing in the 2 seasons. Saltbush plants synthesized more tannins in the spring season, apparently because of more favorable growth factors prevailing in spring compared to fall season, or due to the higher metabolic rate of the younger tissues. Twigs in the fall season had a low

leaf: stem ratio compared to more leafiness in the spring. Since most of tannins exists in the leaves (Van Soest 1994, Barahona et al. 1997), it was expected that spring growth would contain higher levels of total and condensed tannins than the fall growth and regrowth.

Clipping

Clipping of saltbush plants had no effect on the level of total ($P > 0.3$) or condensed tannins ($P > 0.8$). This means that the severity of defoliation of saltbush shrubs was not enough to stimulate or hinder the ability of plants to synthesize tannic compounds. The lenient and confined clipping of selected twigs did not enhance the biosynthesis of total tannins as a defensive mechanism against herbivores.

Shrub Age

Significant difference ($P < 0.001$) in total tannins existed between young and old plants of *A. nummularia* (2.03% and 1.25%, respectively) but not in *A. halimus* (Table 3). However, condensed tannins were higher in various plants of both species. Young plants tended to produce more condensed tannins than old plants because they are more leafy. Young plants of *A. halimus* contained similar levels of total tannins as young seedlings of *A. nummularia*. However, seedlings of *A. nummularia* contained significantly ($P < 0.01$) higher levels of condensed tannins compared to *A. halimus* seedlings (1.57% and 1.47%, respectively).

Potential Toxicity Problems

Allison et al. (1977) reported that sheep ingesting between 39–51 g of calcium oxalate per day are likely to develop acute signs of toxicity. Theoretically, if sheep consume a diet solely of *Atriplex* plants grown in Jordan, they will ingest about 132 g of calcium oxalate (6.6% calcium

oxalate = 66 g per kg DM x 2 kg per day per sheep = 132 g) and are likely to develop acute signs of toxicity. Practically, the potential of toxicoses due to oxalate levels present in the browse of saltbush is low because of selectivity and adaptation of ruminants to high levels of oxalate. James and Butcher (1972) reported that sheep can consume a diet containing 6% oxalate without showing any toxicity signs. However, these animals developed diarrhea and refused to consume such a diet again. Oxalate poisoning occurs at the point where oxalate is absorbed faster than it can be degraded by ruminal microflora. Animals can gradually adapt increasing populations of oxalate degrading microbes in the rumen. Adapted animals can consume 30% more oxalate than unadapted ones (James 1977). In general, oxalate poisoning is a complex issue. Factors such as chemical form of oxalate, animal maturity, adaptation of animals to saltbush, the composition of the diet, and the availability of water for animals could influence the susceptibility of animals to oxalate poisoning.

Several studies dealt with the problem of toxicity due to high levels of tannins ($> 6\%$) in animals diet (Kumar and Singh 1984). However, animals refused to consume diets containing $\geq 2\%$ tannins (Donnelly and Anthony 1969). Moderate levels of tannins (less than 4%) in forages can have beneficial responses in ruminants due to the increased amount of bypass proteins, resulting in higher growth rates (Nunez-Hernandez et al. 1991). The levels of tannins in the saltbushes grown in Jordan are not expected to have adverse effects on sheep grazing these plantations associated with abundance of herbaceous plants.

Conclusion

In summary, our study showed that the 2 saltbush species contained higher levels of

Table 3. Levels¹ of total phenolic compounds, non-tannic phenols, tannic phenols, condensed tannins and hydrolyzable tannins in *Atriplex halimus* and *Atriplex nummularia* seedlings compared to old plants growing in the arid region of Jordan.

	Seedlings		Old Plants	
	<i>A. halimus</i>	<i>A. nummularia</i>	<i>A. halimus</i>	<i>A. nummularia</i>
	(%)			
Total phenols	2.03b ²	2.41a	2.25ab	1.50c
Non-tannic phenols	0.15c	0.37a	0.23b	0.25b
Tannic phenols	1.88a	2.03a	2.01a	1.25b
Condensed tannins	1.47b	1.57a	1.24c	1.08d
Hydrolyzable tannins	0.41b	0.47b	0.78a	0.17c

¹Least square means as % on dry matter basis. Standar errors of least square means are 0.196, 0.089, 0.007, 0.087, 0.027 and 0.071 for total phenols, non-tannic phenols, tannic phenols, condensed tannins and hydrolyzable tannins, respectively.

²Means within a row followed by the same letter are not significantly different at the 0.05 level of probability.

oxalate, tannic phenols and condensed tannins during spring compared to fall season. *Atriplex halimus* is characterized by high levels of oxalate, tannic phenols, condensed and hydrolyzable tannins than *A. nummularia* which explains its low palatability. Spring clipping of saltbush plants had no significant effect on oxalate or tannins concentration of subsequent clippings taken in fall. The levels of secondary metabolites found in our experiments indicate that if sheep were to consume a diet solely of *Atriplex*, they would be likely to develop acute toxicity symptoms. Future work should examine the different chemical forms of oxalates and tannins in the browse of saltbushes in response to different defoliation intensities and under different environmental conditions.

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Defoliation impacts on *Festuca campestris* (Rydb.) plants exposed to wildfire

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Abstract

Wildfires commonly occur in the Fescue Prairie of Alberta, but little information exists to provide a basis for making grazing recommendations after burning. A wildfire in April 1999 provided an opportunity to study the effect of season and intensity of post-burn defoliation on foothills rough fescue (*F. campestris* Rydb.) in southwestern Alberta. A 3 (date of defoliation) x 2 (defoliation intensity) factorial experiment with 10 replicates (plants) was established in both a burned and a non-burned grassland and analyzed as a nested design. Plants were defoliated once during active vegetative growth (17 May), inflorescence development (2 July), or dormancy (30 September), at either 5 or 15-cm clipped stubble heights in the first growing season after fire. Burning increased tiller numbers by 54% compared to non-burned plants but reduced plant ANPP by 51% in the second growing season. While a single defoliation of burned plants, particularly early in the year, had little effect on growth, delaying defoliation into July decreased tillers 1 year later. Increasing defoliation intensity had the greatest impact on non-burned plants, reducing plant height (15%) as well as tiller (21%) and plant (32%) ANPP in the second year. May defoliation reduced etiolated growth 1 year later regardless of burn treatment. A single grazing event after wildfire does not necessarily appear to detrimentally affect rough fescue; however, the low herbage available immediately after fire may not justify the increased risk to the plant with subsequent grazing.

Key Words: defoliation intensity, deferment, etiolated growth, herbage yield, resilience, tillers

The Fescue Prairie of the Northern Great Plains is characterized by the occurrence of plains rough fescue [*Festuca hallii* (Vasey) Piper] and foothills rough fescue (*F. campestris* Rydb) in the prairie-parkland and foothill regions, respectively. Plains rough fescue is shorter than foothills rough fescue and produces short rhizomes compared with the strongly tufted habit of the latter (Pavlick and Looman 1984). Most fire ecology studies in the Fescue Prairie have been conducted in the Parkland (Bailey and Anderson 1978, Anderson and Bailey 1980, Redmann et al. 1993, Gerling et al. 1995). Although the foothills species of rough fescue

Resumen

Comúnmente ocurren fuegos naturales en las praderas de “Fescue” de Alberta, pero existe poca información en que basar las recomendaciones de apacentamiento después del fuego. Un fuego natural que ocurrió en Abril de 1999 brindó la oportunidad para estudiar el efecto de la época e intensidad de defoliación después del fuego en una pradera de “Foothills rough fescue” (*F. campestris* Rydb.) del sudeste de Alberta. Un experimento factorial 3 (fecha de defoliación) x 2 (intensidad de defoliación) con 10 repeticiones (plantas) se estableció en porciones de pastizal quemado y no quemado y se analizó como un diseño anidado. Las plantas fueron defoliadas una vez en las etapas de crecimiento vegetativo activo (17 de Mayo), desarrollo de la inflorescencia (2 de Julio) o dormancia (30 de Septiembre), la defoliación se efectuó a dos alturas del rastrojo, 5 o 15 cm, y se llevo a cabo en la primer estación de crecimiento después del fuego. El fuego aumento el número de hijuelos en 54% en comparación con las plantas no quemadas, pero redujo la ANPP de las plantas en 51% en la segunda estación de crecimiento. Mientras que una sola defoliación de las plantas quemadas, particularmente a inicio del año, tuvo poco efecto en el crecimiento, retrasando la defoliación hasta Julio disminuyo el ahijamiento en el año siguiente. El aumento en la intensidad de defoliación tuvo el mayor impacto en las plantas no quemadas, reduciendo en el segundo año la altura de la planta (15%), el ahijamiento (21%) y la ANPP de la planta (32%). La defoliación en Mayo redujo el crecimiento etiolado al año siguiente, sin importar el tratamiento de quema. Un solo evento de apacentamiento después de un fuego natural no necesariamente parece tener un efecto detrimental en el “Rough fescue”; sin embargo, el poco forraje disponible inmediatamente después del fuego, puede no justificar el aumento en riesgo para la planta que se corre con el apacentamiento subsecuente.

cue might be expected to have a similar response to fire, this premise remains untested.

Rough fescue loses vigor when grazed during the growing season (Looman 1969). Burning may reduce rough fescue abundance (Bailey and Anderson 1978, Antos et al. 1983) and productivity (Jourdonais and Bedunah 1990, Gerling et al. 1995). While considerable research has addressed the effects of grazing on Fescue Prairie (Barker and Erickson 1971, Wright 1974, Willms et al. 1985), no information is available on the cumulative effects of grazing following wildfire on foothills rough fescue plants. Previous research has shown that grazing can affect the subsequent recovery of native bunchgrasses such as Idaho fescue (*F. idahoensis* Elmer) and bluebunch wheatgrass [*Pseudoroegneria spicata* (Pursh) A. Löve subsp. *Spicata*] after wildfire (Bunting et

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al. 1998). Recent increases in wildfire occurrence in the Fescue Prairie (Bork et al. 2002) indicate information specific to foothills rough fescue is needed to develop appropriate guidelines for grazing following fire.

In April 1999, a small wildfire in the Foothills region of Alberta provided an opportunity to study the effects of defoliation following burning on foothills rough fescue plants. The study was specifically designed to evaluate the resilience of plants subjected to variation in the season and intensity of defoliation over a 2 year period.

Materials and Methods

Site Description

The study was conducted in southwest-ern Alberta (50°11'30" N, 113°53'30" W; 1,366 m above sea level) within the Fescue Prairie ecoregion on the eastern slopes of the Porcupine Hills (Strong and Leggat 1992). The area was lightly grazed from 1949 until 1982 when it was fenced to exclude livestock. The plant community was a foothills rough fescue—Parry oat grass (*Danthonia parryi* Scribn.) type indicative of the modal range for the region (Wroe 1972, Strong and Leggat 1992).

The regional landform is rolling moraine upland. The local range site had a slope of approximately 8% with a southerly aspect and is well-drained on loamy parent material. Soils on the site have been classified as Orthic Black Chernozems (Udic Haploboral) developed on till over-lying sandstone (Dormaar and Willms 1990). The climate is dry subhumid with a mean annual precipitation of 444 mm (Table 1). In 1999 and 2000, annual precipitation was 399 and 264 mm, respectively. Growing season (April–August) precipitation during those same years was 123% (351 mm) and 60% (171 mm), respectively, of the long-term mean.

Wildfire Description

The study site was burned by a 1-ha wildfire around 2 pm on 7 April 1999. The average daily wind speed on the day of the fire was 30 km hour⁻¹ (AAFC, unpublished climate data) and air temperatures averaged 6.7° C with a low of 0.9° C and a high of 13° C. Relative humidity in the morning was 50%, dropping to 30% at the time of the fire. The litter fuel load in the area was assessed at 6,372 kg ha⁻¹ in 1999 (AAFRD-Public Lands Division, unpublished data). The fire occurred immediately following snowmelt but before the initiation of plant growth. Although only a small area was burned, the fire was intense and inflicted considerable visible damage (e.g., pitting) to rough fescue tussocks.

Although this study involved a single burn and is therefore unreplicated, variability in fuel loading and microclimatic conditions at the ground surface typically results in variable treatment exposure among individual plants, which was considered the experimental unit in this investigation. Immediate containment of the fire on the windward side ensured that rough fescue plants sampled on either side of the fire boundary were on the same range site.

Methodology

The effects of defoliation intensity following burning were evaluated in a 3 (season of defoliation) x 2 (defoliation intensity) factorial experiment using 10 replicates (plants) of each treatment combination within each of the burned and non-burned areas. Rough fescue plants (N = 120) having a diameter of 15 to 20 cm near the base were randomly selected from within the burned and adjacent non-burned areas following the fire and permanently marked.

Defoliation dates were 17 May (active vegetative growth), 2 July (inflorescence development), or 30 September (dormant). Defoliation intensities were 5 and 15-cm clipped stubble heights. All defoliation treatments were imposed only during

1999, the first growing season following fire, by clipping to the prescribed height. Harvested phytomass was oven-dried and weighed to determine defoliation intensity. An additional 10 plants were randomly selected in each of the burned and non-burned areas for measurement to serve as a check. These plants were added for qualitative comparisons only and were not part of the main design.

In spring 2000, 2 of 10 plants from each treatment were assessed for etiolated growth. Prior to spring green-up, all standing dead plant material was removed to a 5-cm stubble height. Cones were then placed over these plants down to soil around the outside base to exclude light and all etiolated growth clipped bi-weekly to ground level commencing 2 May until growth ceased. All harvested material was oven-dried and weighed.

Tiller counts were made on all plants in September 1999 at the time of the final defoliation treatments. These counts were subsequently repeated on all non-etiolated plants in the third week of May, second week of July, and last week of September 2000, in order to assess the residual treatment effects of burning and defoliation on tiller demography throughout the following growing season. Inflorescences were counted in July 1999 on all plants defoliated earlier in May and of all plants marked for defoliation in September. In addition, inflorescences were counted on all non-etiolated plants in July 2000. Plant heights were measured at the same time as tiller counts were undertaken on all undefoliated plants in 1999 (i.e., September) to assess the effect of burning alone, and of all plants in 2000. Plant height was measured as the average extended length of tillers. Maximum above-ground net primary production (ANPP) was harvested near ground level on 30 September, 2000, oven-dried, and weighed. Average tiller weights (mg tiller⁻¹) were determined for each plant using ANPP and tiller count data.

Table 1. Winter (January to March, November to December), monthly growing season, and 40-year average precipitation on the Fescue Prairie AAFC sub-station near Stavelly, Alberta, from 1997 to 2000.

Year	Jan–Mar	April	May	June	July	Aug.	Sept.	Oct.	Nov–Dec	Total
	(mm)									
1997	21.9	21.4	138	73.1	28	77	34.9	0.2	4.9	399.4
1998	47.5	27.9	169.6	186.9	129.7	16.2	25.3	12.5	31.9	647.5
1999	10.9	66.2 ¹	71.6	109	53.9	50.3	15.6	8.6	12.6	398.7
2000	23	27	16.6	66.2	13.1	48.1	59.9	1.6	8	263.5
40-yr average	76.2 ²	27.2 ²	61.8	84.1	56.1	56.8	40.8	22.6	44.8 ²	444.3 ²

¹Indicates time of wildfire, 7 April 1999.

²Data from the Claresholm Meadows Creek, Alberta climate station, 1961–1990 (Environment Canada 1998).

Statistical Analyses

All data were analyzed using a split-plot design (Steel et al. 1997). Given the lack of replication of fire, burn treatment was considered the whole plot, with defoliation regimes nested within individual burn treatments. Analysis was done using ANOVA (Proc GLM, SAS Institute Inc. 1991), with an emphasis on defoliation and burn by defoliation effects. Where significant results were found, comparisons were made among seasons and/or intensities of defoliation within individual burned and non-burned treatments. Fescue plant responses examined included phytomass removed in 1999, ANPP levels and maximum plant height in 2000, as well as tiller and inflorescence numbers in 1999 and 2000. Probability values for the differences of the least-square-means were adjusted for multiple comparisons according to Tukey's procedure. Inflorescence numbers were analyzed as percent of total tillers to adjust for unequal tiller numbers per plant. Tiller count and weight data were normalized using a square root transformation to meet the conditions of normality based on the Shapiro-Wilk statistic and homogeneity of variance based on Levene's test (Steel et al. 1997).

To evaluate changes in tiller demographics, the percentage change in tiller numbers per plant was analyzed using a repeated measures multivariate analysis of variance (MANOVA, SAS Institute Inc. 1991). This procedure tested for the pattern of correlation between treatment effects and seasonal changes in rough fescue tiller numbers based on sequential sampling from September 1999 through May, July, and September of 2000. The process of evaluating percent changes in tiller numbers through time also circumvented the problem that initial, pre-wildfire tiller counts were not available for use as a covariate. Data on percent change in tillers per plant were also normalized using a square root transformation.

Results

First-Year Effects

Phytomass yields in the first growing season after burning (1999) were partly an artifact of the nature of the harvesting treatments and did not reflect a plant response to clipping (Tables 2 and 3). Nevertheless, the observations provide an opportunity to compare growth and associated opportunities for livestock grazing, as defined by the harvest date, between burned and non-burned plants when cut at

Table 2. Interactive effects of spring wildfire, season of clipping, and clipping height on plant and tiller characteristics of *Festuca campestris* plants (n = 10) in September 1999. Analysis of phytomass harvested and tiller numbers performed on square root transformed data.

Factor	df	Phytomass Harvested		Tillers	
		Tillers (mg • tiller ⁻¹)	Plant (g • plant ⁻¹)	Total (no • plant ⁻¹)	Inflorescence ¹ (% of total)
-----Probabilities-----					
Burn (B)	1	N/a	N/a	N/a	N/a
Season of Clipping (S)	2	<0.001	<0.0001	0.03	0.25
Clipping Height (H)	1	<0.001	<0.0001	0.19	0.01
B x S	2	0.12	<0.001	0.08	0.74
B x H	1	0.88	0.15	0.81	0.01
S x H	2	0.02	0.03	0.43	–
B x S x H	2	0.18	0.70	0.59	–

¹Analysis of % reproductive tillers per plant is based only on spring defoliated and non-defoliated plants due to interference of July clipping with inflorescence production (d.f. = 1 for all variables tested).

the same stubble height. Burned plants had tiller and plant phytomass levels that were 69 and 51% lower, respectively, than non-burned plants (Table 3). Burned plants also exhibited a marked reduction in spring growth leading to a burn by season interaction ($P < 0.001$), which was reflected in lower herbage yields throughout the year. For example, burned plants harvested in May and September yielded only 4 and 41% the phytomass of their non-burned counterparts, respectively (Table 3). As expected, defoliation later into the year increased harvested yields ($P < 0.001$), particularly at the 5-cm clipping height (Table 3).

The reduction of plant and tiller phytomass after burning was associated with a

reduction in plant height by September 1999, from an average of 54 (± 5) to 25 (± 4) cm. Although burning had little effect on tiller numbers at the end of the first growing season, tillering was significantly altered by the phenological stage when defoliation occurred ($P = 0.03$). Tiller counts taken in September indicated that plants harvested in May (active vegetative growth), July (inflorescence development), and September (dormancy) had an average of 120, 98, and 128 tillers, respectively, with burned and non-burned plants responding in a similar manner ($P = 0.08$).

In 1999, inflorescence production was also affected by a burn by clipping height interaction ($P = 0.01$). Burned plants produced few seedheads regardless of clip-

Table 3. Phytomass harvested at 3 dates and 2 stubble heights from burned and non-burned *Festuca campestris* plants (n = 10) during the first growing season (1999) after spring wildfire. Results of ANOVA are given in Table 2.

Treatment	Tiller Phytomass (mg • tiller ⁻¹)	Plant Phytomass (g • plant ⁻¹)
Burn x Season of Clipping		
Burn		
May	6.4	0.4 c ¹
July	23.5	2.9 b
Sept	61.7	5.3 a
Pooled Mean	30.6	2.9
Non-burned		
May	99.1	9.0 b
July	82.4	10.7 ab
Sept	115.8	13.0 a
Pooled Mean	99.1	10.9
Interaction SE mean	10.2	0.9
Clipping Height x Season of Clipping		
5-cm		
May	67.1 b ²	5.7 c ²
July	67.2 b	8.8 b
Sept	128.1 a	12.9 a
15-cm		
May	38.4 a	3.7 b
July	38.6 a	4.8 a
Sept	49.4 a	5.4 a
Interaction SE mean	10.2	0.9

¹Within a column and burn treatment, means followed by the same letter do not differ significantly ($P > 0.05$).

²Within a column and clipping height, means followed by the same letter do not differ significantly ($P > 0.05$).

Table 4. Interactive effects of burning, season of clipping, and clipping height on plant and tiller characteristics of *Festuca campestris* in September 2000 following exposure to spring wildfire and subsequent defoliation in 1999 (n = 8, except for etiolated growth, where n = 2). Analysis for tillers and ANPP performed on square root transformed data.

Factor	df	ANPP ¹		Height (cm)	Tillers		Etiolated growth	
		Tiller (g • plant ⁻¹)	Plant (no • plant ⁻¹)		Total (no. • plant ⁻¹)	Inflorescence (% of total)	Tiller (mg • tiller ⁻¹)	Plant (g • plant ⁻¹)
(mg • tiller ⁻¹)								
-----Probabilities-----								
Burn (B)	1	N/a	N/a	N/a	N/a	N/a	N/a	N/a
Season of Clipping (S)	2	0.89	0.31	0.65	0.15	<0.0001	0.02	<0.01
Clipping Height (H)	1	0.02	0.05	<0.001	0.47	0.97	0.62	0.78
B x S	2	0.18	0.05	0.13	0.05	0.04	0.16	0.70
B x H	1	0.01	0.02	0.04	0.36	0.70	0.93	0.43
S x H	2	0.24	0.69	0.84	0.74	0.27	0.31	0.42
B x S x H	2	0.91	0.38	0.40	0.17	0.17	0.13	0.55

¹Aboveground net primary production.

ping height (< 0.11% of tillers), while plants not exposed to fire but clipped at 5 and 15-cm stubble heights had 0.43 and 1.76% of their tillers produce an inflorescence, respectively.

Second-Year Effects

Responses in 2000 represented residual effects of defoliation in 1999 (Table 4). In 2000, burned plants continued to have lower tiller and plant yields (i.e. ANPP) compared to non-burned plants, by 69 and 51%, respectively (Table 5). The observed reduction in plant ANPP in September of 2000 with burning coincided with a continued reduction in plant height (58% of non-burned; Table 5) and tillers that weighed 32% that of non-burned tillers (Table 5). Burned plants remained about 60% the height of non-burned plants throughout the summer of 2000 (data not shown).

In contrast to these results, burned fescue plants had greater tiller numbers (203 tillers plant⁻¹) compared to those not exposed to fire (132 tillers plant⁻¹). While the increase in tillers within burned plants occurred primarily before May 2000 (Fig. 1), tiller emergence in non-burned plants was most abundant between May and July of 2000.

Plants defoliated to a 5-cm height in 1999 had reduced tiller (P = 0.02) and plant ANPP (P = 0.05), as well as plant height (P < 0.001) in 2000. These effects, however, were confined to non-burned plants (P < 0.05, Table 5), suggesting burning reduced the impact of the intensive clipping treatment.

Variation in the response of plants to different seasons of clipping was also evident within the burn treatments (P = 0.05). Examination of these data indicated ANPP levels were stable among non-burned plants defoliated at different times the year before (Table 5). In contrast, defoliation of burned plants in July resulted in the lowest

plant ANPP the following year, although post-hoc mean comparisons revealed no significant difference (at P = 0.05). Year-end tiller numbers in 2000 also varied among the seasonal defoliation treatments within the burned and non-burned plants (P = 0.05). Defoliation of non-burned plants prior to September 1999 stimulated tillering the following year (140, 140, and 118 tillers plant⁻¹, with May, July, and September defoliation, respectively), but depressed tillering if applied in July to burned plants (234, 168, and 207 tillers plant⁻¹, with May, July, and September defoliation, respectively). Tiller numbers

within burned and non-burned plants defoliated in September were also similar to the non-defoliated controls for both burned (207 vs 195, respectively) and non-burned (118 vs 114, respectively) plants.

Additional effects were observed of burning and defoliation season on inflorescence production (P = 0.04) in 2000. Defoliation in July resulted in the greatest reduction of inflorescences (Fig. 2), but was most apparent within non-burned plants. Notably, inflorescence production also appeared to increase within the September defoliated plants in both burned and non-burned plants relative to the unde-

Table 5. Effects of different clipping heights and seasons of defoliation on the mean height and ANPP of burned and non-burned rough fescue plants (n = 8), as measured in September 2000 following spring wildfire and defoliation in 1999. ANOVA results are given in Table 4.

Treatment	Plant Height (cm)	Tiller ANPP ¹ (mg • tiller ⁻¹)	Plant ANPP ¹ (g • plant ⁻¹)
Burn x Clipping Height			
Burned			
5-cm	24 a ²	44 a	9.6 a
15-cm	26 a	43 a	8.8 a
Undefoliated	23	46	9.7
Pooled Mean	25	44	9.3
Non-burned			
5-cm	39 b	122 b	15.3 b
15-cm	46 a	153 a	22.4 a
Undefoliated	46	172	20.1
Pooled Mean	43	143	19.0
Interaction SE	1	0.6	1.4
Burn x Season of Clipping			
Burned			
May	25	47	11.5 a
July	23	38	6.5 a ³
September	22	45	9.6 a
Non-burned			
May	38	132	19.5 a
July	43	144	20.3 a
September	39	137	16.7 a
Interaction SE	1	0.8	1.7

¹Aboveground net primary production.

²Within a column and burn treatment, means followed by the same letter do not differ significantly (P > 0.05).

³Burned July plant ANPP differs from May (0.05 < P < 0.10).

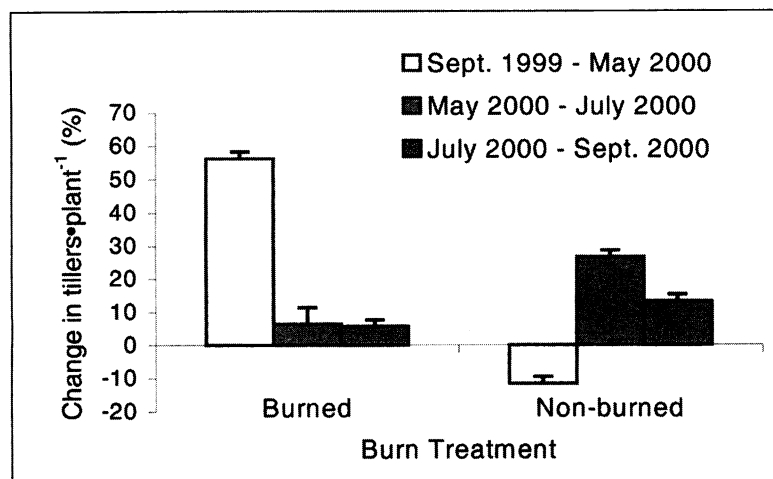


Fig. 1. Seasonal changes in tiller numbers (\pm SE) from September 1999 to September 2000 on burned and non-burned plants following a spring wildfire in 1999 ($n = 8$). Changes in tiller number were affected ($P < 0.0001$) by the measurement interval and the burning treatment as evaluated by multivariate analysis of variance for repeated measures.

foliated controls (Fig. 2). In contrast, clipping intensity had no effect ($P > 0.05$) on inflorescence production (Table 4).

Finally, burned plants had 44% less etiolated growth of tillers compared to non-burned plants (Table 6), and May defoliation the previous year resulted in significantly less ($P < 0.05$) etiolated growth at both the tiller and plant level (Table 6). The effect of defoliation intensity and season, however, were similar ($P > 0.05$) between burned and non-burned plants.

Discussion

Response to Burning

Foothills rough fescue plants had reduced yields the first and second growing seasons after spring burning, which is comparable to Redmann et al. (1993) and Gerling et al. (1995) for plains rough fescue. The yield reductions in the present study were related to burning resulting in shorter, lighter tillers, and occurred despite a 50% increase in tiller numbers in burned plants during the second year. These results indicate that tiller recruitment by burning could not compensate for depressed tiller weights over the 2 years of monitoring conducted here. This pattern may be related to re-allocation of limited plant resources such as carbohydrates to a greater number of tillers, particularly as they become larger with age throughout the growing season, post-burn conditions related to litter removal (Redmann 1978, Savage 1980) and precipitation.

Precipitation during the first growing season after fire was near average, however, precipitation to the end of the second growing season was only about 54% of the long-term average (Table 1). Reduced precipitation may have limited plant growth in the second year. Given the loss of litter with burning and its importance for growth (Willms et al. 1986), moisture deficits were also likely exacerbated by the fire.

Although burning decreased plant ANPP, height and inflorescence production, suggesting a negative response to burning, a more reliable indicator of plant response may be tiller numbers as it represents longer-term productive potential. Using tiller numbers as a standard, burning may have improved plant vigor by stimulating tillering, thereby supporting the notion that rough fescue is both adapted to, and the beneficiary of, fire. Coincident changes in etiolated growth, however, showed no effect ($P > 0.05$) of burning on the plant but a reduction for individual tillers (Table 6). Etiolated growth is positively correlated with carbohydrate levels in the roots and crowns of grasses (Raese and Decker 1966, Dorvat et al. 1972). The reduction in energy at the tiller level in burned plants suggests some susceptibility to further damage should tiller development be impeded. Burning foothills rough fescue has been shown to increase individual plant production 3 years after wildfire, but increased plant mortality of burned plants resulted in lower total fescue production compared to non-burned areas (Antos et al. 1983).

Therefore, enhanced tiller numbers following burning are likely to benefit future production only when plant mortality is limited. No mortality was documented in the current study.

Although the results here focus on rough fescue plants, their response is not necessarily indicative of the entire grassland because the reproductive capacity of many plant species are uniquely adapted to filling ecological niches in the post-fire environment. Increased forb biomass after a late winter wildfire helped compensate for a reduction in grass production by the second year after burning in a grassland similar to the present study (Bork et al. 2002).

Response to Post-Burn Defoliation

Given that post-burn grazing or regrowth by wildlife was likely common prior to European settlement, the postulation might be made that rough fescue can tolerate this pattern of disturbance. However, the decision to graze with livestock in the year after burning might be based as much on the benefits to animals as on the effect to the plant. By May, the time when grazing normally begins on Fescue Prairie, burned plants had produced only 5% the biomass of non-burned plants, which subsequently increased to only 40% by September. Thus, available forage for grazing declined markedly with burning.

Results indicate that clipping of burned plants in early spring did not produce a cumulative negative effect on plant recovery. Burning appeared to increase plant resilience to post-burn harvesting by slowing growth and minimizing exposure of regrowth to defoliation. Nevertheless, plant energy reserves were lowest in

Table 6. Effects of spring wildfire and subsequent date of defoliation in 1999 on the ANPP¹ of etiolated tillers and plants in May 2000.

Plant	Treatment (mg • tiller ⁻¹)	Tiller (g • plant ⁻¹)
Burn Treatment ($n = 12$)		
Burned	9.0	1.6
Non-burned	16.2	1.8
SE mean	1.8	0.23
Season of Clipping ($n = 8$)		
May	7.4 b ²	1.2 b
July	14.0 ab	1.5 ab
September	16.3 a	2.5 a
SE mean	2.2	0.28
Undefoliated Control ($n = 4$)	16.3	1.5

¹Aboveground net primary production.

²Within a column and burn treatment, means followed by the same letter do not differ significantly ($P > 0.05$).

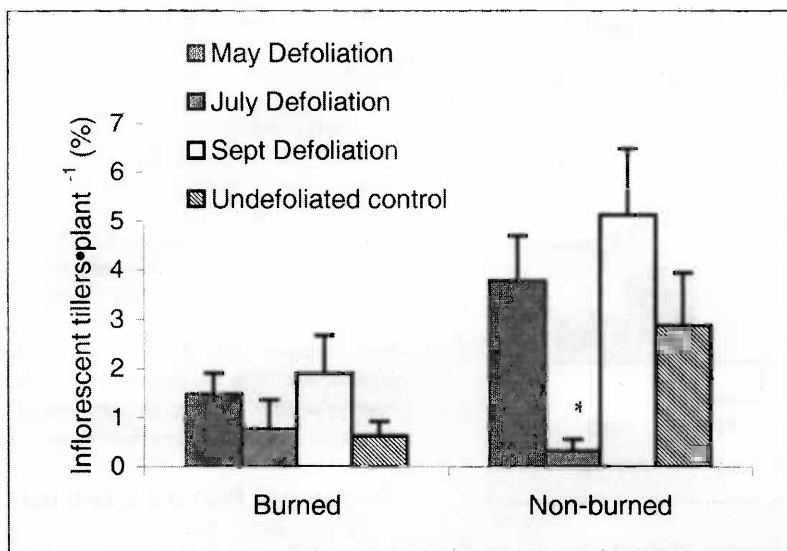


Fig. 2. Changes in the proportion of inflorescences (\pm SE) in July, 2000 on burned and non-burned plants following a spring wildfire in 1999 and subsequent defoliation at 3 dates ($n = 8$). Within the unburned treatments, the July clipping (denoted with a *) differs from May and September ($P < 0.05$).

plants defoliated the previous year in May (Table 6), regardless of their burn status, which indicates vulnerability to spring grazing and supports the commonly held belief that grazing should be delayed in spring to benefit plant vigor. Burned plants of Idaho fescue had greater mortality when defoliated in early summer compared to early fall (Bunting et al. 1998). Although plants tend to become more vulnerable to defoliation at the time of inflorescence development (i.e., July) due to the re-allocation of energy to seed production (Branson 1953), rough fescue plants in this study produced very few inflorescences relative to the total number of tillers (Fig. 2). Inflorescence production in 2000, however, did exhibit a general reduction the following year within plants defoliated the previous July (Fig. 2). This observation, coupled with a marginal trend towards a decline in plant ANPP (Table 5) and a marked reduction in tiller numbers within burned plants defoliated during July, suggests deferral of grazing beyond inflorescence development is warranted, particularly if plant recruitment is desired.

In contrast to the season of defoliation, severity of defoliation had no effect ($P > 0.05$) on any plant response variable measured within burned plants. Burned plants had a linear pattern of growth from May to September, which may indicate that sufficient photosynthetic tissue remained after severe defoliation to restore the plant energy requirements under conditions favorable for growth in the first year.

More severe defoliation of non-burned plants, particularly those defoliated at 5 cm, resulted in declines in height as well as tiller and plant ANPP 1 year after defoliation. The different response to clipping between burned and non-burned plants may be partly related to the relative proportion of herbage removed from plants and the photosynthetic area remaining after clipping. Clipping at a fixed height will remove a greater proportion of total herbage from tall, rapidly growing non-burned plants compared with shorter, burned plants, and likely accounts for the differing phytomass levels harvested in 1999. This resulted in clipped, non-burned plants having greater treatment differences than burned plants. Similar mechanisms have been suggested for the effect of water stress on subsequent defoliation in grasses (Simone and Baruch 1991), and highlights a limitation of the common practice of using fixed clipping heights as a replacement for actual grazing.

Morphological differences in burned and non-burned plants may also be important. Unlike burned plants, tiller sheaths in non-burned plants remained intact below the height of defoliation, shielding the enclosed leaf tissue. Clipping at 15 cm, however, may still leave some photosynthetic surface exposed. Additionally, the clipping height of 5 cm used in this investigation represents a relatively severe defoliation, which livestock grazing may only achieve when stubble had previously been removed by burning or severe grazing.

It should be noted that the single defoliation treatment we applied more closely simulates the effect of short duration or high intensity-low frequency grazing rather than season-long grazing. Multiple harvests during the growing season, as might occur under season-long grazing, has been shown to severely reduce yields of rough fescue plants and increase mortality (Willms and Fraser 1992). However, the results found here do support the findings of Willms (1991) suggesting that the effects of defoliation on plant yield may only be fully evident in the second year after treatment.

Plant responses to burning or defoliation are also dependent on previous disturbances. In our study, individual fescue plants had a long history of protection from grazing, which was likely to produce stability within plant vigor and its local environment. Although tiller demographics have not been documented for rough fescue, it appears that individual tillers can be several years old prior to producing an inflorescence. In our study, very few plants produced inflorescences in either year and tillers became more robust over time. Therefore, it is likely that initial disturbances have the greatest impact in upsetting the energy dynamics within fescue plants, while the effect of subsequent disturbance is dependent on factors such as recovery time. In our study, clipping represented the initial disturbance of non-burned plants and could be expected to have a greater effect than in slower growing burned plants.

Tillering is perhaps the most important response to disturbance as it determines the future potential productivity within the plant (Murphy and Briske 1992). Both burning and clipping increased overall tiller numbers, which implies enhanced productive potential. However, this trend also coincided with a decline in the potential for sexual reproduction, as evidenced by a decrease in the proportion of inflorescent tillers. July defoliation appeared to be particularly detrimental, reducing the proportion of seedheads 1 year later from about 5% to less than 1% of all tillers, indicating longer-term impacts due to defoliation can occur on sexual recruitment within rough fescue.

Management Implications

Although burning may impede various aspects of development in foothills rough fescue plants, it also represents a potential mechanism for plant renewal through

enhanced tiller production. Its also appears that spring burned fescue plants can be safely grazed in a single defoliation event during the early part of the first growing season if the environmental conditions are favorable for recovery. This tolerance is probably linked to slow plant growth limiting the impact of subsequent defoliation. Despite this, limited available forage from burned plants may not warrant the potential risk to the plant under most grazing systems as burning could facilitate grazing close to the crown and lead to a loss of plant vigor. In addition, burned plants appear to increase in sensitivity to July defoliation during the post-burn recovery growing season, potentially due to a delay in plant growth coinciding with burn-induced stress. In conclusion, both plant physiological (carbohydrate) and morphological (height, ANPP, tillers, and inflorescence) characteristics exhibited marked responses into the second year following burning and defoliation, suggesting that the risk associated with grazing burned fescue plants may be greater than any potential benefits in the short-term. Finally, these results also highlight the importance of longer-term monitoring and management to maximize the recovery of foothills rough fescue plants exposed to defoliation or fire.

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Vegetation indices, CO₂ flux, and biomass for Northern Plains Grasslands

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Abstract

Native grasslands are a sink for atmospheric CO₂ sequestration, but ways for extending site-specific CO₂ flux measurements to a regional scale are lacking. Objectives of this study were to determine the utility of using canopy radiometric reflectance for estimating CO₂ fluxes for semiarid grasslands. The relationship between the normalized difference vegetation index (NDVI) calculated from spectral reflectance data obtained with hand-held radiometers was compared to CO₂ flux calculated from Bowen ratio/energy balance measurements. Carbon dioxide flux was measured during the plant growing season over a nongrazed prairie, grazed prairie, and a shrub dominated prairie site near Mandan, N.D. Measurements were also made of evapotranspiration (ET), green biomass, and green leaf area index (LAI). Correlation coefficients of NDVI with vegetation parameters of biomass and LAI for each site and year exceeded 0.84 in 1999, 0.74 in 2000, and 0.91 in 2001; with CO₂ flux correlations exceeded 0.63 in 1999, 0.68 in 2000, and 0.69 in 2001; with ET correlations exceeded 0.91 in 1999, 0.92 in 2000, and 0.90 in 2001. Regression analysis over all years and sites produced a nonlinear relation between NDVI and both biomass ($R^2 = 0.83$) and LAI ($R^2 = 0.77$) and a linear relationship between NDVI and both CO₂ flux ($R^2 = 0.51$) and ET ($R^2 = 0.81$). The relationships between NDVI and biomass, LAI, CO₂ flux, and ET for the 3 grassland sites, which differed in management and vegetation, were generally quite similar suggesting that NDVI has potential for use in predicting canopy CO₂ flux rates for semiarid grasslands in the Northern Great Plains.

Key Words: global carbon cycle, rangelands, Bowen ratio, remote sensing, sequestration

Carbon dioxide flux measurements have shown that grasslands function as a net sink for sequestration of atmospheric CO₂ (Kim et al. 1992, Dugas et al. 1999, Frank et al. 2000, Frank and Dugas 2001, Sims and Bradford 2001). Tropical forests are the largest terrestrial biomass sink for C, containing about 40% of the total C stored in terrestrial ecosystems (Dixon et al. 1994). Grassland ecosystems comprise about one-fifth of the earth's land surface and contain more than 10% of the global C stocks (Eswaran et al.

Resumen

Los pastizales nativos son un depósito de fijación de CO₂ atmosférico, pero faltan maneras de extender los mediciones del flujo de CO₂ realizadas en un sitio específico a una escala regional. Los objetivos de este estudio fueron determinar la utilidad de usar la reflexión radiométrica de la copa para estimar los flujos de CO₂ de pastizales semiáridos. La relación entre el Índice de la Diferencia Normalizada de Vegetación (NDVI) calculada a partir de los datos de reflexión espectral obtenidos con radiómetros manuales se comparó con los flujos de CO₂ calculado a partir de mediciones de la relación Bowen/balance de energía. El flujo de dióxido de carbono se midió durante la estación de crecimiento de las plantas en una pradera no apacentada, en una apacentada y en una pradera dominada por arbustos, situadas cerca de Mandan, N.D. También se hicieron mediciones de evapotranspiración (ET), biomasa verde índice de área foliar verde (LAI). Los coeficientes de correlación del NDVI con los parámetros de vegetación y LAI para cada sitio excedieron 0.84 en 1999, 0.74 en 2000 y 0.91 en 2001, con coeficientes de correlación del flujo de CO₂ mayores a 0.63 en 1999, 0.68 en 2000, y 0.69 en 2001; y correlaciones con ET superiores a 0.91 en 1999, 0.92 en 2000 y 0.90 en 2001. El análisis de regresión a través de todos los años y sitios produjo una relación no lineal entre NDVI y biomasa ($R^2 = 0.83$) y LAI ($R^2 = 0.77$) y una relación lineal entre NDVI y el flujo de CO₂ ($R^2 = 0.51$) y la ET ($R^2 = 0.81$). Las relaciones entre NDVI y la biomasa, el LAI, el flujo de CO₂ y la ET en los 3 sitios de pastizal, los cuales difirieron en el manejo y vegetación, fueron generalmente muy similares, sugiriendo que el NDVI tiene el potencial para ser usado en predecir las tasas de flujo de CO₂ de la copa de la vegetación de los pastizales semiáridos de las Grandes Planicies del Norte.

1993). Temperate-region grassland ecosystems have extensive fibrous root systems for storing C compounds and may be important C sinks for balancing the global C budget (Rastetter et al. 1992, Sundquist 1993, Gifford 1994, Schimel 1995, Keeling et al. 1996, Batjes 1998, Fan et al. 1998).

Native grasslands are a diverse mixture of species that generally occupy landscape sites that have less productive soils than cropland and are often located in regions that receive less precipitation. Although considerable heterogeneity is present in grasslands, the use of remotely sensed data to predict biomass production (Tucker 1977, Aase et al. 1987, Burke et al. 1991, Anderson et al. 1993, Wylie et al. 2002a) and C flux (Wylie et al. 2002b) has been encouraging. A positive relationship between NDVI and biomass or above ground net primary production has been shown for several grassland ecosystems (Pearson et al. 1976, Paruelo et

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al. 1997, Tucker 1977, Aase et al. 1987). Wylie et al. (2002a) showed a strong relationship, an R^2 of 0.85, for the relationship between biomass vs. NDVI for diverse grasslands ranging from about 36° to 52° N latitude in the Great Plains. Others have shown a strong relationship between canopy absorbed photosynthetically active radiation and canopy indices based on reflectance in the red and infrared bands (Anderson et al. 1993, Paruelo et al. 1997), which provides support for the use of vegetative indices, such as NDVI, as an indicator of CO_2 fluxes.

Although prediction of biomass from vegetative indices has shown considerable promise, information on estimating CO_2 fluxes from vegetative indices is limited. Some have used the relation between NDVI and absorbed photosynthetically active radiation (Monteith et al. 1964) as estimates of canopy photosynthesis (Paruelo et al. 1976, Wylie et al. 2002a). Wylie et al. (2002b) found that the time-integrated normalized vegetative index was a strong predictor of day time CO_2 fluxes in a sagebrush-steppe ecosystem, suggesting that this index could be used to scale ecosystem CO_2 fluxes to the regional level. Scaling-up of vegetation responses from the site specific to the regional-global level was identified by Schimel (1995) as a critical area for future research.

Ecosystem CO_2 flux measurements are being made by researchers in coordinated efforts over diverse landscapes; the USDA-Agricultural Research Service Rangeland CO_2 flux Project (Svejcar et al. 1997), Ameriflux Network (Wofsy et al. 1993, Hollinger et al. 1999), and Euroflux Network (Aubinet et al. 2000). There is a need to extend these data from site of measurement to the regional and global scale. The objectives of this study were to evaluate the relationship between NDVI and CO_2 flux, above ground biomass, and leaf area index from 3 semiarid grasslands for purposes of extending CO_2 flux data to a regional scale.

Materials and Methods

Three grassland sites located at the Northern Great Plains Research Laboratory, Mandan, N.D. (latitude 46°46'N, longitude 100°55'W, elevation 518 m) were used in this study. The sites are typical Northern Great Plains mixed-grass prairie dominated by western wheat-grass [*Pascopyrum smithii* (Rydb) Löve], needle-and-thread (*Stipa comata* Trin. and

Rupr.), *Carex* (*Carex* spp.), little bluestem [*Schizachyrium scoparium* (Michx.) Nash], side-oats grama [*Bouteloua curtipendula* (Michx.) Torr.], Kentucky bluegrass (*Poa pratensis* L.) and blue grama [*Bouteloua gracilis* (H.B.K.) Lag. ex Griffiths]. The sites included a long-term (86 yr) continuously grazed historical site (grazed prairie), a site that was grazed prior to 1992 and again after 1999 (prairie), and a grazed site with about 20% of the land area occupied by dense shrub thickets of mainly buffalo berry (*Shepherdia argentea* Nutt.), western snowberry (*Symphoricarpos occidentalis* Hook), and several other tree and shrub species with the remainder of the area being typical grassland (shrub prairie). The grazing intensity for all sites was moderate or about 2.6 ha per steer. Soil at the sites belong to the Werner-Sen-Chama complex (loamy, mixed, superactive, frigid shallow Entic Haplustoll; fine-silty, mixed, superactive, frigid Typic Haplustoll; fine-silty, mixed, superactive, frigid Typic Calcistoll). The sites never had fertilizer or herbicides applied.

Canopy reflectance measurements were obtained with an Exotech 100-BX 4 band radiometer (Exotech Inc., Gaithersburg, Md) with a 15° field of view. The unit was mounted on a portable mast at 2 m above the soil surface. Reflectance in bands 1 (450–520nm) and 2 (520–600nm) were not used in calculations. Reflected radiation in bands 3 or the RED band (630–690nm) and 4 or the NIR band (760–900nm) were measured looking vertically downward from the mast height. Ten readings were taken near the location of each biomass sampling within each site and averaged. Measurements were made on clear days between 1300–1500 hours CDT at 15–21 day intervals from spring greenup in April to fall dormancy in late October in 1999, 2000, and 2001. The radiometer was calibrated prior to taking readings at each site using measurements of a barium sulfate standard panel. The normalized difference vegetative index ($\text{NDVI} = (\text{NIR} - \text{RED}) / (\text{NIR} + \text{RED})$) was calculated as described by Jackson (1983).

Green biomass and leaf area were measured at each site by clipping 4 representative 0.25 m² quadrats within 40 m of the Bowen ratio/energy balance towers on the same day, or if biomass sampling days were cloudy, within several days of making the radiometric measurements. The taller and dense shrub thickets constituted about 20% of the area in the shrub prairie site and were sampled for leaf area index (LAI) during mid-June each year. Leaves

were manually separated from stems, and LAI was measured using a belt-driven photoelectric area meter. Leaves and stems were oven dried (70° C) and weighed to obtain total above-ground biomass.

Concentrations of CO_2 and water vapor were measured every 20 minutes during the growing period from spring greenup in April to late October in 1999, 2000, and 2001 using Bowen ratio/energy balance instrumentation towers (Model 023/ CO_2 Bowen ratio system, Campbell Scientific, Inc., Logan, Ut.) located centrally at each site to provided at least 200 m of fetch in all directions from the towers. Evapotranspiration (ET) was measured simultaneously with CO_2 flux. Fluxes were calculated using methods described by Dugas (1993) and Dugas et al. (1999). Bowen ratios were calculated from temperature and humidity gradients measured every second at 1 and 2 m above the canopy. Sensible heat flux was calculated from the Bowen ratio, average net radiation was measured using a model Q*7.0 and 7.1 net radiometer (REBS, Seattle, Wash.), and soil heat flux was calculated from 2 soil heat flux plates (Model HFT, REBS) with soil temperature measured by thermocouples above the plates. Net radiometers were calibrated against a laboratory standard (Model 7.1, REBS) over grass each year before use. Plant height was measured at least 3 times each growing season and was occasionally used in calculation of turbulent diffusivity (Dugas et al. 1999). The turbulent diffusivity, assumed equal for heat, water vapor, and CO_2 , was calculated using the 20-minute sensible heat flux and temperature gradient measurements. Twenty-minute averages of CO_2 and water vapor flux, corrected for vapor density differences at the 2 heights (Webb et al., 1980), were calculated as a product of turbulent diffusivity and the 20-minute average CO_2 and water vapor gradient measured every second at 1 and 2 m above the canopy. When the Bowen Ratio/Energy Balance (BREB) method for calculating turbulent diffusivity was not valid because of differences in the sign of the flux and the gradient, diffusivity was calculated using wind speed, atmospheric stability, and canopy height (Dugas et al. 1999). This alternate method of calculation of diffusivity was used very infrequently to calculate the daytime flux measurements. Carbon dioxide and water vapor concentration gradients between the 2 heights were measured with infrared gas analyzers (Model 6262, Li-Cor Inc., Lincoln, Nebr.) that were calibrated week-

ly. Fluxes were not corrected for temperature differences in the 2 air streams because in a separate test, fine-wire thermocouples indicated air temperatures from the 2 heights did not differ when entering the gas analyzer (unpublished observations). Soil water content was measured at 3.8 cm depth with time-domain reflectometry methods (Model CS615 Water Content Reflectometer, Campbell Scientific Inc.) every 20 minutes and averaged daily. All data generated from the Bowen ratio/energy balance system were stored in a model 21X data logger (Campbell Scientific Inc.).

The Bowen ratio/energy balance method is an indirect method compared to the direct eddy covariance method of measuring CO_2 fluxes. Bowen ratio calculations use measurements of air temperature and humidity gradients, net radiation, and soil heat flux for estimating surface latent heat flux. The Bowen ratio may become highly variable especially during instances of stable atmospheric conditions when diffusivities for heat and water vapor become very small. Such conditions generally occur near dusk and dawn and would be excluded from our data set since we removed fluxes at radiation levels less than 25 W m^{-2} . Reports using the Bowen ratio/energy balance method for measuring CO_2 fluxes over grasslands have been made by Dugas et al. (1997), Dugas et al. (1999), Frank et al. (2000), Frank and Dugas (2000), Sims and Bradford (2001), and Frank (2002). Angell et al. (2001) showed CO_2 fluxes from the Bowen ratio/energy balance method were very similar to those for closed chamber measurements for both daytime and nighttime flux measurements on a sagebrush steppe site.

Daily CO_2 flux and ET was calculated for the daylight period or when net radiation exceeded 25 W m^{-2} , which approximates the period between sunrise and sunset. Daily flux were then averaged for the time interval between reflectance readings. Regression and correlation analysis were used to evaluate the relationship between CO_2 flux, ET, biomass, and LAI with NDVI using SAS (SAS Institute 1989).

Results and Discussion

Precipitation received during the flux measurement period was 520 mm in 1999, 337 mm in 2000, and 392 mm in 2001 compared to the long-term average of 320 (Figs 1–3). The long-term (85 yr) annual precipitation total at Mandan is 404 mm. Historically, the greatest average monthly

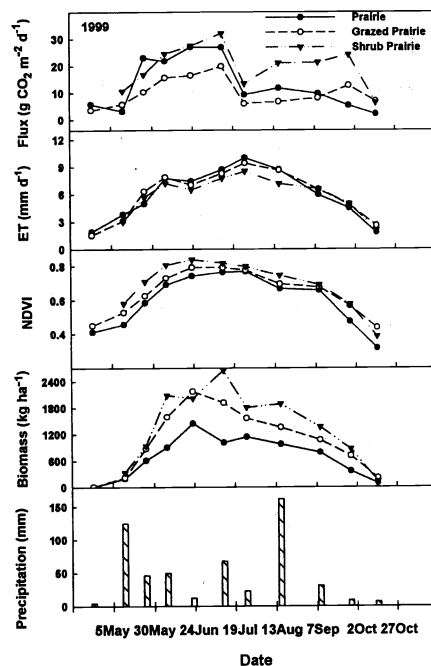


Fig. 1. Seasonal trends of CO_2 flux, ET, NDVI, biomass, and precipitation for a prairie, grazed prairie, and shrub prairie site in 1999.

precipitation occurs in June, when 21% of the annual precipitation is received. Unusually high amounts of precipitation were received in single-day, high-intensity events during May and August 1999.

The temporal dynamics of the biophysical parameters measured at each site were characteristic of cool-season grassland ecosystems in that activities of CO_2 flux, ET, and biomass accumulation increased rapidly in the spring, peaked in early summer, and decreased in late summer through early autumn (Figs. 1, 2, 3). The season-long data for CO_2 flux, ET, and biomass exhibited a similar response pattern across sites and years. This relationship is typical for Northern Great Plains grasslands where air temperature and soil water are the primary driving factors controlling cool-season grass phenology and biomass accumulation (Frank and Bauer 1995). Periods of peak biomass differed slightly among years, but generally occurred during the late-June to late-July period. Peak biomass across all years and sites ranged from $1,804 \text{ kg ha}^{-1}$ for 2000 to $2,088 \text{ kg ha}^{-1}$ in 1999 with an average of $1,936 \text{ kg ha}^{-1}$, which along with an LAI of < 1 (as shown in Fig. 4), indicated that the canopy of these grasslands was generally sparse when viewed from the nadir position.

Flux of CO_2 showed greater variation among sampling periods throughout the 3

years compared to the other measured biophysical parameters (Figs. 1–3). This was especially apparent during a drought period from 12 July to 26 July 1999 or between the sixth and seventh sampling when fluxes decreased sharply for all 3 sites (Fig. 1). The difference in CO_2 flux among sites for periods following the 1999 drought period were greater between the shrub prairie site compared to the prairie and grazed prairie sites than during similar periods in 2000 and 2001. This response may have been due to less leaf senescence following the drought period for the shrubs in the shrub prairie site compared to mainly grass species in the prairie and grazed prairie sites. Differences in CO_2 fluxes for the grazed prairie vs. the prairie (grazed only in 2000) varied only slightly over all periods (Fig. 2).

Period of maximum CO_2 flux varied across years and sites and occurred prior to mid-July each year except for the grazed prairie site in 2000. Peak CO_2 flux per period across years ranged from $28.8 \text{ g CO}_2 \text{ m}^{-2} \text{ day}^{-1}$ for the prairie in 2001 (Fig. 3) to $32 \text{ g CO}_2 \text{ m}^{-2} \text{ day}^{-1}$ for the shrub prairie in 1999 (Fig. 1). The greater CO_2 uptake for the shrub prairie site compared to the prairie and grazed prairie in 1999 was probably due to the greater shrub

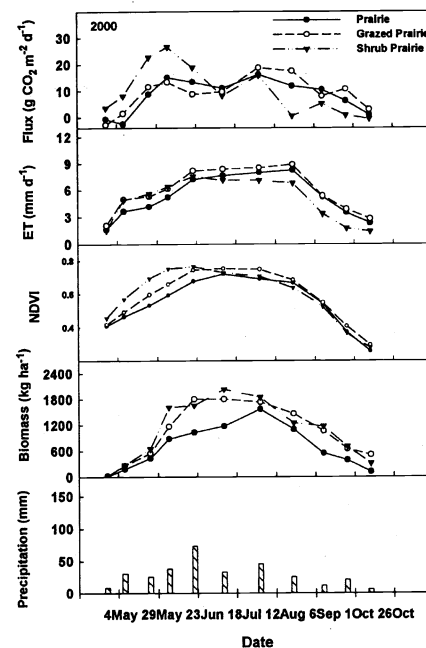


Fig. 2. Seasonal trends of CO_2 flux, ET, NDVI, biomass, and precipitation for a prairie, grazed prairie, and shrub prairie site in 2000.

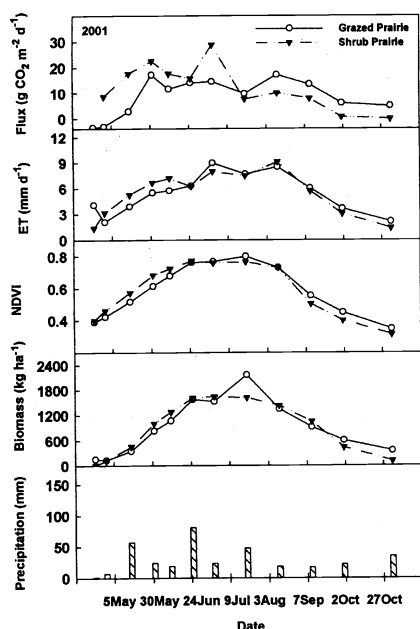


Fig. 3. Seasonal trends of CO₂ flux, ET, NDVI, biomass, and precipitation for a grazed prairie and shrub prairie site in 2001.

green leaf area available for fixing CO₂. Peak LAI of the shrub thicket alone for the shrub prairie site averaged 4.6 compared to 0.7 for the grazed prairie and prairie sites.

Rates of ET showed a similar seasonal pattern as that observed for biomass and CO₂ flux, except that peak ET rates occurred later than those for biomass and CO₂ flux. Peak ET rates ranged from a low of 7.6 mm day⁻¹ for the shrub prairie site in 2000 to 10.0 mm day⁻¹ for the prairie site in 1999. These Northern Great Plains grasslands are typically exposed to high atmospheric evaporative demand and relatively low annual precipitation (404 mm), which results in pan evaporation often exceeding precipitation. Also, cool-season grasslands characteristically have high rates of transpiration as grassland vegetation typically extract all available

soil water to about 120 cm depth by end of the growing season. The slight increase in ET during the drought period in 1999 was probably due to a greater reduction in photosynthesis than plant transpiration in response to water stress causing stomatal conductance to decrease (Cowan 1982) which is similar to that reported by Frank and Berdahl (2001) for Russian wildrye [*Psathyrostachys juncea* (Fisch.) Nevski].

Values of NDVI for each period showed a very similar seasonal responses for the 3 sites. The NDVI was low in the spring, then increased until about 1 June, changed little during June, July and August, and then decreased as plants senesced in autumn. There were only slight differences in NDVI across years within sites and between sites, which was expected because the difference in biomass among sites across years averaged only 284 kg ha⁻¹. Correlation coefficients between NDVI and the vegetation parameters of biomass and LAI for each site and year exceeded 0.84 in 1999, 0.74 in 2000, and 0.91 in 2001 (Table 1). Regression analysis showed a nonlinear relationship with the general shape of the regression line being similar for both biomass and LAI vs. NDVI (Fig. 4). Values of R² with NDVI were relatively high as evidenced by values of 0.83 for biomass and 0.77 for LAI (Fig. 4). The uniformly high correlation coefficients (r) and regression coefficient of determination (R²) suggested that a single regression equation based on data from all years and sites should reliably predict biomass and LAI from NDVI. Aase et al. (1987) showed a similar relationship between LAI and NDVI for 2 managed native prairie sites, but a unique relationship existed for crested wheatgrass [*Agropyron desertorum* (Fisch. Ex Link) J. A. Schultes]. Wylie et al. (1996) showed a linear relationship between NDVI and biomass for hand-held radiometer spectral data and a nonlinear relationship for satellite derived spectral data (Wylie et al.

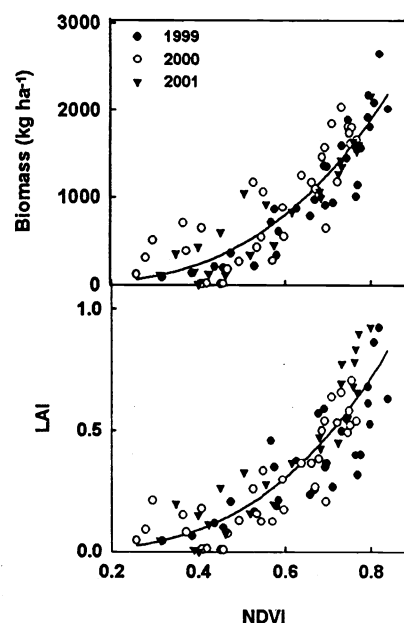


Fig. 4. Relationship between biomass and NDVI (top) and LAI and NDVI (bottom) for data combined across prairie, grazed prairie, and shrub prairie sites for 1999, 2000, and 2001. For biomass the equation for the fitted line is: biomass = 2.698 + (3709.449 × NDVI³); R² = 0.83 (P ≤ 0.05); standard error of regression is 266, and for LAI the fitted line is: LAI = -0.093 + (-0.192/lnNDVI); R² = 0.77 (P ≤ 0.05); standard error of regression is 0.13.

2002a). Values of NDVI have been shown to provide a good estimate of biomass for a shortgrass prairie (Anderson et al. 1993) and across a range of precipitation amounts ranging from 280 to 1,150 mm year⁻¹ (Paruelo et al. 1997).

The range in correlation coefficients for NDVI and CO₂ flux were greater among years than sites within years (Table 1). Within years the greatest range in correlation coefficients was from 0.68 for the grazed prairie in 2000 to 0.79 for the prairie in 2000, whereas, over years correlation coefficients ranged from 0.63 for the grazed prairie in 1999 to 0.79 for the prairie in 2000. Correlation coefficients were lowest in 1999 compared to 2000 and 2001, but the range in correlation coefficients were similar over years. Correlation coefficients within years for NDVI vs. CO₂ flux exceeded 0.63 in 1999, 0.68 in 2000, and 0.69 in 2001. The reason for the lower correlations in 1999 was probably due to the drought period in mid July (Fig. 1) causing greater variation among factors affecting plant CO₂ uptake. For example, precipitation in 1999 exceeded 100 mm twice during the data

Table 1. Correlation coefficients between NDVI and biomass, LAI, CO₂ flux and ET for a prairie, grazed prairie, and shrub prairie site in 1999, 2000, and 2001. All correlation coefficients are significant at P ≤ 0.05.

	1999			2000			2001	
	Prairie	Grazed prairie	Shrub prairie	Prairie	Grazed prairie	Shrub prairie	Grazed prairie	Shrub prairie
Biomass	0.95	0.97	0.90	0.88	0.86	0.74	0.93	0.92
LAI	0.88	0.87	0.84	0.87	0.83	0.79	0.93	0.91
CO ₂ flux	0.73	0.63	0.70	0.79	0.68	0.77	0.76	0.69
ET	0.95	0.93	0.91	0.92	0.93	0.94	0.90	0.93

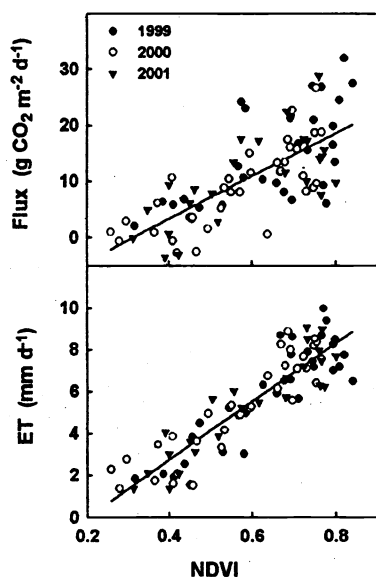


Fig. 5. Relationship between CO₂ flux and NDVI (top) and ET and NDVI (bottom) for data combined across prairie, grazed prairie, and shrub prairie sites for 1999, 2000, and 2001. For CO₂ flux the equation for the fitted line is: $\text{flux} = -11.49 + (37.99 \times \text{NDVI})$; $R^2 = 0.51$ ($P \leq 0.05$); standard error of regression is 5.74, and for ET the fitted line is: $\text{ET} = -2.81 + (13.92 \times \text{NDVI})$; $R^2 = 0.81$ ($P \leq 0.05$); standard error of regression is 1.04.

collection period, but never during 2000 and 2001. Law et al. (2000) reported that water stress in conifer tree significantly reduced the association between CO₂ flux and NDVI. The regression analysis of NDVI vs. CO₂ flux across years and sites (8 site years) was linear with an R^2 of 0.51 (Fig. 5). The greater variability at the higher NDVI and CO₂ flux values in 1999 contributed mostly to the lower R^2 across all sites and years. Because the greatest difference in the NDVI vs. CO₂ flux relationship occurred over years and not among sites within years suggested that the seasonality of biomass accumulation and environmental factors affecting CO₂ uptake may have a significant effect on the NDVI vs. CO₂ flux relationship.

A major difference in the biomass response curves for 1999 and 2000 that may have affected the CO₂ flux and NDVI relationship was that peak biomass occurred on the 23 June 1999 sampling, whereas in 2000 peak biomass occurred on the 11 July sampling or 18 days later. Another factor that may have contributed to the greater variability between NDVI and CO₂ flux occurred between 12 July and 26 July 1999 when drought conditions caused a large decrease in CO₂ flux, but not NDVI or biomass.

Wylie et al. (2002b) reported a strong relationship between satellite derived time-integrated normalized vegetative index and CO₂ flux measurements for a sagebrush-steppe ecosystem (*Artemisia* spp.) which suggested that the time-integrated normalized vegetative index could be used for mapping regional CO₂ fluxes for semiarid grasslands. Our point measurements of canopy radiometric reflectance when matched with CO₂ flux data provides further evidence for using NDVI for scaling data to a regional level. Correlation coefficients between NDVI and the daily 24 hour day and night CO₂ flux were lower for all sites and years than for only daylight CO₂ flux measurements; however the same general trend existed (data not presented).

The relationship between NDVI and ET was less variable than NDVI vs. CO₂ flux as evident by the greater R^2 of 0.81 (Fig. 5). The range in correlation coefficient across years and sites for NDVI vs. ET were similar, ranging from 0.90 to 0.95 (Table 1), which supports the higher R^2 obtained for the regression analysis that used data across all years and sites.

Conclusions

The relationships between NDVI and biomass, LAI, CO₂ flux, and ET for 3 grassland sites that differed in management and plant composition were generally quite similar, suggesting that NDVI has good potential for use in predicting canopy CO₂ flux rates for grasslands in the Northern Great Plains. The relatively high correlation coefficient and regression R^2 values for NDVI with CO₂ flux, ET, biomass, and LAI were similar among sites within years, but greater variation was observed for 1999 when drought conditions occurred.

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Restoring riparian corridors with fire: Effects on soil and vegetation

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Abstract

In many riparian corridors of the semi-arid west, stream incision has resulted in lowered water tables, basin big sagebrush (*Artemisia tridentata* var. *tridentata* Nutt.) encroachment and the loss of the dominant herbaceous vegetation. To determine the potential for restoring basin big sagebrush-dominated riparian corridors to greater herbaceous cover, a fall prescribed burn on sites with relatively shallow (–153 to –267 cm) and deep (–268 to \geq –300 cm) water tables was conducted. We evaluated the separate and interacting effects of water table depth and burning on total soil C and N, soil nutrient availability, and soil enzyme activities by microsite (sagebrush subcanopy, sagebrush interspace), and soil depth (ash/liter, 0–2, 2–5, and 10–20 cm). Three years after the prescribed burn, tissue nutrient content in silvery lupine (*Lupinus argenteus* Pursh) and Douglas sedge (*Carex douglasii* Boott), by microsite, growing in burned and unburned areas of 1 shallow water table site was measured. Influence of fire on soil attributes was largely limited to the top 5 cm. As a consequence of prescribed burning, deep water table sites lost relatively more N and C from litter horizons and released more aqueous-soluble Ca^{+2} from 0–2 cm mineral horizons than did corresponding horizons from shallow water table sites. Overall, compared to unburned controls, burning: (1) increased aqueous-extractable SO_4^{-2} , K^+ , and KCl-extractable NH_4^+ , (2) decreased activities of the enzymes asparaginase, urease and acid-phosphatase, and (3) decreased KCl-extractable NO_3^- and aqueous-soluble ortho-P. Out of 16 measured soil attributes reported, 7 were influenced by a microsite main effect and/or interaction. New tissue of silvery lupine on burned plots had greater N, greater Zn and Fe (only on subcanopy microsites) and less Ca than plants on control plots; new tissue of Douglas sedge had greater S and less Na, P, and Zn. The results indicate that burning alone is an appropriate restoration treatment for shallow water table sites because of minimal C and N loss and increased available nutrients for regrowth of understory herbaceous species. Deep water table sites require a burning prescription that minimizes fire severity because of higher potential C and N loss, and reseeding due to a lack of perennial understory herbaceous species and more xeric conditions.

Key Words: restoration, riparian ecosystems, water table depth

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Resumen

En muchos corredores ribereños del oeste semiárido la incisión de corrientes ha resultado en mantos freáticos mas bajos, la expansión de “Basin big sagebrush” (*Artemisia tridentata* var. *tridentata* Nutt.) y la perdida de vegetación herbácea dominante. Para determinar el potencial para restaurar los corredores ribereños dominados por “Basin big sagebrush con una mayor cobertura herbácea se llevo a cabo un fuego prescrito en otoño en sitios con mantos freáticos relativamente poco profundos (–153 to –267 cm) y mantos freáticos profundos (–268 to \geq –300 cm). Evaluamos los efectos separados e interactuantes de la profundidad del manto freático y la quema en el C y N total del suelo, la disponibilidad de nutrientes del suelo y las actividades enzimáticas del suelo por micrositio (“Sagebrush” subcoba, “Sagebrush” interespacio) y profundidad del suelo (ceniza /mantillo, 0–2, 2–5 y 10–20 cm). Tres años después del fuego prescrito se midió por micrositio, el contenido de nutrientes de los tejidos de “Silvery lupine” (*Lupinus argenteus* Pursh) y “Douglas sedge” (*Carex douglasii* Boott), creciendo en áreas quemadas y sin quemar de un sitio con manto freático somero. La influencia del fuego en los atributos del suelo se limito principalmente a los 5 cm superiores. Como consecuencia del fuego prescrito, los sitios con manto freático profundo perdieron relativamente más N y C de los horizontes con mantillo y liberaron mas Ca^{+2} soluble en agua de los horizontes minerales de 0–2 cm que los horizontes correspondientes en los sitios con manto freático poco profundo. En general, comparado con los controles sin quemar, la quema (1) incremento el SO_4^{-2} extractables en agua, K^+ y KCl-extractable NH_4^+ , (2) Disminuyo la actividad de las enzimas asparaginasa, ureasa y ácido- fosfatasa y (3) disminuyo el KCl-extractable, NO_3^- y los ortho-P soluble en agua. De los 16 atributos de suelo medidos, 7 fueron influenciados por un efecto principal de micrositio y/o interacción. El tejido nuevo de “Silvery lupine” en las parcelas quemadas tuvo mayor contenido de N, Zn y Fe (solo en los micrositios de abajo de la copa) y menos Ca que las plantas en las parcelas control; el nuevo tejido del “Douglas sedge” tuvo más S y menos Na, P y Zn. Los resultados indican que la quema sola es un tratamiento apropiado para restauración de sitios con agua freática somera debido a las pérdidas mínimas de C y N y el aumento en la disponibilidad de nutrientes para el rebrote de especies herbáceas. Los sitios con manto freático profundo requieren de una prescripción de fuego que minimice la severidad del fuego por el alto potencial de perdida de C y N y la resiembra debido a la falta de especies herbáceas perennes y a condiciones mas xéricas.

Streams in the central Great Basin are in an incisional phase (Miller et al. 2001), that is being exacerbated by anthropogenic disturbance (Chambers et al. 1998). Stream incision often results in lowered water tables and encroachment and dominance of basin big sagebrush (*Artemisia tridentata* var. *tridentata* Nutt.) in riparian corridors, and the loss of grass and forb-dominated meadow ecosystems. For riparian meadow ecosystems in general, the hydrologic regime, as indicated by water table depth, determines both soil properties (Chambers et al. 1999) and riparian ecosystem characteristics (Castelli et al. 2000). Thus, the potential for restoring sagebrush-dominated ecosystems to grass and sedge meadows depends on whether or not an abiotic threshold defined by water table depth has been crossed (Chambers and Linnerooth 2001). The characteristics of the soils and their response to restoration treatments are critical determinants of the restoration potential.

A restoration experiment was conducted to determine the potential for restoring basin big sagebrush-dominated riparian corridors to dry meadows. Two ecological site types were identified that occur naturally in the drainages and that have similar soils and landforms to serve as models for the restoration effort. The ecological site types are: (1) the dry meadow ecological site type which is dominated by grasses and sedges and has relatively shallow water tables; and (2) the basin big sagebrush/basin wild rye (*Leymus cinereus* Scribn. & Merr.) type. This type is dominated by basin big sagebrush and basin wild rye with lesser amounts of dry meadow species and has relatively deep water tables (Weixelman et al. 1996). A restoration treatment was applied to sites with relatively shallow and deep water tables that included a prescribed burn to remove basin big sagebrush followed by seeding herbaceous species typical of both ecological site types.

In this component of the larger restoration study, we examined the effects of both water table depth and prescribed burning on the soil and plant nutrient status of basin big sagebrush-dominated riparian corridors. The effects of fire on soil nutrient status in sagebrush steppe ecosystems are generally known (Blank et al. 1994a), but fires' effects on riparian corridors or interactions with water table depth have yet to be addressed. Moreover, there is limited data on how plant nutrient content is influenced when growing in post-fire soil. Therefore, this study asks 3 questions: 1) Does soil nutrient status dif-

fer between sites with different water tables or in response to burning? 2) Does microsite influence post-fire soil nutrient status and nutrient uptake? 3) Do plants acquire soil nutrients at different rates in burned and unburned plots?

Materials and Methods

Study Sites

In July 1996, we located 4 basin big sagebrush-dominated study sites along Willow (39°33'12"N, 116°59'30"W), Ledbetter (39°45'30"N, 117°30'W), and Marysville (39°02'30"N, 117°24'27"W) Creeks in the Toiyabe Mountain Range of central Nevada that represented progressive stages of modification of the dry meadow ecosystem type. Study sites were on drainageways and stream terraces at elevations ranging from 2,000 to 2,300 m, and were characterized by incised stream reaches. The climate is semiarid, and on average 72% of the 30 to 40 cm of average annual precipitation falls from Mid-October through May. Average temperature ranges from -4°C in January to 20°C in July. Soil parent material is Quaternary alluvium of mixed mineralogy. The Willow Creek drainage is derived from granite, chert, shale, quartzite, limy sandstone and siltstone, and limestone. The Marysville and Ledbetter drainages are derived from quartz latite with a lesser amount of andesite and basalt.

Site selection was based on presence of species typical of the dry meadow and basin big sagebrush/giant wild rye ecosystem types (Weixelman et al. 1996), and depths to water table determined from hand-augered wells. Two hydro-geomorphic positions were included. Two study sites were located on lower benches and were characterized by relatively shallow water tables (Willow wet and Ledbetter Creeks; -153 to -267 cm below the surface). An additional 2 sites were located on higher benches and had deeper water tables (Willow dry and Marysville Creeks; -268 to \geq -300 cm below the surface). Sites with shallow water tables had higher cover of perennial graminoids and forbs, lower densities and volumes of basin big sagebrush, and were more similar to the model dry meadow type than shallow water table sites (Linnerooth et al. 1998). Graminoid species which typify the sites included Nevada bluegrass (*Poa secunda* spp. *juncifolia* [Scribn.] R. Soreng), mat muhly (*Muhlenbergia richardsonis* [Trin] Rydb.), creeping wild rye (*Leymus triticoides* [Buckley] Pilger), basin wild rye,

and Douglas sedge (*Carex douglassi* Boott). Common forbs included lupines (*Lupinus* sp.) and asters (*Aster* sp.). The shrubs, basin big sagebrush and green rabbitbrush (*Chrysothamnus viscidiflorus* ssp. *viscidiflorus* [Hook.] Nutt.), occurred with high constancy indicating that the study sites were relatively drier than the model dry meadow ecosystem type.

Holocene pedogenesis of Quaternary-aged sediments under herbaceous vegetation has produced deep, highly organic and relatively undifferentiated profiles. The soils on all sites are classified as Pachic Haplocryolls with < 2-mm textures of loam and silt loam. Willow Creek dry and the Marysville site occur on slightly higher benches and are characterized by deeper water tables, the soils have lighter-colored mollic epipedons. Coarse fragment content for all soils lies between 5 and 50%.

Experimental Design and Data Collection

A paired plot approach was used in which 1 plot at each of the 4 sites received the restoration treatment (prescribed burn and seeding), and the other plot served as a control. Burning was conducted on 19–21 Oct. 1996 to remove both woody and understory vegetation. Plots were between 740 and 900 m² in size, and fencing was used to reduce grazing and trampling by livestock and wildlife. Soils were sampled from 29 Oct. to 4 Nov. 1996. Sampling included both subcanopy and interspace microsites because of the effects of sagebrush plants on soil characteristics in these ecosystems. At each site, soil samples (n = 4) were collected for all restoration treatment/microsite combinations, and included the surface litter for unburned plots, surface ash for burned plots, and mineral soil depths of 0–2 cm, 2–5 cm, and 10–20 cm (2 water tables x 2 replicate sites x 2 burn treatments x 2 microsites x 4 depths x 4 subsamples). Surface samples were obtained with a trowel; deeper samples with a 10 cm diameter soil auger. From the time of the prescribed burn to when soil sampling occurred, approximately 12 cm of snow fell on the Willow Creek shallow and deep water table sites. Cold temperatures, however, limited snow melt and only the ash/litter layers and the upper 2 cm of the mineral soil became wet.

Vegetation was sampled in late June 1999 for both treatment/microsite combinations on the Willow Creek site with the deep water table. Three replicate transects were established within both the burned

and unburned plots, 6 or 7 sample points were randomly located along each transect ($n = 20$), and sample quadrats (0.25 m^2) were placed in both the subcanopy and interspace microsites closest to the random point (2 burn treatments \times 2 microsites \times 3 replicate transects \times 6 or 7 subsamples). All plant material was clipped at the soil surface and separated by species. The vegetation samples were dried at 60°C for 48 hours and weighed (biomass is expressed as g m^{-2}). Only silvery lupine (*Lupinus argenteus* [Pursh]) and Douglas sedge on the Willow Creek site with the deep water table had sufficient biomass within all treatment/microsite combinations for analyses. This experimental design limits inferences of the results only to this site (see Hurlbert 1984).

Laboratory Methods

Soil samples were stored in an ice cooler in the field and at 2°C between all preparatory steps in the lab. All soil, ash, and litter material was passed through a 2-mm sieve prior to analysis. Some samples were dried slightly to facilitate sieving. All analyses were done on the $< 2\text{-mm}$ fraction. The dichromate oxidation procedure with supplemental heating was used to quantify organic carbon (OC) (Nelson and Sommers 1982). Total N was assayed by the micro-Kjeldahl procedure (Isaac and Johnson 1976). Aqueous soil extracts were prepared by shaking 10 grams soil with 20 ml of deionized water for 1 hour (high organic matter samples required more water). The samples were centrifuged at $9400 \times g$ for 10 minutes. Chloride, HPO_4^{2-} , and SO_4^{2-} were quantified by gradient elution ion chromatography. Ion chromatography was used to quantify Na^+ , K^+ , Mg^{+2} and Ca^{+2} . Ammonium and NO_3^- were extracted with 0.5 M KCl (10g soil 30 ml extractant with shaking for 30 min). Ammonium was quantified using flow-injection membrane diffusion colorimetric methodology. Nitrate was quantified by ion chromatography with spectroscopic detection at 210 nm. Standards were made up from reagent grade chemicals. Soil enzyme bioassays of asparaginase, urease, and acid-phosphatase followed standard procedures (Tabatabai 1994). All data were corrected to 105°C soil weight.

Individual vegetation samples were ground in a Udy Mill and homogenized. Dry ashing followed by addition of HCl and HNO_3 was used to solubilize metals (Campbell and Plank 1998). Calcium, Mg, Fe, Cu, Mn, and Zn were quantified by atomic absorption spectroscopy; Na and K

were quantified by atomic emission spectroscopy; P was quantified colorimetrically using molybdenum-blue chemistry. Nitrogen in ground plant tissue was quantified by the micro-Kjeldahl method (Isaac and Johnson 1976). We used the method of Kowalenko and Van Laerhoven (1998) to solubilize total plant S which was quantified using ion chromatography.

Statistical Analyses

The overall study design was a split, split, split plot that was completely randomized at the main plot level. Water table depth (shallow, deep) was the main plot factor, treatment (burned, unburned) was the split plot factor, microsite (subcanopy, interspace) was the split, split plot factor, and depth was treated as a split, split, split plot factor (ash/litter, 0–2 cm, 2–5 cm, 10–20 cm). Sites within water tables were the main plot error term. For significant F values in the ANOVA model, Duncan's tests, at the ≤ 0.05 probability level of significance, were used to separate means (SAS 1996). All significant main effects and interactions were examined, but only significant treatment main effects or interactions are reported. Vegetation data were analyzed separately by species (silvery lupine and Douglas sedge) using a 2-way ANOVA. Factors were treatment and microsite (subcanopy, interspace). For significant F values, treatment differences were discerned at the $P \leq 0.05$ level using L.S. means (SAS 1996).

Results and Discussion

Visible Effects of Prescribed Burning

Following prescribed burning, the pattern of fire effects mirrored the heterogeneous distribution of plant materials. Shrub subcanopies were covered with 1 to 5 cm of grayish to whitish ash which suggests temperatures greater than 750°C at the soil surface with lethal penetration of heat through the surface soil seedbank (Bentley and Fenner 1958). Lighter fuel loads in interspaces contributed to a darker ash generally less than 1 cm thick, which suggests temperatures somewhat greater than 350°C at this soil surface with lethal levels of heat only reaching to approximately 2 cm (Bentley and Fenner 1958). There were no visible differences in surface fire effect patterns between shallow water table and deep water table sites, but shallow water table sites had lower soil temperatures than deep water table sites (Chambers and Linnerooth 2001).

Influence of Water Table Depth

The response of the shallow and deep water table sites to the burn was more a function of the vegetation composition and structure than of the hydrologic regime. Depth to water table was not a significant main effect for any of the measured attributes (Table 1). Shallow water table sites had significantly more organic carbon (OC) in undershrub microsites than interspace microsites following the burn (water table \times microsite interaction; Table 1) (Table 2), whereas deep water table sites had no significant differences in OC content between microsites. The different response was the result of a greater proportional loss of OC, due to burning, in subcanopy microsites of deep rather than shallow water table sites. Similarly, prescribed burning reduced total soil N, averaged over all soil depths, but significantly more N was lost on deep rather than shallow water table sites (water table \times treatment interaction; Table 1) (Table 2). Because the shallow water table sites support greater herbaceous plant cover and biomass and are generally moister than the deep water table sites (Wright 2001, Chambers and Linnerooth 2001), we expected them to contain more total soil C and N. This was not the case. For unburned sites, there were no differences in soil C and N between deep and shallow water table sites for any depth. The relatively greater loss of C and N from subcanopy microsites due to burning on deep rather than shallow water table sites can be attributed to greater fuel loads of sagebrush on deep water table sites (Linnerooth et al. 1998).

In the 0–2 cm depth increment, burning released significantly more Ca^{+2} from deep rather than shallow water table sites (water table depth \times treatment \times soil depth interaction; Table 1) (Table 3). For shallow water table sites, burning released much higher levels of Mg^{+2} in interspace microsites than in corresponding deep water sites (water table depth \times treatment \times microsite \times soil depth interaction; Table 1) (Table 3). Increases in aqueous-soluble cations in upper soil layers and ash are often reported following fires (Smith 1970, Marion et al. 1991, Blank and Zamudio 1998). Greater shrub fuel loads on deep water table sites may have fostered a proportionally greater increase in aqueous-soluble Ca^{+2} and Mg^{+2} due to burning than occurred on shallow water table sites. For the shallow water table sites, large increases in post-burn levels of Mg^{+2} in ash layers of interspace microsites are possibly due to transfer of ash from subcanopy microsites.

Table 1. ANOVA results for measured soil attributes showing f-values and significance levels with an asterisk.

	df	Measured attributes							
		OC ¹	N	C:N	pH	SO ₄ ⁻²	Ortho-P	Asp	Urease
WT ²	1	0.78	0.09	0.09	1.86	0.03	0.02	0.24	0.01
S(WT)-Err A	2								
TR	1	156.46**	352.52**	21.59*	83.58*	437.00**	11.00	35.37*	81.77*
WTxTR	1	2.24	20.73*	0.35	0.37	0.08	0.26	4.11	0.00
SxTR(WT)-ErrB	2								
MS	1	11.16*	0.44	0.03	0.95	0.81	39.57**	0.01	0.12
WTxMS	1	11.38*	1.27	1.16	0.13	0.20	6.02	0.70	0.15
TRxMS	1	38.05**	5.51	0.70	0.00	0.43	23.19**	0.39	0.11
WTxTRxMS	1	5.94	0.00	1.59	0.59	0.35	2.36	0.10	0.36
SxTRxMS(WT)-Err C	4								
D	3	61.02***	51.50***	4.16*	30.50***	7.83**	19.81***	9.24***	16.69***
WTxD	3	0.27	0.41	0.10	1.74	0.65	0.36	2.42	0.00
TRxD	3	13.30***	8.25***	0.87	34.79***	5.50**	17.59***	8.54***	20.42***
WTxTRxD	3	0.70	0.71	0.17	0.19	0.48	1.30	1.32	0.06
MSxD	3	2.36	1.99	0.38	3.64*	1.60	4.08	1.11	0.30
WTxMSxD	3	0.54	0.30	0.36	0.36	0.13	2.71	0.09	0.10
TRxMSxD	3	5.23**	2.58	0.43	2.22	0.98	5.66**	0.96	0.11
WTxTRxMSxD	3	1.09	0.06	1.70	0.58	0.39	0.99	0.02	0.09
SxTRxMSxD(WT)-Err D	22								

	df	Measured attributes							
		Ptase	NO ₃ ⁻	NH ₄ ⁺	K ⁺	Mg ⁺²	Ca ⁺²	Na ⁺	SAR
WT ²	1	1.75	0.40	2.10	0.28	0.01	0.59	0.04	0.50
S(WT)-Err A	2								
TR	1	42.86*	4.46	0.80	2.93	36.71*	100.26**	22.18*	19.8*
WTxTR	1	0.93	1.02	0.14	0.23	2.64	6.19	0.33	0.95
SxTR(WT)-ErrB	2								
MS	1	0.48	0.65	0.43	1.88	0.29	5.42	2.02	3.50
WTxMS	1	0.64	0.72	10.81*	0.30	0.70	0.17	0.36	0.83
TRxMS	1	1.75	0.00	0.28	0.82	0.08	0.49	0.65	0.76
WTxTRxMS	1	4.80	0.44	0.04	0.55	2.03	1.67	1.11	1.16
SxTRxMS(WT)-Err C	4								
D	3	40.37***	5.76**	8.42***	2.46	28.55***	34.37***	14.78***	8.03***
WTxD	3	1.92	0.48	0.18	0.12	2.11	8.27***	0.37	0.44
TRxD	3	55.48***	4.20*	7.95***	1.23	7.81**	12.71***	5.42**	4.21*
WTxTRxD	3	0.98	0.50	0.41	0.22	4.48*	5.54**	0.24	0.41
MSxD	3	0.31	2.30	0.33	1.43	0.16	3.56*	1.92	2.30
WTxMSxD	3	0.30	0.24	3.14*	0.15	0.56	1.30	0.50	1.06
TRxMSxD	3	1.93	1.97	0.49	1.02	0.11	4.55*	1.02	1.51
WTxTRxMSxD	3	0.64	0.23	0.36	0.47	3.90*	1.10	2.13	1.77
SxTRxMSxD(WT)-Err D	22								

Abbreviations: ¹OC = organic carbon; N = total Kjeldahl nitrogen; C:N=carbon to nitrogen ratio; SO₄⁻²=sulfate; Ortho-P=ortho-phosphate; Asp=asparaginase; Ptase = acid phosphatase; SAR=sodium adsorption ratio. ²WT=water table depth (shallow, deep); S = site (Willow wet, Willow dry, Ledbetter, and Marysville); TR=treatment (burned, control); MS=microsite (subcanopy, interspace); D = depth; * denotes p ≤ 0.05; ** denotes p < 0.01; *** denotes p < 0.001.

Table 2. Soil organic C, Kjeldahl N, and C:N ratios by site water table depth, microsite, soil depth, and treatment¹.

Depth	Shallow water table				Deep water table			
	Subcanopy		Interspace		Subcanopy		Interspace	
	Burned	Unburned	Burned	Unburned	Burned	Unburned	Burned	Unburned
-----Organic-C (g kg ⁻¹)-----								
ash/litter	106±16	236±36	90±16	140±29	43±13	271±25	136±18	156±9
0-2 cm	47±5	83±13	39±6	60±16	58±13	85±9	64±8	93±14
2-5 cm	35±4	51±7	33±6	46±9	35±3	55±6	56±12	63±7
10-20 cm	17±2	22±4	17±3	23±4	19±1	22±1	20±1	21±2
-----Kjeldahl-N (g kg ⁻¹)-----								
ash/litter	7.2±0.9	15.7±1.9	9.4±1.5	8.6±1.8	5.2±1.0	17.0±1.9	8.6±2.3	12.9±1.7
0-5 cm	4.6±0.5	7.0±1.3	4.6±1.2	5.6±1.4	4.7±0.5	7.5±1.2	7.2±1.6	8.9±1.8
5-10 cm	2.7±0.3	3.4±0.5	2.9±0.6	3.2±0.7	2.8±0.3	4.1±0.5	4.5±1.1	4.6±0.8
20-30 cm	1.4±0.2	1.5±0.2	1.4±0.3	1.8±0.3	1.6±0.2	1.7±0.1	1.5±0.1	1.7±0.2
-----C:N -----								
ash/litter	13.8±1.9	15.2±1.3	9.7±1.0	16.4±1.3	7.8±1.0	16.8±2.0	14.0±1.3	12.4±2.0
0-5 cm	10.3±0.5	12.3±0.3	10.4±1.4	11.2±0.6	12.1±2.4	11.8±0.6	9.2±1.0	11.3±1.0
5-10 cm	13.0±0.6	15.4±0.5	12.2±0.7	14.8±0.5	12.1±1.0	13.9±1.0	13.6±1.1	14.5±0.9
20-30 cm	12.8±0.7	14.3±1.3	12.3±0.6	13.2±0.3	12.2±1.4	13.0±0.3	13.2±0.5	12.8±0.5

¹Variation in data shown by standard errors.

Table 3. Aqueous-soluble cations and KCl-extractable ammonium by site water table depth, microsite, soil depth, and treatment¹.

Depth	Shallow water table				Deep water table			
	Subcanopy		Interspace		Subcanopy		Interspace	
	Burned	Unburned	Burned	Unburned	Burned	Unburned	Burned	Unburned
	-----Organic-Ca ⁺² (mmol kg ⁻¹)-----							
ash/litter	3.4±0.3	4.3±0.7	4.1±1.0	2.2±0.8	2.3±0.7	3.2±0.5	2.6±0.7	3.2±0.8
0-2 cm	2.9±1.0	1.1±0.3	1.3±0.4	0.9±0.1	7.4±1.6	1.4±0.3	3.1±0.9	1.3±0.4
2-5 cm	1.6±0.4	0.8±0.1	1.5±0.4	0.5±0.1	2.6±0.4	1.6±0.7	1.8±0.5	1.2±0.2
10-20 cm	0.6±0.1	0.6±0.1	0.5±0.2	0.4±0.1	0.5±0.1	0.4±0.1	0.6±0.2	0.4±0.1
	-----Mg ⁺² (mmol kg ⁻¹)-----							
ash/litter	8.0±1.9	2.8±0.5	13.0±5.0	1.1±0.4	7.7±1.1	2.3±0.3	2.7±1.4	4.8±3.6
0-2 cm	2.0±0.5	0.7±0.1	1.8±0.9	0.5±0.1	4.6±0.7	1.0±0.2	2.2±0.7	0.7±0.1
2-5 cm	1.2±0.3	0.4±0.1	1.0±0.3	0.3±0.1	2.3±0.5	1.1±0.5	1.4±0.6	0.6±0.1
10-20 cm	0.3±0.1	0.2±0.1	0.3±0.1	0.2±0.1	0.4±0.1	0.3±0.1	0.3±0.1	0.2±0.1
	-----Na ⁺ (mmol kg ⁻¹)-----							
ash/litter	4.0±0.9	1.8±0.5	4.0±1.4	0.8±0.2	5.8±1.0	0.9±0.2	1.3±0.5	1.3±0.8
0-2 cm	1.3±0.3	0.5±0.1	0.7±0.2	0.3±0.1	2.2±0.5	0.4±0.1	1.5±0.4	0.3±0.1
2-5 cm	0.7±0.1	0.4±0.1	0.7±0.1	0.3±0.1	0.8±0.1	0.5±0.2	0.6±0.2	0.3±0.1
10-20 cm	0.4±0.1	0.4±0.1	0.4±0.1	0.4±0.1	0.5±0.1	0.4±0.1	0.3±0.1	0.2±0.1
	-----K ⁺ (mmol kg ⁻¹)-----							
ash/litter	112±38	40.3±13.6	46.4±8.0	6.8±2.9	241±95	17.2±3.1	8.1±2.9	16.6±12.4
0-2 cm	13.5±3.0	7.0±1.7	15.3±5.6	2.2±0.5	16.5±4.2	9.1±3.4	9.3±2.9	1.7±0.4
2-5 cm	10.1±1.9	4.7±1.2	13.7±5.2	1.2±0.1	14.4±1.8	10.0±4.7	9.7±4.9	1.6±0.2
10-20 cm	2.3±0.5	2.2±0.7	3.3±1.2	1.9±0.6	4.0±2.0	2.7±0.8	1.9±0.8	1.0±0.2
	-----KCl-NH ₄ ⁺ (mmol kg ⁻¹)-----							
ash/litter	2.5±1.1	10.9±8.4	1.1±0.5	4.6±1.9	1.6±0.3	3.8±1.0	8.3±4.3	10.4±1.8
0-2 cm	8.4±2.1	0.6±0.1	3.6±0.9	0.7±0.3	7.5±0.8	1.5±0.7	7.1±1.2	2.4±0.5
2-5 cm	4.3±1.1	0.7±0.3	3.1±1.0	0.3±0.1	5.2±1.1	1.3±0.7	3.3±1.6	0.9±0.3
10-20 cm	0.3±0.1	0.1±0.1	0.6±0.3	0.1±0.1	0.6±0.2	0.1±0.1	0.5±0.3	0.1±0.1

¹Variation in data shown by standard errors.

In shallow water table sites, levels of NH₄⁺ tended to be lower with increasing soil depth for both microsites (water table x microsite x soil depth interaction; Table 1) (Table 3). For deep water table sites, levels of NH₄⁺ declined significantly with soil depth in interspace microsites, but were nearly constant for the first 3 depths in the subcanopy microsite and then declined significantly.

Effects of Prescribed Burning on Soil Attributes

Significant loss of enzyme activity due to burning was largely limited to ash layers, but acid phosphatase activity was reduced to the 5 cm soil depth (urease, asparaginase and acid phosphatase all influenced by treatment x depth interaction; Table 1) (Table 4). Although not significant, enzyme activity in burned subcanopies generally was lower compared to

unburned controls. Soil enzyme activities declined due to heat deactivation (Saa et al. 1993, Hernandez et al. 1997, Staddon et al. 1998). The insulating properties of soil and brief exposure of the soil surface to high temperatures generally limits the depth of deactivation to 2 cm (Aston and Gill 1976). Greater loss of acid phosphatase activity deeper in the soil due to burning, relative to urease and asparaginase, may have occurred because acid

Table 4. Soil enzyme activities of urease, asparaginase, and acid phosphatase by site water table depth, microsite, soil depth, and treatment¹.

Depth	Shallow water table				Deep water table			
	Subcanopy		Interspace		Subcanopy		Interspace	
	Burned	Unburned	Burned	Unburned	Burned	Unburned	Burned	Unburned
	-----Urease (μmol g ⁻¹ hr ⁻¹)-----							
ash/litter	1.7±0.9	36.4±7.6	1.2±0.5	45.8±23.3	0.9±0.2	41.5±6.9	3.8±1.9	34.6±7.8
0-2 cm	2.6±1.3	6.6±0.9	4.9±1.1	9.9±1.6	1.3±0.4	9.3±1.0	3.9±1.1	8.8±1.8
2-5 cm	1.4±0.5	3.5±0.7	3.8±1.1	8.2±0.9	1.8±0.6	4.4±0.6	4.4±1.2	5.3±1.1
20 cm	5.0±0.8	6.6±0.7	4.0±0.9	6.2±1.0	4.2±0.7	5.6±0.7	4.6±0.7	5.7±0.9
	-----Asparaginase (μmol g ⁻¹ hr ⁻¹)-----							
ash/litter	0.9±0.4	10.7±6.6	0.6±0.2	8.2±2.0	0.8±0.1	5.7±1.7	1.0±0.5	3.4±1.5
0-2 cm	0.0±0.9	1.0±0.1	1.3±0.8	0.8±0.2	0.7±0.4	1.1±0.2	2.6±1.3	1.6±0.5
2-5 cm	0.8±0.2	0.4±0.2	0.0±0.3	0.9±0.1	0.7±0.3	0.4±0.2	0.7±0.3	2.5±2.0
10-20 cm	0.2±0.1	0.7±0.3	0.1±0.2	0.8±0.2	0.3±0.1	0.3±0.1	0.6±0.3	0.7±0.2
	-----Acid Phosphatase (μmol g ⁻¹ hr ⁻¹)-----							
ash/litter	0.1±0.1	9.0±1.4	0.1±0.1	10.4±3.3	0.1±0.1	13.3±1.0	0.9±0.8	11.7±1.1
0-2 cm	1.0±0.3	6.1±0.8	2.0±0.8	5.5±0.8	0.7±0.3	8.4±0.7	2.2±0.7	6.2±1.0
2-5 cm	2.8±0.9	4.2±0.4	2.3±0.7	5.8±1.0	1.0±0.3	6.0±0.8	2.9±0.6	4.9±0.7
10-20 cm	1.6±0.2	1.6±0.2	1.3±0.2	2.6±0.6	1.1±0.1	2.1±0.4	1.3±0.2	2.2±0.4

¹Variation in data shown by standard errors.

Table 5. Soil pH and water-soluble sulfate and ortho-P and KCl-extractable nitrate by site water table depth, microsite, soil depth, and treatment¹.

Depth	Shallow water table				Deep water table			
	Subcanopy		Interspace		Subcanopy		Interspace	
	Burned	Unburned	Burned	Unburned	Burned	Unburned	Burned	Unburned
-----pH-----								
ash/litter	8.6±0.2	6.3±0.3	8.8±0.3	5.8±0.2	9.2±0.3	5.9±0.1	7.9±0.4	5.6±0.2
0-2 cm	7.1±0.1	5.9±0.1	7.4±0.4	5.8±0.2	6.8±0.3	5.4±0.1	6.9±0.3	5.3±0.2
cm	6.4±0.2	6.0±0.2	6.8±0.4	5.7±0.1	6.3±0.1	5.5±0.1	6.0±0.3	5.1±0.1
10-20 cm	6.7±0.1	7.1±0.2	6.6±0.3	6.5±0.2	6.9±0.2	6.5±0.1	6.4±0.2	6.5±0.1
-----Sodium adsorption ratio-----								
ash/litter	1.12±0.19	0.65±0.12	0.94±0.17	0.47±0.13	1.83±0.29	0.39±0.06	0.54±0.15	0.37±0.12
0-2 cm	0.58±0.06	0.41±0.06	0.43±0.05	0.28±0.03	0.62±0.11	0.28±0.05	0.60±0.09	0.24±0.03
2-5 cm	0.46±0.04	0.38±0.08	0.45±0.05	0.35±0.03	0.39±0.02	0.28±0.05	0.36±0.04	0.20±0.03
10-20 cm	0.56±0.09	0.51±0.05	0.63±0.18	0.53±0.17	0.53±0.07	0.44±0.07	0.33±0.05	0.33±0.06
-----SO ₄ ⁻² (mmol kg ⁻¹)-----								
ash/litter	17.40±5.01	2.70±0.98	14.96±5.17	0.43±0.24	17.32±3.26	1.28±0.27	5.02±1.24	0.65±0.27
0-2 cm	5.62±1.47	0.28±0.06	4.11±1.63	0.15±0.03	9.40±2.46	0.48±0.22	5.41±1.78	0.27±0.08
2-5 cm	2.73±0.86	0.14±0.03	3.65±1.30	0.12±0.03	4.17±0.94	0.48±0.33	3.84±1.74	0.20±0.04
10-20 cm	0.28±0.11	0.35±0.28	0.85±0.39	0.13±0.07	1.52±0.54	0.17±0.08	0.97±0.51	0.28±0.16
-----ORTHO-P (mmol kg ⁻¹)-----								
ash/litter	0.26±0.11	2.77±0.77	0.18±0.05	0.65±0.26	0.25±0.06	1.64±0.55	0.49±0.19	1.10±0.45
0-2 cm	0.31±0.04	0.65±0.12	0.22±0.06	0.14±0.01	0.31±0.07	0.66±0.13	0.21±0.04	0.20±0.04
2-5 cm	0.30±0.05	0.59±0.09	0.17±0.04	0.12±0.01	0.35±0.05	0.60±0.14	0.23±0.06	0.23±0.05
10-20 cm	0.26±0.04	0.33±0.05	0.15±0.04	0.13±0.03	0.18±0.04	0.23±0.06	0.09±0.02	0.17±0.04
-----KCl-NO ₃ ⁻ (mmol kg ⁻¹)-----								
ash/litter	0.13±0.04	2.87±2.15	0.10±0.05	0.66±0.55	0.05±0.01	4.18±1.30	0.53±0.28	3.44±2.49
0-2 cm	0.50±0.31	0.54±0.13	1.05±0.50	1.34±0.27	0.10±0.07	0.53±0.14	0.59±0.26	3.33±1.53
2-5 cm	0.29±0.22	0.29±0.07	0.37±0.15	0.52±0.10	0.04±0.01	0.31±0.09	0.23±0.07	1.41±0.45
10-20 cm	0.13±0.02	0.09±0.01	0.13±0.03	0.23±0.15	0.05±0.01	0.19±0.07	0.08±0.03	0.16±0.03

¹Variation in data shown by standard errors.

phosphatase is more sensitive to heat, or compound(s) created by the fire may be inhibitory to acid phosphatase activity. Reduced enzyme activities of urease, asparaginase, and acid phosphatase can potentially lower mineralization rates of N and P, at least in ash layers. The large reduction of acid phosphatase enzyme activity in burned subcanopies suggests possible interactions with P nutrition for plant establishment and regrowth.

Burned plots had lower organic carbon (OC) in the ash/litter and 0–2 cm depths than controls, with the greatest loss of OC occurring in shrub subcanopy microsites (treatment x microsite x soil depth interaction; Table 1) (Table 2). Nitrogen content was lower for all depths on burned than control plots, but was significantly lower only in ash/litter layers (treatment x depth interaction; Table 1) (Table 2). Carbon to N ratios were lower on burned plots (Table 2). Vegetation combustion and concomitant soil heating often leads to system loss of C and N and the level of loss is a function of microsite fuel levels (Schnitzer and Hoffman 1964, Raison 1979, DeBell and Ralston 1970, White et al. 1973, Blank et al. 1994a, Johnson et al. 1998). A consequence of lowered C:N ratios following the burns may be greater N mineralization potential (Christensen

1973, Stock and Lewis 1986, Dyrness et al. 1989, Kutiel and Naveh 1987).

Aqueous-soluble Na⁺ and KCl-extractable NH₄⁺ exhibited a significant treatment x soil depth interaction (Table 1). Prescribed burned plots had greater content of Na⁺ in the ash/litter, 0–2 cm, and 2–5 cm depths than control plots (Table 3). Content of KCl-extractable NH₄⁺ was lower in the ash layer and higher in the 0–2 cm and 2–5 cm depths of the burned than control plots (Table 3). Large quantities of NH₄⁺ can be liberated after burns (Raison 1979, Khanna and Raison 1986, Overby and Perry 1996) depending on soil burn temperature (Marion et al. 1991). Extremely high temperatures, as occurred in the ash layers, fostered a slight increase in ammonium or slight loss relative to unburned litter layers. Beneath the ash layers where soil temperature was lower, ammonium levels increased markedly. The elevated extractable ammonium values in ash and mineral layers in burned treatments relative to controls suggests enhanced N nutrition for plants. High data variability and a conservative statistical approach negates any post-fire inferences regarding aqueous-soluble K⁺. However, K⁺ was consistently higher in burned than control plots for all depths except 10–20 cm (Table 3).

Soil pH, sodium adsorption ratio (SAR), aqueous-soluble SO₄⁻², and KCl-extractable NO₃⁻ exhibited significant treatment x depth interactions (Table 1). Burning resulted in an increase in soil pH, SAR, and SO₄⁻² in all depths except 10–20 cm (Table 5). Elevated soil reaction often occurs after fire and has been attributed to hydrolyses of basic cations (Sampson 1944). The pH's attained in our study due to burning, at least in ash layers, would negatively influence nutrient availability (Marschner 1995). The increase in SAR is due to a greater proportional release of Na⁺ than Ca⁺² plus Mg⁺² due to burning. The SARs are below threshold values of about 10 which could lead to soil dispersion (Bohn et al. 1979). However, prescribed fires undertaken in soils with higher initial SARs may result in soil dispersion. Of all attributes measured, aqueous soluble SO₄⁻² increased the most following the burn, and was over 10 times greater in ash and mineral layers to 5 cm in burned than control plots. Although S readily volatilizes from vegetation heated above 300° C (Tiedemann 1987), oxidation of S-containing functional groups, possibly aided by catalysis on soil mineral surfaces, results in elevated soil sulfate levels after fires (Blank et al. 1994a). The large increase of aqueous-soluble SO₄⁻²

due to fire should favorably affect S nutrition of plants as the macronutrient is assimilated dominantly by root uptake (Marschner 1995).

In subcanopy microsites, ash layers had less ortho-P than the litter layer (treatment x microsite x depth interaction; Table 1) (Table 5). Soil content of ortho-P following vegetation fires is difficult to predict due to its involvement in numerous sorption and precipitation reactions, and to the interaction of these reactions with factors such as soil type, burn temperature, and potential volatilization (Raison et al. 1985). A decline in labile pools of ortho-P following fire can be due to precipitation with Fe, Al, and Ca (Smith 1970).

Burning resulted in loss of NO_3^- relative to controls for the litter/ash and 0–2 cm depths (treatment x soil depth interaction; Table 1) (Table 5). Loss of nitrate in surface soil layers following wildfire is almost universally reported in the literature and likely results from conversion to nitrogen gas and/or gaseous oxides of nitrogen at temperatures greater than 200°C (DeBell and Ralston 1970, White et al. 1973). There may not be much ecological significance to these NO_3^- losses in sagebrush communities where mineralization can rapidly replenish NO_3^- (Blank et al. 1994a).

Biomass and Nutrient Content of Vegetation

In 1999, three years after the prescribed burn, total above ground herbaceous biomass for both the shallow and deep water table sites averaged 1,243 g m⁻² on the burned plots and 469 g m⁻² on control plots (Wright 2001). At the Willow Creek site with the shallow water table, the nitrogen fixing legume, silvery lupine, had higher aboveground biomass on the burned than control plot (Table 6). Aboveground biomass of Douglas sedge was higher on burned interspaces, but lower on burned subcanopies than corresponding controls. Tissue nutrient content of the 2 species varied considerably by treatment and microsite (Table 6). Silvery lupine had higher tissue content of N and lower content of Ca on the burned than control plot. Also, tissue content of Zn and Fe was higher on subcanopies than interspaces of the burned plot. For Douglas sedge, only tissue S was higher on the burned than control plot. Tissue Zn and K of Douglas sedge were higher in plants growing on the control than burned plot, and tissue P was higher in subcanopies than interspaces on the control.

The stimulation of plant growth following fires or “ash-bed effect” is attributed to increased nutrient availability and uptake by plants (Cromer 1967, Kutiel and Naveh 1987). Luxury consumption of nutrients

after fires may promote growth and reproduction in low nutrient soils (Rundel and Parson 1980). The influence of the “ashbed effect” may be short-lived, lasting less than one year (Renbuss 1968, Griffen and Friedel 1984). This may explain why we did not see overwhelming evidence of elevated nutrient uptake in burned plots. In a pot study, Blank et al. (1994b) grew big sagebrush (*Artemisia tridentata* spp. *Wyomingensis* Beale & A. Young), cheatgrass (*Bromus tectorum* L.), bottlebrush squirreltail (*Elymus elymoides* (Raf.) Swezey), and Indian ricegrass (*Achnatherum hymenoides* (Roemer & Schultes) Barkworth) in the surface 5 cm of burned and unburned sagebrush subcanopy soil. Bottlebrush squirreltail and cheatgrass produced significantly more aboveground biomass when grown in burned soil, yet aboveground tissue concentrations of N, K, P, Ca, and Mg (S and micronutrients were not quantified in this study) did not differ significantly between treatments. Although higher tissue concentrations of S, Fe, and Zn suggest increased uptake due to elevated soil availability on the burned plot, other factors may contribute to the increased abundance of herbaceous vegetation. Removal of sagebrush can enhance water availability (Sturges 1983), and the burned plots had higher late season moisture availability than the control plots (Chambers and

Table 6. Biomass and elemental content of aboveground plant material of Silvery lupine and Douglas sedge, by microsite and treatment, for the Willow Wet study site ¹.

Attribute	Subcanopy		Interspace		Microsites Pooled				
	Burned	Unburned	Burned	Unburned	Burned	Unburned			
<i>Silvery lupine</i>									
Biomass (g 0.25m ⁻²)	2.21±1.35	*	1.24±0.52	9.64±3.98	*	2.67±1.34	5.19±1.07	1.61±0.73	
N (mol kg ⁻¹)	2.6±0.1		1.9±0.1	2.3±0.2		1.8±0.1	2.4±0.1	*	1.9±0.1
Zn (mmol kg ⁻¹)	0.58±0.05	*	0.37±0.02	0.39±0.03	*	0.50±0.03	0.46±0.04		0.69±0.03
Mn (mmol kg ⁻¹)	0.78±0.12		0.68±0.16	0.52±0.04		0.71±0.15	0.62±0.07		0.69±0.10
Fe (mmol kg ⁻¹)	8.8±3.4	*	1.7±0.1	2.7±0.9		4.3±1.1	5.0±1.7		3.0±0.7
P (mmol kg ⁻¹)	74±6		72±1	78±4		75±5	76±3		73±3
K (mol kg ⁻¹)	0.38±0.03		0.45±0.03	0.38±0.04		0.36±0.05	0.38±0.03		0.41±0.03
Na (mmol kg ⁻¹)	9±1		19±8	17±7		33±10	14±5		26±6
Ca (mol kg ⁻¹)	0.22±0.01		0.30±0.02	0.27±0.03		0.30±0.02	0.25±0.02	*	0.30±0.01
S (mmol kg ⁻¹)	39.0±13.7		35.9±0.7	32.9±3.8		29.5±2.7	35.2±2.6		32.7±1.7
<i>Douglas sedge</i>									
Biomass (g m ⁻²)	5.53±1.61	*	1.28±0.63	0.49±2.84	*	4.81±1.76	3.36±0.79		2.21±1.35
N (mol kg ⁻¹)	1.1±0.1		1.0±0.1	1.3±0.2		1.2±0.1	1.2±0.1		1.2±0.1
Zn (mmol kg ⁻¹)	0.41±0.02		0.54±0.05	0.35±0.02		0.50±0.05	0.37±0.02	*	0.51±0.03
Mn (mmol kg ⁻¹)	0.58±0.06		0.52±0.09	0.57±0.05		0.67±0.07	0.57±0.04		0.62±0.06
Fe (mmol kg ⁻¹)	5.7±1.0		4.6±1.0	3.2±0.6		3.0±0.4	4.3±0.7		3.5±0.5
P (mmol kg ⁻¹)	53±2	*	79±3	55±4		59±1	54±2		65±3
K (mol kg ⁻¹)	0.37±0.02		0.49±0.02	0.41±0.01		0.44±0.03	0.39±0.01	*	0.46±0.02
Na (mmol kg ⁻¹)	11±2	*	69±27	13±2		24±11	12±1		39±13
Ca (mol kg ⁻¹)	0.14±0.01		0.11±0.01	0.13±0.01		0.14±0.01	0.13±0.01		0.13±0.01
S (mmol kg ⁻¹)	49.2±4.3		49.2±1.3	57.7±5.0		45.8±2.1	53.9±3.5	*	46.4±1.5

¹An asterisk denotes significant differences due to treatment; significance judged at the p≤0.05 level using Fisher's protected least significant difference. Variation in data shown by standard errors.

Linnerooth 2001). Shading by sagebrush can reduce nutrient uptake by herbaceous vegetation (Cui and Caldwell 1997). Kutiel and Naveh (1987) report significant increase in shoot and root biomass and elemental content of N, P, Mg, K, Ca, and Fe 2 months after fire for plants grown on ash.

Conclusions and Implications

This and companion studies show that while shallow water table sites can be restored to graminoid dominance with prescribed fire, deep water table sites appear to have crossed thresholds and will require both burning and reseeding. Three years after the burns, the shallow water table sites were dominated by species that characterize the dry meadow ecological site as a result of seedling establishment (Chambers and Linnerooth 2001) and especially vegetative growth and expansion of preexisting understory species (Wright 2001). In contrast, the deep water table sites were dominated by annual weedy species that occurred in the seed bank, including lambsquarter (*Chenopodium album* L.) and tansy mustard (*Descurainia pinnata* [Walt.] Britt.) (Wright 2001, Chambers and Wehking, unpublished data).

The soil response to the burns on the shallow vs deep water table sites was only indirectly related to the water table regime. There were no detectable differences between shallow and deep water table sites for the soil attributes measured. However, deep water table sites lost proportionately more C and N from subcanopy microsites, and released more aqueous soluble Ca^{+2} and Mg^{+2} , than shallow water table sites. Also, higher mortality of both seeds and vegetative propagules occurred in subcanopy than interspace microsites, especially on deep water table sites (Wehking and Chambers, unpublished data). These differences can be attributed to higher fuel loads of basin big sagebrush (Linnerooth et al. 1998) and higher burn temperatures on deep rather than shallow water table sites. The water table regime influences the persistence and growth of basin big sagebrush in riparian corridors. Moreover, the biomass of basin big sagebrush, relative to understory herbaceous vegetation in degraded riparian corridors, can influence the effects of prescribed burns on both soils and vegetation. Prescribed burns on sites with high volumes of sagebrush and deep water tables can have more negative effects than on sites with lower volumes of sagebrush and shallower water tables.

The response of the soil chemical properties to prescribed burning were consistent with the existing literature, i.e., there is a general increase in water-soluble Ca^{+2} , Mg^{+2} , Na^{+} , SO_4^{-2} , and K^{+} , and KCl-extractable NH_4^{+} and a loss of extractable NO_3^{-} . The increase in available nutrients undoubtedly influenced the response of both the perennial and herbaceous species following the burns. Even 3 years after burning, the content of selected nutrients in both silvery lupine and Douglas sedge was higher on burned than control plots on the deep water table site in Willow Creek. Our overall results indicate that prescribed burns on basin big sagebrush dominated sites with shallow water tables and a preexisting understory of dry meadow species result in minimal C and N loss and increased available nutrients for vegetative regrowth and seedling establishment. Burning sites with deep water tables, high sagebrush biomass, and few perennial herbaceous species can result in proportionately greater C and N loss, and increase available nutrients for weedy species. While burning alone is an appropriate restoration treatment for shallow water table sites, deep water table sites will require a burning prescription that minimizes fire severity, and reseeding with species adapted to more xeric conditions.

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Book Reviews

Desert Puma: Evolutionary Ecology and Conservation of an Enduring Carnivore. By Kenneth A. Logan and Linda L. Sweanor. 2001. Island Press, Washington D.C. 463 p. US \$70.00 hardcover, US \$48.00 paper. ISBN 1559638664.

Studying animals with long-life spans and large home ranges is often doomed to exiguous results, low sample sizes, and weak statistical power. When the animals are secretive carnivores, things only get worse. Having spent the last 2 years on a puma (*Puma concolor*) project, I might be slightly biased, but I believe that these elusive cats are among the most challenging animals to study. Therefore, when Kenneth Logan and his life-partner Linda Sweanor finally published the results of the most extensive study of pumas ever done in the Southwestern United States, I ran at the library and checked out *Desert Puma: Evolutionary and Conservation of an Enduring Carnivore*, a meticulous report of their premier research. I discovered a gold mine of information about every aspect of puma ecology.

From 1985 to 1995, Kenneth Logan and Linda Sweanor devoted their energy (lives may be a more appropriate term) capturing, monitoring, and studying 107 pumas and their progeny—for a total of 241 marked animals, in the rugged terrain of the San Andres Mountains of New Mexico. Collecting as much data as possible, the authors attempted to describe and analyze the pumas' life history strategies and population dynamics, behavioral and social organization, and relationships with multiple prey species—with a particular emphasis on the precarious desert bighorn sheep (*Ovis canadensis mexicana*) and desert mule deer (*Odocoileus hemionus crooki*). In the light shed by their observations, they also explicitly recommended management and conservation actions to assure a sound future for pumas—not only in New Mexico, but throughout their range as well.

Possibly as a natural consequence of such an exhaustive and extensive project, Logan and Sweanor integrated a wide scope of disciplines in their analysis. In addition to the ecological components inherent to a wildlife population study, such as estimation of vital parameters or home range characteristics, they widened their approach to the subjects of paleontology, taxonomy, ethology, and evolution. Evolutionary aspects are especially dominant from cover to cover, as life history traits and pumas' relationships with their relatives, competitors, and prey are closely scrutinized and interpreted in relation with fitness of the animals. This comprehensive aspect of their analysis will tease the interest of a broad range of scientists.

Desert Puma: Evolutionary and Conservation of an Enduring Carnivore also distinguishes itself by its scientific rigor. Throughout 5 key parts and 21 chapters, the authors use a lively yet pragmatic prose to share their data, detailing them enough to enable other researchers to recreate most of their analyses. Hence, the reader is steadily enlightened by flows of facts, numbers, statistics, and figures. Logan and Sweanor thoroughly explore the carnivore literature, and no statement is left to stand alone without a rationale behind it. Appendixes also provide the reader detailed morphological information, mating history of every pair, a discussion of the home range estimation method and results, and parameters used to model mule deer population dynamics. Although this high level of quantitative precision could repel the non-scientific reader, it is thoughtfully balanced by anecdotal field stories describing particularities of individual pumas. For example, the description of a mother and its kittens purring at

each other while researchers were watching the nursery 20 m away, or the behavioral response of pumas when researchers were approaching them, to name only these examples, were truly enjoyable to me.

With this impressive report, Kenneth Logan and Linda Sweanor establish the puma as a keystone and an umbrella species that can play an ultimate role in landscape level conservation strategies. The result is an indispensable reference for the bookshelf of any researcher interested in pumas, or any elusive species that requires long-term monitoring. Logan and Sweanor set new standards in that category. Overall, though, I believe that the greatest contribution of *Desert Puma: Evolutionary and Conservation of an Enduring Carnivore* goes to the puma itself, as a controversial species that needs wildlife professionals to understand what their role in nature is and what they need to thrive.—Catherine Lambert, Large Carnivore Conservation Laboratory, Washington State University, Pullman, Washington.

Water Management in Islam. Edited by Naser I. Faruqi, Asit K. Biswa and Murad J. Bino. 2001. United Nations University Press, New York. 149 p. US\$19.95 paper. ISBN 0-88936-924-0.

Using international experience and expertise gained through participation in both local and international conferences and workshops on water issues, and their current positions, Faruqi, Biswas and Bino have assembled a collection of papers by experts in water management. The book is based on the findings of a workshop on Water Resources Management in Islamic World, organized by the IDRC and held in Amman, Jordan, in December, 1998. Following the workshop, Naser Faruqi a senior program specialist with the IDRC, Ottawa, Canada, Asit R. Biswas, President of the Third World Center for Water Management in Mexico City, Mexico, and Murad J. Bino, Executive Director of the INWRDAM, Amman, Jordan, edited the contributed papers.

The objective of the book is to examine the role that culture and religion play in water demand management (WDM), which is defined as "a measure designed to reduce the volume of fresh water being withdrawn, but without decreasing consumers' satisfaction, or output, or both (p. 90)". This book makes clear that Islamic water management principles together with other economic and non-economic instruments have a significant role in promoting water management and conservation.

The Arabic word for water 'ma' appears 63 times in the Quran (p. 1, p. 40)." Water has special importance in Islam for its use in wudu (ablution, bathing before prayers) and ghusl (bathing).

An overriding principle of Islam is that of ensuring equity in water distribution and access to water. Muslims believe that ensuring social justice and equity in society is the cornerstone of Islam and that the Prophet Muhammad (pbuh) set the example for them (p. 2). All the Islamic laws (hadith) focus on morality, and fair distribution of resources, including water. But the current situation in MENA countries indicate skewed distribution of, and access to water, especially between the rich and the poor, except in Iran, where the lifeline volume of water offered for free seems to be more fair and equitable.

The book addresses non-economic instruments, including water conservation, wastewater reuse and family planning, and economic instruments such as water rights and ownership in Islam,

water tariffs, and markets and privatization and intersectoral water markets. Family planning was actively not discussed at the workshop, but the authors shed some light on the extent to which it is allowed in Islam and its role in preventing further reductions in overall water availability per person.

The 12 chapters of the book start with an introduction based on the 'Dublin Principles,' followed by an overview and principles of Islam and water management, which summarizes the papers presented at the workshop and concludes with a comparison of international and Islamic law on WDM.

The series of documented papers indicates that Islam can promote water management through awareness and educational campaigns. The experts believe that policy makers could "maximize on religion and the desire for salvation to design and implement an islamically inspired water management strategy (p. 46)." The book encourages public awareness campaigns and education through mosques and religious schools, in order to reach the majority of people through the influence of Islam. This education could be done through the religious leaders, known as Imams, during their Friday teachings in mosques.

Case studies from a few countries exemplify the role of NGOs and international institutions such as the WHO in promoting health education. These institutions rely on clean water and public awareness campaigns through training of Imams. Wastewater management is acceptable in Islam as long as it does not cause harm, and has been successful in Saudi Arabia, and to a certain extent, in Palestine.

Water rights and ownership is based on 3 categories: (1) water as a private property awards the owner the right to trade; (2) water as a restricted private property enables the landowner to have limited but special rights over others; and (3) water as a public property cannot be traded. Islam allows cost recovery for providing water and it is believed that a fair tariff will achieve "greater equity across society (p. 13)". Islam allows free markets in water trading and discourages governments from fixing prices.

The book is explicit in emphasizing that Islam is based on the notion of social justice and equity. "Islam promotes moral self-regulation to enhance social justice and to combat corruption, then sets forward a system of laws to enforce its moral code (p. 88)." But what is not clear is the extent to which religion has been applied and pursued in societies to promote and achieve equitable distribution of and access to water. The case studies analyzed indicate that the poor often lack piped water and need to buy water from vendors, who charge much higher prices than the municipalities do for piped water. This situation implies that the poor are paying more (4 to 10 times) for water than the rich, while they consume less water (about 14 liters a day), compared to the rich, who consume 62 liters a day (p. 87). This inequity is a challenge to the overriding principle of Islam, equity, as supported by Faruqi in the following statement. "Clearly, the current situation is inequitable, and the primary water right under Islam – *haq al shafa* (the right to quench your thirst) – is being compromised (p. 5)."

Nevertheless, the documented papers and recommendations from the workshop indicate that equity can and should be maintained in order to achieve a sound water management strategy, based on Islamic principles. Equity has been achieved in some countries, like Iran, although the use of economic instruments might argue against it as block rates offer no incentives to conserve water (p. 86). It is clear that awareness campaigns through religious teachings based on Islamic water management principles would promote water conservation and better management of water demand. The existing system in most of the MENA countries supports most of the principles recommended at the workshop, but what is lacking is a strategy to implement them.—*Selma T. Kavezeri-Karuaihe*, Windhoek, Namibia, currently with the Department of Natural Resource Sciences, Washington State University, Pullman, Washington.

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