Journal of Range Management

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

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

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

*—to create a public appreciation of the economic and social benefits to be obtained from the range environment;*

*—to promote professional development of its members.*

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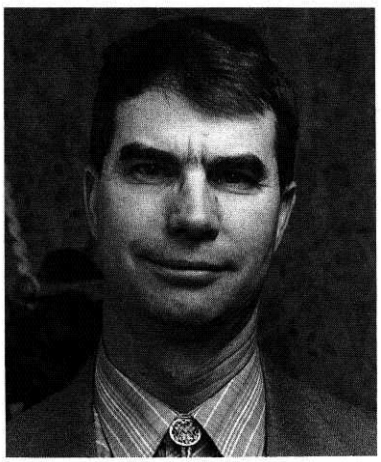

# President's Address:

# Defining failures and successes

DAVID FISCHBACH

*This address was given by David Fischbach, 1994 President of the Society for Range Management, on January 17, 1995, at the Society's Annual Meeting in Phoenix, Ariz.*

I'll never forget 3 years ago when the telephone rang one evening, early in December. It was Stan Tixier who called to inform me that I had been elected as your 2nd vice president. Stan and I visited for a little while. When we were finished, I hung up the phone and went to the living room where my wife was and explained to her that Stan Tixier had just called to congratulate me on being elected. Eldora was quilting that evening, as she frequently does. She didn't even look up and said "That was the dumbest thing you ever did in your life!"

We have a lot of challenges in front of us my friends. I would just like to pose some of these challenges to you, as I see them right now. They are not going to be specific. They are going to be quite general.

One of the challenges we are going to have is to renew our commitment as SRM members and as people who are dedicated not only to SRM but to the range resource. Some of you are really going to have a challenge with the cuts that we have seen recently in the United States government. Some of you have challenges in your work load and how you are going to perform your job. I would like to address specifically the challenges of what you are going to do from now on with, and for, the Society for Range Management. With funding cuts, many of you will have reductions in your travel accounts. I submit to you, this reduction in your travel accounts will bring out your dedication to the Society, to the goals of all range management. That is what dedication really is. Dedication frequently comes, and has to come from sacrifice. When you have to dig in to your own pocket to work for an organization or a cause, that's where dedication and sacrifice come in. I really look forward to all of you coming back to our future meetings, even though many of you might have to dig into your own pockets to come. I tell you very simply that we need all of you to continue to participate and support the Society and it's goals.

In our English language we have 2 words that we don't frequently think about today. Those 2 words are opposite words. One of them is failure; and one is success.

What is failure? What does it mean to fail? Failure quite simply is the lack of success. It doesn't have to be. We can learn much from our failures if we pay attention to them. Capitalize on what we have learned from our mistakes and turn these mistakes and failures into successes. I offer these challenges to you as individuals as well as the Society for Range Management. Let's analyze our failures, see how we can capitalize on them and turn them into successes. Actually when you think about it, success wouldn't be very valuable if it weren't for an occasional failure. If everything we did and said was 100% successful, it really wouldn't have the value that it has when we compare it to our failures.

Let's look at success. What really is success. It is seen by most of us in very different ways. Some of us call it successful when we climb the professional ladder, when we accumulate wealth, or when we have hard goods. Maybe we need to look at it differently. My favorite definition of success is quite simply, **we are successful when we are perceived by our peers as we would have them perceive us**. Here again I address this to each of us as individuals and to all of us as a group of people who work with and for the profession of range management.

In this definition of success we have to analyze 2 or 3 things, and maybe ask ourselves some questions. Question number one might be, who are our peers? Question number two might be, how do they perceive us? Question three, whom would we have be our peers, and how do they perceive us. And from there, what are we going to do to have our peers perceive us as we would have them. My challenge to us is to capitalize on our failures and turn them into successes, to evaluate our successes and improve on them wherever we can, determine who we would have our peers be and do what we can to have them perceive us as we would have them.The best way for all of us to do this is to constantly, everyday, keep in mind that we must do and say the things that we know in our hearts are the right things to do. Maybe not politically correct, maybe not bureaucratically expedient, maybe not individually, personally beneficial to us as individuals, or as a group at this particular time. To look at where we are headed, and do and say the things that we know are right.

In order to do that, it is a further challenge of ours to be as informed as possible on **many** different fronts. There is nothing more frightening than ignorance in action. If we don't get the facts right, there is no way we can make the decisions right. When we criticize or disagree with people we must criticize or disagree from our hearts to an idea or an objective, not to an indi-

vidual or group. Criticize constructively from our hearts, to an idea, not destructively from our emotions to an individual.

Someone told me once I've never disagreed with a person who couldn't be my friend, if that person wanted to be. I've never lost a friend because we disagreed. When people deem themselves or are deemed by others to be leaders, it frequently behooves them to look over their shoulders and see who is following.

During this 3 year tenure as an officer in the Society for Range Management:

My eyes have been opened, to many different views
and some have really seemed strange.
Like the way so many people perceive this resource
that we refer to as range.

It's been a fun trail, a valuable experience
that's added a lot to my life.
But I can go no further, without giving
thanks to my parents, my son and my wife.

Without their support and continuous sacrifice,
it would have been impossible for me to serve,
as President of your SRM, for without them,
I wouldn't have had the nerve.

So when the grass is parched and the waterholes
are dry, and we look up for clouds to see only blue sky;
We give thanks to those on earth and above;
to all who have helped us, and blessed us with love.

Those back home have managed to get by,
sometimes on just a lick and a promise.
I guess I'll just head on back now,
if I can only remember where home is.

The time has come to saddle up and
ride the trail to camp.
I can tell I haven't been here long,
cause the saddle blanket's still damp.

So with the saddle in place and a foot in
the stirrup, I put my hand on the horn;
And swing back into a familiar saddle,
Maybe feelin' kind of forlorn.

Now some places we've been it seems we've left
without leaving much for evidence or traces;
But I do remember a hotel in Spokane,
where we had fun with some "Friends in Low Places"

That piano player was a super talent, and the
microphone he certainly didn't hog;
But after six nights, he still hadn't learned,
"The Dirty Old Egg-Suckin' Dog".

As we grow older though, we continue to learn,
but some things will just never change.
I'm still the same guy, who enjoys a piano sing-along,
and a few verses of "Home on the Range."

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# Redberry juniper-herbaceous understory interactions

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## Abstract

**Basal cover, density, biomass, and species richness of the understory were measured in concentric zones from the stem bases of large redberry juniper (*Juniperus pinchotii* Sudw.) trees to 6 m beyond their canopy edges on a shallow, rocky soil and 2 deep soils in the northern Edwards Plateau of Texas. The juniper-driven successional processes of tree dominance, debilitation of understory dominants, influx of subsidiary species, and the general reduction in diversity, density, and biomass of the herbaceous species were evident on all 3 sites. Juniper interference intensified with increasing proximity to the stem bases. Biomass and basal cover of the herbaceous understory responded to a greater extent than did density and species richness 2 years after large redberry junipers were killed with soil injections of picloram (4-amino-3,5,6-trichloro-2-pyridinecarboxylic acid). Herbaceous biomass responses after junipers were killed indicated that the sphere of influence of large junipers was more extensive on the shallow soil than on the deep soils. Herbaceous biomass in the presence of interference by large junipers on the Kimbrough, Angelo clay loam, and Tulia loam soils was 1,300, 1,780, and 1,290 kg ha$^{-1}$, respectively, compared to 2,140, 2,140, and 1,560 kg ha$^{-1}$ 2 years after the junipers were killed on the 3 sites, respectively. Projected herbaceous biomass when juniper populations on the sites develop into closed-canopy woodlands was 320, 880, and 270 kg ha$^{-1}$ for the Kimbrough, Angelo clay loam, and Tulia loam soils, respectively.**

**Keywords: *Juniperus pinchotii*, ecology, species richness, succession, competition, picloram**

Redberry juniper (*Juniperus pinchotii* Sudw.) is a sprouting evergreen conifer that occurs in Oklahoma, New Mexico, Arizona, and Texas (Correll and Johnston 1979). It is a major woody species on about 4.7 million ha of Texas rangeland (Soil Conservation Service 1985). The increase of redberry juniper in grasslands since the late nineteenth century has been attributed to overgrazing, reduced frequency and intensity of fire, periodic droughts, and climatic conditions more favorable for woody plants (Ellis and Schuster 1968, Smeins 1983). Redberry juniper is considered an invader species on most range sites and it has little economic value. Forage production declines dramatically as redberry juniper canopy cover increases (McPherson and Wright 1990), and dense stands interfere with livestock handling and movement. Many grasslands on the Edwards Plateau of Texas have been converted to juniper-dominated woodlands or to closed-canopy juniper stands.

Grass yield on a redberry juniper-infested site on the Edwards Plateau was 514 kg ha$^{-1}$ compared to 1,942 kg ha$^{-1}$ on an adjacent site where the junipers were controlled with pelleted picloram (4-amino-3,5,6-trichloro-2-pyridinecarboxylic acid) (Robison and Cross 1970). Grass production decreased linearly on ungrazed areas and logarithmically on grazed areas in the Texas High Plains as redberry juniper canopy cover increased (McPherson and Wright 1990). McPherson et al. (1991) reported a distance-independent interaction between herbaceous vegetation biomass and redberry junipers 1 to 4 m tall on Texas high plains grasslands. They attributed this to the effect of variable tree sizes sampled, understory species composition, overlapping lateral root systems of the junipers, and to an environment sufficiently favorable to overshadow competition for soil water beyond the juniper canopy edges.

Other *Juniperus* species have been reported to have major effects on associated herbaceous vegetation. Basal area of grasses at the stem base of oneseed juniper (*Juniperus monosperma* [Engelm.] Sarge.) in a New Mexico study was only 2 to 5% compared to 31 to 35% at the canopy edge (Schott and Pieper 1985). The relationship between total herbaceous biomass and overstory canopy cover was best expressed by a negative 2$^{nd}$ degree polynomial curve in a pinyon-juniper (*Pinus edulis* [Engelm.]-*J. monosperma*) woodland in south-central New Mexico (Pieper 1990). Herbage production was significantly reduced beneath canopies and at the canopy edges of eastern redcedar (*Juniperus virginiana* L.) in north-central Oklahoma, but the trees did not affect herbage production 1 m or farther beyond the canopy edges (Engle et al. 1987). Herbaceous biomass at the edge of western juniper (*Juniperus occidentalis* Hook.) canopies increased from near 0 to about 1,400 kg ha$^{-1}$ within 4 years after the trees were killed with granular picloram (Evans and Young 1985).

Redberry juniper is an important overstory species in the semiarid Edwards Plateau of Texas that is rapidly increasing in abundance and dominance, yet its relations with the herbaceous understory have not been studied. Such information is critical to understanding successional mechanisms and the effects of woody species on livestock carrying capacity and wildlife habitat and

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watershed values of rangeland. The objectives of this study were to quantify the relationship between large redberry junipers and basal cover, density, biomass, and species richness of the herbaceous understory on a shallow, rocky soil and 2 deep soils in the northern Edwards Plateau and to quantify short-term responses of the herbaceous understory to control of large junipers.

## Materials and Methods

The study was conducted on the Hugh Stone Ranch, 16 km northwest of San Angelo (Tom Green County), Texas. The area is comprised of approximately 12,800 ha of short- and mid-grass rangeland with a dominant overstory of redberry juniper and honey mesquite (*Prosopis glandulosa* Torr. var. *glandulosa*). Average annual precipitation is 519 mm, with peaks generally occurring in late spring and early autumn. The average annual temperature is 18°C and the average frost-free period is 232 days (Wiedenfeld and Flores 1976).

Study sites were selected less than 1.6 km apart on soils designated as a Kimbrough association, an Angelo clay loam, and a Tulia loam. The Kimbrough soils (loamy, mixed, thermic, shallow Petrocalcic Calciustolls) are very shallow-to-shallow gravelly loams on undulating topography with 1 to 8% slopes. They have a low available water capacity and loss of rainfall as surface runoff is medium. The surface soil, 10 to 38 cm thick, is underlain by a 3 to 46-cm thick layer of indurated caliche. Major grasses on the site included Wright threeawn (*Aristida wrightii* [Nash] Allred), red grama (*Bouteloua trifida* Thurb.), hairy tridens (*Erioneuron pilosum* [Buckl.] Nash), and Reverchon bristlegrass (*Setaria reverchonii* [Vasey] Pilger). Major forbs were needleleaf bluet (*Hedyotis acerosa* Gray var. *acerosa* Gray ex Benth & Hook), Parks groomwell (*Lithospermum parksii* I.M. Johnst.), mouse ear (*Tiquilia canescens* [DC.] A. Richards.), and longstalk greenthread (*Thelesperma longipes* Gray.). The Kimbrough soil supported 290 redberry junipers >2.0 m tall ha$^{-1}$ along with 250 redberry junipers ha$^{-1}$ 1-2 m tall and 5,981 redberry junipers ha$^{-1}$ <1 m tall (total redberry juniper canopy cover 31%) (Dye 1993).

The Angelo clay loam (fine, mixed, thermic Torrertic Calciustolls) had high available-water capacity, moderately slow permeability, and occurred on <1% slopes. The solum of this soil is 150 to 300 cm thick. Major grasses on the Angelo clay loam were Wright threeawn, common curlymesquite (*Hilaria belangeri* [Steud.] Nash), fall witchgrass (*Leptoloma cognatum* [Schult.] Chase), and Texas wintergrass (*Stipa leucotricha* Trin. & Rupr.). Major forbs included croton (*Croton dioicus* [Cav.] Rosval and *C. potsii* [Klotzch] Muell. Arg.), and gray coldenia. The Angelo clay loam supported 89 redberry junipers >2.0 m tall ha$^{-1}$ along with 70 redberry junipers ha$^{-1}$ 1-2 m tall and 749 redberry junipers ha$^{-1}$ <1 m tall (total redberry juniper canopy cover 7%) (Dye 1993).

The Tulia loam (fine-loamy, carbonatic, thermic Calciorthidic Paleustalfs) had high available-water capacity, moderate permeability, and occurred on 1 to 3% slopes. The solum of this soil is 50 to 100 cm thick over a buried B horizon 50 to 200 cm thick. Dominant grasses were Wright threeawn, Texas grama (*Bouteloua rigidiseta* [Steud.] A.S. Hitch.), fall witchgrass, and buffalograss (*Buchloe dactyloides* [Nutt.] Engelm.). Dominant forbs were croton, gray coldenia, and Parks groomwell. The redberry juniper stand on the Tulia loam included 125 redberry junipers ha$^{-1}$ >2.0 m tall along with 141 redberry junipers ha$^{-1}$ 1-2 m tall and 1,396 redberry junipers ha$^{-1}$ <1 m tall (total redberry juniper canopy cover 12%) (Dye 1993).

Ten of the tallest redberry juniper trees on each site were permanently marked in August 1991. Mean tree heights (±standard deviations) were 3.7 ± 0.3, 3.2 ± 0.3, and 3.3 ± 0.5 m on the Kimbrough, Angelo clay loam, and Tulia loam sites, respectively, and mean canopy diameters were 4.6 ± 0.9, 3.6 ± 0.9, and 3.4 ± 0.7 m on the 3 sites, respectively. Herbaceous vegetation was sampled at 6 locations along a line transect placed in the 4 cardinal directions from each juniper in August 1991. Basal cover, density, standing crop, and species richness were sampled within 6 concentric sampling zones (at stem base, mid-canopy, canopy edge, and at 1, 3, and 6 m beyond canopy edge). Basal cover was estimated by the 10-point frame method (pins 3.8 cm apart) (Brown 1954, Bonham 1989) with one placement of the frame perpendicular to the transect at each sampling location on each transect. Basal cover within each concentric zone on each site was estimated from 400 points in 1991 (10 trees × 4 transects × 10 points) and from 200 points for each zone for both live and dead trees in 1992 and 1993 (5 trees × 4 transects × 10 points). Density was recorded by species within a 60.0 × 33.33-cm quadrat placed at each sampling location on each transect. The herbaceous plants within the quadrat were subsequently harvested at ground level, separated into grasses and forbs, oven dried to a constant weight at 52°C, and weighed. Species richness within each concentric zone was the total number of herbaceous, woody, and succulent species encountered while recording plant densities (Ludwig and Reynolds 1988).

Five of the permanently marked redberry junipers on each site were killed in September 1991 by injecting picloram at 20 ml m$^{-1}$ of tree height 10 to 15 cm into the soil beneath the tree canopies. Other redberry junipers ≥ 0.5 m tall within a 12-m radius of the treated junipers were also killed to eliminate their influence on the herbaceous vegetation. The herbaceous vegetation around live and dead redberry junipers was sampled by the methods given above in late August of 1992 and 1993 to quantify response to the reduction of juniper interference. Sampling locations were shifted 30° from the cardinal directions during sampling in 1992 and 1993. To express whole-tree influence on herbage biomass, total herbage biomass (kg ha$^{-1}$) within the circular area from stem bases to 6 m beyond the canopy edges of live and dead junipers on each site in 1993 was calculated by summing the product of area (ha) within each concentric sampling zone and the respective biomass estimate (kg ha$^{-1}$), and dividing this total (kg) by the total area (ha) within this circle.

The experiment was arranged in a completely randomized design with 10 replications (trees) on each site in 1991 and 5 replications each of live and dead trees on each site in 1992 and 1993. Analysis of variance on basal cover, density, biomass, and species richness data revealed significant site × year interactions, so data for each site and year were subjected to separate analyses of variance, and means were separated ($P \leq 0.05$) by LSD where necessary. Since cardinal direction was not significant, data within a sampling zone were pooled over direction. Density data for major understory species were transformed by log (x + 0.5) before analysis of variance, the means were separated ($P \leq 0.05$ or $P \leq 0.10$) by LSD where necessary, and the means were reverse transformed for presentation. Total numbers of species encountered within each sampling zone for each treatment (live or dead

trees) during density sampling in 1993 (observed values) were compared to the numbers recorded in 1991 (expected values) by chi-square analyses to evaluate for treatment effects on species richness.

## Results

### Interaction of Mature Junipers with Understory Species

Monthly precipitation recorded in a rain gauge 10 km from the study area exceeded the long-term average during 9 months of 1991, and total precipitation for the year (798 mm) was 54% above the long-term average. Data collected in 1991 (n= 10 trees/site) generally indicated basal cover of the herbaceous understory was significantly lower adjacent to juniper stems and at mid-canopy compared to canopy edges and beyond on all 3 sites (Fig. 1). A dense mat of dead juniper leaves covered 92 to 97% (ranges of means among 3 sites) of the soil surface at the juniper stem bases, 82 to 90% at mid-canopy, and 55 to 63% at canopy edge (Dye 1993). Basal cover 6 m beyond canopy edges

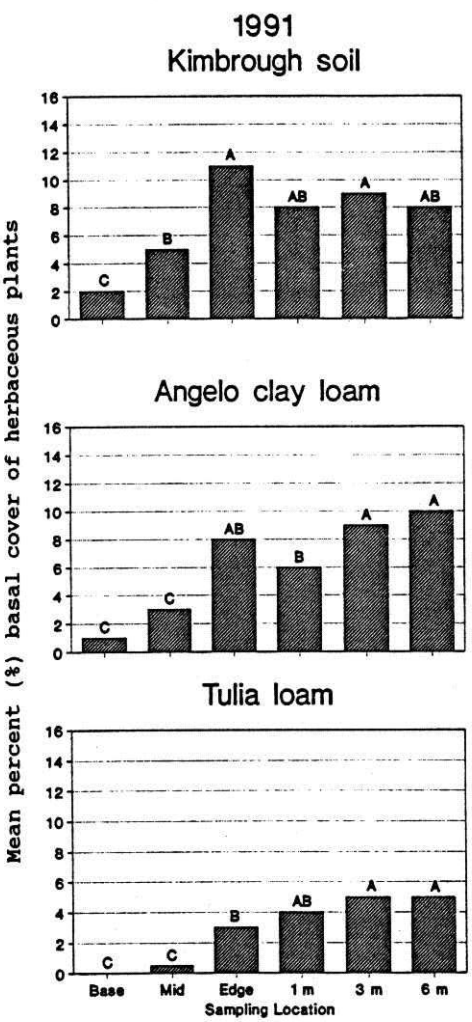


**Fig. 1. Mean basal cover (%) of herbaceous plants in 6 sampling locations around redberry junipers on 3 sites (n= 10 trees/site) near San Angelo, Tex. in 1991. Means within a site that subtend different uppercase letters are different ($P \leq 0.05$).**

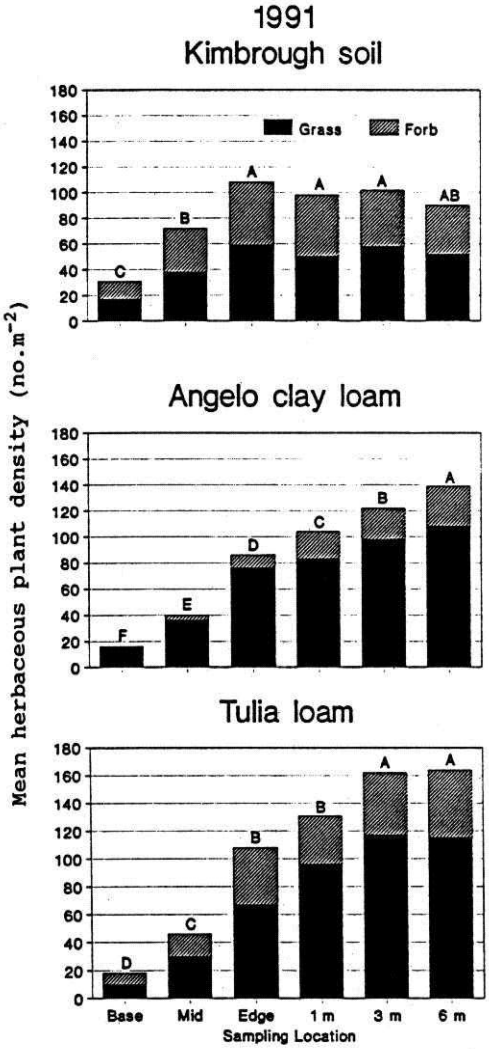


**Fig. 2. Mean herbaceous plant densities (no. m$^{-2}$) in 6 sampling locations around redberry junipers on 3 sites (n= 10 trees/site) near San Angelo, Tex. in 1991. Means within a site that subtend different uppercase letters are different ($P \leq 0.05$).**

ranged from 4- to >10-fold greater than that at the stem bases. Herbaceous plant basal cover at the edge of juniper canopies on the Kimbrough and Angelo clay loam soils was similar to that 1 to 6 m beyond canopy edges, whereas basal cover at canopy edges on the Tulia loam was significantly lower than that 3 to 6 m beyond juniper canopy edges (Fig. 1).

Density of grasses and forbs in 1991 was lowest at the base of juniper stems and greatest at the edge of juniper canopies (Kimbrough site) or at 6 m beyond canopy edges (Angelo clay loam and Tulia loam sites) (Fig. 2). Mean densities of herbaceous plants 6 m beyond canopy edges ranged from about 3- to 9-fold greater than at the stem bases.

Total herbaceous biomass increased from stem bases to 6 m beyond canopy edges on the Kimbrough and Angelo clay loam and to 3 m beyond canopy edges on the Tulia loam in 1991 (Fig. 3). Total herbaceous biomass at stem bases on the 3 sites ranged from 120 to 140 kg ha$^{-1}$ compared to a range from 1,160 to 1,990 kg ha$^{-1}$ 6 m beyond juniper canopy edges. Our finding of distance-dependent interactions between large redberry junipers and standing crop of the herbaceous understory is in contrast to the distance-independent interaction found by McPherson et al.

(1991) at 2 sites occupied by the species on the Texas high plains. They reported a reduction in standing crop only midway between the juniper stems and canopy edge, although they did not sample at the stem bases.

Species richness of grasses and forbs was lower ($P \leq 0.05$) in the zone adjacent to juniper stem bases compared to that at the canopy edges and beyond on all 3 sites (Table 1). Furthermore, there were generally fewer herbaceous species in the mid-canopy zone than in other zones outward to 6 m beyond canopy edges. However, species richness of shrubs and succulents was greater ($P \leq 0.05$) in the zones adjacent to juniper stems and at mid-canopy than at canopy edges and in the interspace between large junipers. Total understory species richness was lower ($P \leq 0.05$) in the zone adjacent to juniper stems than in the other zones surrounding large junipers on the Angelo clay loam and Tulia loam sites but not on the Kimbrough association site (Table 1).

Herbaceous species that were most tolerant of redberry juniper interference, i.e. those that were abundant at juniper canopy edges and beyond and also present in lower numbers ($\geq 1$ m$^{-2}$) at the stem bases, included threeawns, hairy tridens, buffalograss, needleleaf bluet, and longstalk greenthread (Tables 2-4). Herbs with lesser tolerance, i.e. those that were abundant at canopy edges and beyond but absent or rare ($<1$ m$^{-2}$) at stem bases, included red grama, common curlymesquite, Texas grama, Reverchon bristlegrass, leather-weed croton, gray coldenia, and spreading sida (*Sida abutifolia* Mill.). Texas wintergrass, a grass with the $C_3$ photosynthetic pathway, was the only herbaceous plant more abundant beneath juniper canopies than in the interspaces. Several shrubs and succulents, including redberry juniper, agarito (*Berberis trifoliolata* Moric.) and pricklypear (*Opuntia* spp.) were more abundant beneath large junipers than in the interspaces (Tables 2-4). Littleleaf sumac (*Rhus microphylla* Engelm.), lime pricklyash (*Zanthoxylum hirsutum* Buckl.), and Mormon tea (*Ephedra antisyphylitica* C.A. Meyer) were also present beneath large junipers but absent or rare in the interspaces.

**Table 1. Mean species richness in 6 sampling locations around large redberry junipers on a Kimbrough association, Angelo clay loam, and Tulia loam near San Angelo, Tex. in 1991[1].**

| | Distance from juniper | | | | | |
|---|---|---|---|---|---|---|
| | Beneath juniper canopy | | | Beyond canopy edge | | |
| | Stem base | Mid canopy | Canopy edge | 1 m | 3 m | 6 m |
| | (number of species) | | | | | |
| Kimbrough Association | | | | | | |
| Grasses | 1.6 c | 2.7 bc | 4.5 a | 4.1 ab | 4.3 a | 3.9 ab |
| Forbs | 2.7 b | 4.6 a | 5.5 a | 5.5 a | 5.1 a | 4.4 a |
| Shrubs/succulents | 2.9 a | 2.0 b | 1.2 c | 0.9 cd | 0.3 d | 0.3 d |
| Total | 7.2 c | 9.3 abc | 11.2 a | 10.5 ab | 9.7 abc | 8.6 bc |
| Angelo clay loam | | | | | | |
| Grasses | 2.3 c | 3.9 b | 6.2 a | 5.9 a | 5.3 a | 6.2 a |
| Forbs | 0.5 d | 1.6 c | 2.3 bc | 3.2 ab | 2.9 ab | 3.8 a |
| Shrubs/succulents | 1.6 a | 1.2 a | 0.3 b | 0.1 b | 0.1 b | 0.3b |
| Total | 4.4 d | 6.7 c | 8.8 ab | 9.2 ab | 8.3 bc | 10.3a |
| Tulia loam | | | | | | |
| Grasses | 2.3 c | 4.8 b | 8.0 a | 8.0 a | 7.7 a | 8.1 a |
| Forbs | 1.6 b | 2.7 b | 4.5 a | 5.1 a | 5.4 a | 4.5 a |
| Shrubs/succulents | 2.5 a | 1.8 a | 1.0 b | 0.3 bc | 0.4 bc | 0.2 c |
| Total | 6.4 c | 9.3 b | 13.5 a | 13.4 a | 13.5 a | 12.8 a |

[1]Means within a row followed by the same lowercase letter are not different ($P \leq 0.05$).

**Table 2. Mean density of major species in 6 sampling locations around large redberry junipers on a Kimbrough soil near San Angelo, Tex. in 1991[1,2].**

| | Distance from juniper | | | | | |
|---|---|---|---|---|---|---|
| | Beneath juniper canopy | | | Beyond canopy edge | | |
| | Stem base | Mid canopy | Canopy edge | 1 m | 3 m | 6 m |
| | (plants m$^{-2}$) | | | | | |
| Grasses | | | | | | |
| Threeawn | 8.8 c | 23.0 ab | 29.1 a | 14.4 bc | 11.6 bc | 16.2 abc |
| Sideoats grama | 1.6 AB | 1.8 A | 1.6 AB | 0.1 BC | 0.0 C | 0.2 BC |
| Hairy tridens | 1.6 c | 5.0 bc | 14.2 a | 20.4 a | 18.7 a | 14.4 ab |
| Fall witchgrass | 0.2 | 0.4 | 0.4 | 0.4 | 0.5 | 0.6 |
| Reverchon bristlegrass | 0.1 | 0.6 | 0.7 | 1.1 | 0.8 | 2.1 |
| Slim tridens | 0.2 | 0.3 | 0.6 | 0.7 | 0.6 | 0.9 |
| Other grasses | 0.4 | 0.8 | 1.3 | 1.4 | 1.7 | 0.8 |
| Forbs | | | | | | |
| Plains lazydaisy[3] | 0.2 | 0.5 | 0.9 | 0.9 | 1.0 | 0.8 |
| Needleleaf bluet | 1.7 b | 6.8 a | 11.5 a | 13.3 a | 10.6 a | 6.4 a |
| Parks groomwell | 0.4 b | 5.2 a | 5.7 a | 3.8 ab | 2.0 ab | 0.5 b |
| Longstalk greenthread | 2.4 B | 6.0 AB | 10.1 A | 8.6 A | 6.2 AB | 11.3 A |
| Other forbs | 5.2 | 5.7 | 6.0 | 8.0 | 3.6 | 3.9 |
| Shrubs/Succulents | | | | | | |
| Agarito | 1.7 a | 0.7 b | 0.0 b | 0.0 b | 0.1 b | 0.0 b |
| Redberry juniper | 4.0 ab | 6.5 a | 6.5 a | 1.4 bc | 0.2 c | 0.0 c |
| Other shrubs | 1.8 a | 0.3 b | 0.2 b | 0.0 b | 0.0 b | 0.0 b |

[1]Means within a row followed by the same lowercase letter are not different ($P \leq 0.05$).
[2]Means within a row followed by the same uppercase letters are not different ($P \leq 0.10$).
[3]*Aphanostephus ramosissimus* DC.

## Response to Reducing Juniper Interference

Growing conditions were favorable during 1992 with total precipitation of 749 mm. Precipitation exceeded the long-term average 5 months in 1992. Responses of the herbaceous understory to reduced redberry juniper interference within the first year after herbicide applications reflected the growing conditions and resiliency of the herbaceous species. Responses recorded at the end of the first growing season (August 1992) after mature junipers were killed included: 1) increases ($P \leq 0.05$) in basal cover of herbaceous plants from stem bases out to mid-canopy on the Kimbrough soil; 2) increases ($P \leq 0.05$) in density of herbaceous plants at stem bases and out to mid-canopy on the Kimbrough soil and at the stem bases on the Angelo clay loam; and 3) increases ($P \leq 0.05$) in herbaceous biomass from stem bases out to 3 m beyond canopy edges on the Kimbrough soil and Tulia loam and out to the canopy edges on the Angelo clay loam (Dye 1993).

Growing conditions were less favorable during 1993 than during 1991 and 1992. Rainfall received during January-August 1993 (349 mm) was near the long-term average. However, the preceding autumn was extremely dry. Basal cover of herbaceous plants increased ($P \leq 0.05$) beneath the canopies of dead junipers 2 growing seasons after treatment (Fig. 4). Total basal cover at dead stem bases ranged from 6 to 12 percentage units greater than that at live stem bases, and total basal cover at midcanopy of dead junipers was 10 percentage units greater than that at mid canopy of live trees. Basal cover was similar from the stem bases of dead junipers to 6 m beyond their canopy edges at all 3 sites after 2 growing seasons. In contrast, basal cover around live junipers followed the same pattern observed in 1991, i.e. basal cover generally decreased from 6 m beyond canopy edges to the stem bases on all 3 sites. Basal cover of herbaceous plants at the canopy edges

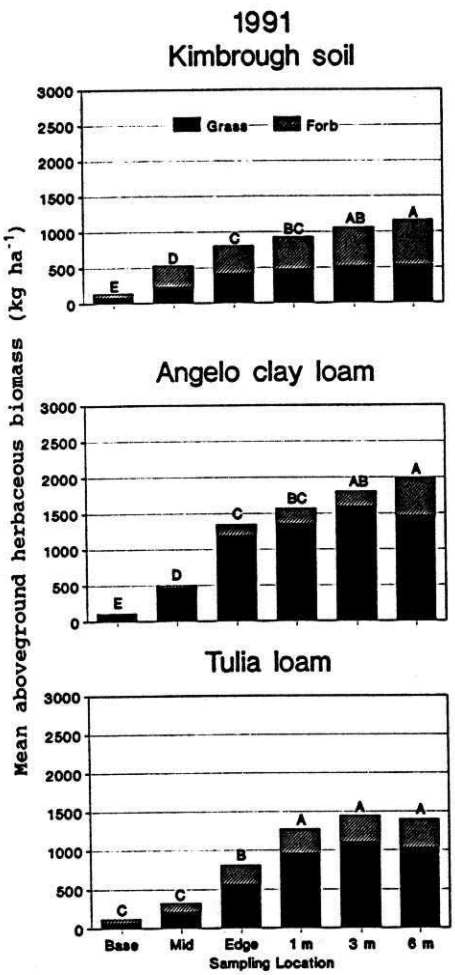


**Fig. 3. Mean grass and forb aboveground biomass (kg ha$^{-1}$) in 6 sampling locations around redberry junipers on 3 sites (n= 10 trees/site) near San Angelo, Tex. in 1991. Means within a site that subtend different uppercase letters are different ($P \leq 0.05$).**

or beyond was not affected by killing junipers on the 3 sites.

Mean density of herbaceous plants beneath canopies of dead junipers was greater ($P \leq 0.05$) than beneath live juniper canopies on the Kimbrough site in 1993, but densities from the canopy edges out to 6 m beyond canopy edges were similar for live and dead trees (Fig. 5). Densities of the herbaceous plants were not affected by killing junipers on the Angelo clay loam site. Herbaceous plant densities were greater at canopy edges and at 1 m beyond canopy edges of dead juniper compared to live juniper on the Tulia loam site in 1993.

Compared to live trees, herbaceous biomass production increased ($P \leq 0.05$) in 1993 after junipers were killed on all 3 sites (Fig. 6). Increases ($P \leq 0.05$) in biomass occurred from the stem bases out to at least 6 m beyond canopy edges on the Kimbrough soil, from stem bases out to the canopy edges on the Angelo clay loam, and from stem bases to 1 m beyond canopy edges on the Tulia loam. Relative increases in herbaceous biomass were greatest beneath juniper canopies. Total biomass at dead stem bases was 2,520, 2,410, and 1,620 kg ha$^{-1}$ compared to 60, 360, and 110 kg ha$^{-1}$ at live stem bases on the Kimbrough soil, Angelo clay loam, and Tulia loam, respectively. Grass biomass was greater ($P \leq 0.05$) beneath dead juniper canopies compared to live juniper canopies on all 3 sites. Reduction of juniper interference resulted in herbage production beneath the canopies similar to that in the interspaces (6-m sampling location) within 2 years, whereas herbage yields around live junipers decreased greatly from the interspaces toward the stem bases as was observed in 1991.

**Table 3. Mean density of major species in 6 sampling locations around large redberry junipers on an Angelo clay loam soil near San Angelo, Tex. in 1991[1,2].**

| | Distance from juniper | | | | | |
|---|---|---|---|---|---|---|
| | Beneath juniper canopy | | | Beyond canopy edge | | |
| | Stem base | Mid canopy | Canopy edge | 1 m | 3 m | 6 m |
| | (plants m$^{-2}$) | | | | | |
| Grasses | | | | | | |
| Threeawn | 1.9 B | 4.2 AB | 5.3 A | 5.8 A | 6.1 A | 8.5 A |
| Silver bluestem[3] | 0.1 | 0.2 | 0.6 | 1.5 | 1.5 | 1.2 |
| Red grama | 0.0 c | 0.4 c | 8.0 b | 11.6 b | 6.4 b | 29.8 a |
| Common curlymesquite | 0.3 b | 4.9 b | 28.2 a | 26.9 a | 39.2 a | 31.9 a |
| Fall witchgrass | 1.9 | 3.4 | 4.7 | 3.0 | 1.4 | 1.3 |
| Texas wintergrass | 2.1 ab | 3.4 a | 3.5 a | 0.2 b | 0.0 b | 0.0 b |
| Other grasses | 0.8 c | 2.8 bc | 4.8 ab | 8.8 a | 5.2 ab | 7.9 a |
| Forbs | | | | | | |
| Croton | 0.1 c | 0.9 c | 1.5 bc | 4.8 b | 13.2 a | 14.5 a |
| Gray coldenia | 0.7 bc | 0.1 c | 1.1 abc | 1.4 abc | 1.6 ab | 3.1 a |
| Other forbs | 0.3 c | 2.0 bc | 4.3 ab | 7.6 a | 6.0 ab | 6.4 ab |
| Shrubs/Succulents | 2.3 a | 1.8 ab | 1.2 abc | 0.1 c | 0.1 c | 0.3 bc |

[1]Means within a row followed by the same lowercase letter are not different ($P \leq 0.05$).
[2]Means within a row followed by the same uppercase letters are not different ($P \leq 0.10$).
[3]*Bothriochloa saccharoides* (Sw.) Rydb.

Calculation of total herbaceous biomass within the entire circular area from stem bases to 6 m beyond canopy edges of live and dead junipers (1993 data) revealed that individual, large junipers reduced herbage standing crops by 18.1, 6.8, and 5.0 kg on the Kimbrough, Angelo clay loam, and Tulia loam soils, respectively. Total biomass within these circular areas around live trees in 1993 was 1,300, 1,780, and 1,290 kg ha$^{-1}$ on the Kimbrough, Angelo clay loam, and Tulia loam soils, respectively, compared to 2,140, 2,140, and 1,560 kg ha$^{-1}$ around dead trees for the 3 soils, respectively.

Chi-square analyses comparing 1991 versus 1993 data on species richness for live and dead junipers revealed no consistent patterns. There were no significant changes within any of the sampling zones in total numbers of understory species on the Tulia loam or within most sampling zones on the Kimbrough soil and Angelo clay loam (data not shown).

## Discussion

### Redberry Juniper Interference

Interference of large redberry junipers with the herbaceous understory was evident on 2 deep soils with high water-holding capacities and on a shallow, rocky soil with low water-holding capacity. The magnitude of interference, relative to herbaceous plant basal cover, density, herbage biomass, and species richness, intensified with increasing proximity to the juniper stems. Differential responses among the 3 sites in herbage biomass after killing the junipers indicated that the area affected by a juniper was greatest on the more xeric, shallow, rocky Kimbrough soil and least on the deep, nearly level Angelo clay loam. Herbage biomass increased in all zones from juniper stem bases to 6 m beyond juniper canopy edges on the Kimbrough soil, but only out to 1 m beyond canopy edges on the Tulia clay loam and out to

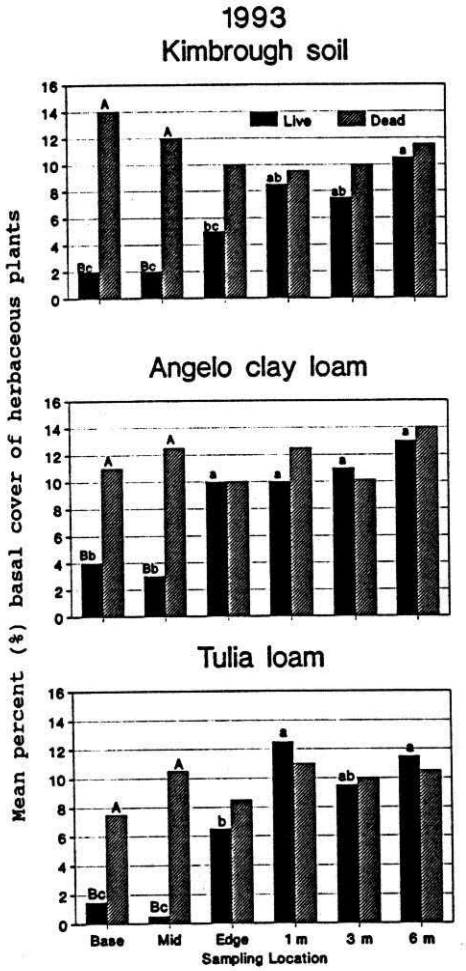


**Fig. 4. Mean basal cover (%) of herbaceous plants in 6 sampling locations around live (L) and dead (D) redberry junipers on 3 sites near San Angelo, Tex. in 1993. Means within a site and sampling location that subtend different uppercase letters are different ($P \leq 0.05$). Means within a site and treatment (live or dead) that subtend different lowercase letters are different ($P \leq 0.05$).**

the canopy edges on the Angelo clay loam within 2 years after the junipers were killed.

Competition between large junipers and the herbaceous understory for soil water or nutrients was evidently more intense on the Kimbrough soil because it has less soil mass and a lower available-water status compared to the Angelo clay loam and Tulia loam. Junipers growing on shallow soils may have more extensive lateral root systems than those growing on deep soils, and they may rely more heavily upon soil moisture and nutrients within the root zone of the herbaceous plants. The interference of oneseed junipers with the herbaceous understory in northern Arizona was greater on sandy soils than on clay loam soils (Johnsen 1962). The diameter of bare areas beneath oneseed junipers averaged 0.6 m on clay loam soils compared to 1.8 m on sandy soils. The bare areas extended beyond the canopy edges of oneseed junipers ≥ 0.6 m tall on sandy soils, but were only evident on trees >1.8 m tall on clay loam soils. Eastern redcedars 2 and 6 m tall on tallgrass prairie in Oklahoma reduced herbage production significantly beneath their canopies, but the reduction at canopy edges was slight and effects beyond canopy edges only occurred in a year of below-normal precipitation (Engle et al. 1987).

Other factors that may contribute to mature redberry juniper interference, in addition to competition for soil water and nutrients, are litter, shade, allelopathy and interception of rainfall by the juniper canopies and litter. Juniper litter cover ranged from 92 to 97% at the juniper stem bases and from 82 to 90% at mid-canopy prior to application of picloram treatments. Picloram defoliated the trees, thus thickening the litter layer and possibly increasing litter cover. The greatest responses to killing junipers in this study were the increases in herbage production and basal cover in the zones with greatest litter cover that had previously been most heavily shaded. This suggests that juniper litter was not allelopathic to grasses and forbs present in these zones, although leachates from the live juniper leaves may have suppressed growth of herbaceous plants beneath the canopies. Our results suggest that juniper interference directly beneath the tree canopies was associated with shading, competition for soil water, nutrients and interception of rainfall. Thurow and Carlson (1994) reported that 62% of the precipitation received in closed-canopy juniper woodlands was lost to interception by the juniper canopies, and about 14.5% of that reaching the soil surface would be intercepted by the juniper litter layer. Juniper interference beyond canopy edges may have been associated with competition for soil water or nutrients, although allelopathic effects from juniper root exudates cannot be ruled out.

## Influence of Redberry Junipers on Rangeland Values

The data presented have significant implications relative to the

**Table 4. Mean density of major species in 6 sampling locations around large redberry junipers on a Tulia loam soil near San Angelo, Tex. in 1991[1].**

| | Distance from juniper | | | | | |
|---|---|---|---|---|---|---|
| | Beneath juniper canopy | | | Beyond canopy edge | | |
| | Stem base | Mid canopy | Canopy edge | 1 m | 3 m | 6 m |
| | (plants m$^{-2}$) | | | | | |
| Grasses | | | | | | |
| Threeawn | 3.1 c | 4.6 bc | 10.4 ab | 13.0 a | 13.6 a | 20.2 a |
| Texas grama | 0.0 b | 0.7 b | 2.2 ab | 5.5 a | 5.7 a | 6.1 a |
| Red grama | 0.0 c | 0.1 c | 3.2 b | 20.1 a | 27.1 a | 27.6 a |
| Buffalograss | 1.0 | 5.6 | 7.2 | 5.8 | 10.0 | 7.9 |
| Fall witchgrass | 0.9 | 1.9 | 3.2 | 3.1 | 1.9 | 2.1 |
| Reverchon bristlegrass | 0.4 c | 3.3 b | 5.7 ab | 7.2 ab | 7.6 ab | 11.8 a |
| Slim tridens[2] | 0.2 b | 0.2 b | 1.6 ab | 3.1 a | 2.1 a | 1.6 ab |
| Sand dropseed[3] | 0.5 d | 1.0 cd | 4.7 a | 3.4 ab | 2.1 bc | 2.2 bc |
| Other grasses | 0.4 c | 3.0 b | 7.2 ab | 5.9 ab | 4.5 ab | 8.2 a |
| Forbs | | | | | | |
| Croton | 0.0 c | 0.5 c | 2.3 bc | 4.2 ab | 8.0 a | 5.8 ab |
| Parks groomwell | 2.1 | 4.7 | 10.1 | 3.6 | 2.4 | 1.9 |
| Spreading sida | 0.3 c | 1.2 c | 4.7 b | 8.2 ab | 9.7 ab | 12.1 a |
| Gray coldenia | 0.0 d | 0.7 cd | 2.5 bc | 3.2 ab | 5.5 ab | 6.7 a |
| Other forbs | 1.9 | 2.1 | 3.3 | 4.1 | 4.5 | 3.3 |
| Shrubs/Succulents | | | | | | |
| Redberry juniper | 2.2 a | 1.4 ab | 1.2 abc | 0.3 bcd | 0.1 cd | 0.0 d |
| Pricklypear | 2.6 a | 1.0 b | 0.2 bc | 0.1 bc | 0.2 bc | 0.0 c |
| Other shrubs | 0.9 a | 1.2 a | 0.4 ab | 0.0 b | 0.0 b | 0.1 b |

[1]Means within a row followed by the same lowercase letter are not different ($P \leq 0.05$).
[2]Means within a row followed by the same uppercase letters are not different ($P \leq 0.10$).
[3]*Tridens muticus* (Torr.) Nash.
[4]*Sporobolus cryptandrus* (Torr.) Gray.

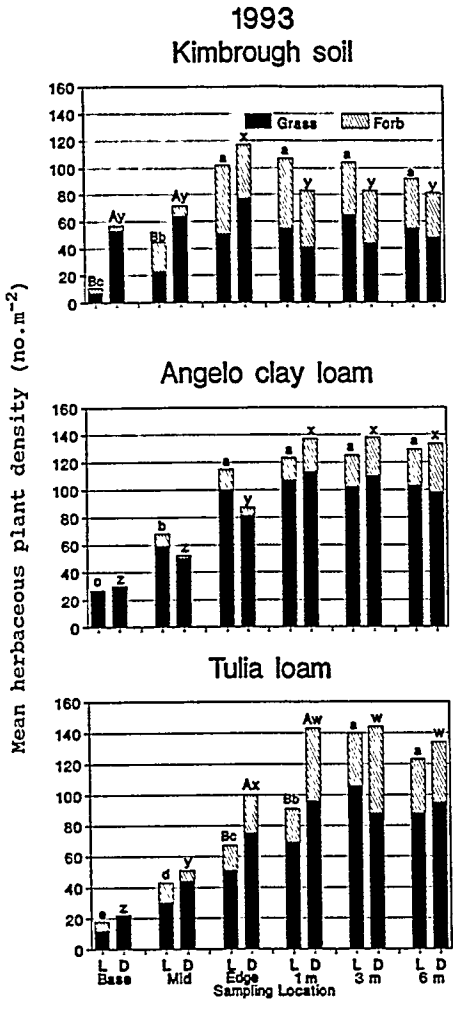


**Fig. 5. Mean herbaceous plant density (no. $m^{-2}$) in 6 sampling locations around live (L) and dead (D) redberry junipers on 3 sites near San Angelo, Tex. in 1993. Means within a site and sampling location that subtend different uppercase letters are different ($P \leq 0.05$). Means within a site and treatment (live or dead) that subtend different lowercase letters are different ($P \leq 0.05$).**

future values of redberry juniper woodlands for livestock and wildlife production and as watersheds. We project that annual herbage production will decrease to the current weighted average for the stem base and mid-canopy sampling zones for live trees, i.e. 320, 880, and 270 kg $ha^{-1}$ for the Kimbrough, Angelo clay loam, and Tulia loam soils, respectively, as the redberry junipers currently present on these sites mature and create closed-canopy woodlands. These values represent decreases of about 85, 59, and 82% compared to our estimates of potential herbage production for the 3 sites, respectively. The carrying capacity of these sites would be reduced to a greater extent because a substantial proportion of the forage would not be accessible to large herbivores. The dramatic decline in herbaceous species diversity would further degrade the wildlife habitat values of these sites. Vast, dense stands of juniper are not ideal wildlife habitat, nor are they conducive to wildlife management (Rollins and Armstrong 1994). Redberry juniper may contribute >20% of deer diets during winter (Sowell et al. 1985), but it is not considered a "good" forage because its monoterpenes may limit consumption, kill rumen microbes, and be inefficiently detoxified by multifunctional oxidase enzyme systems in the livers of ruminants (Huston et al. 1994). Armstrong (1991) rated juniper as only a "fair" deer forage that was utilized only where more desirable browse was unavailable. In relation to watershed values, dense stands of junipers have negative impacts on deep drainage and recharge of underground aquifers because a high percentage of the rainfall received is lost to interception by juniper canopies and litter and to meet juniper's transpiration requirements (Thurow and Carlson 1994). The negative effects of junipers on herbaceous plant cover in the interspaces decreases the quality of runoff by increasing the sediment load (Thurow and Carlson 1994).

### Influence of Redberry Juniper on Succession

The redberry juniper trees observed reflected the successional processes of "tree dominance, debilitation of understory dominants, influx and promotion of subsidiary species, and the overall reduction of understory density" as were reported in single-leaf pinyon (*Pinus monophylla* Torr. and Frem.) stands by Everett et al. (1983). The influx and promotion of other shrub and half-

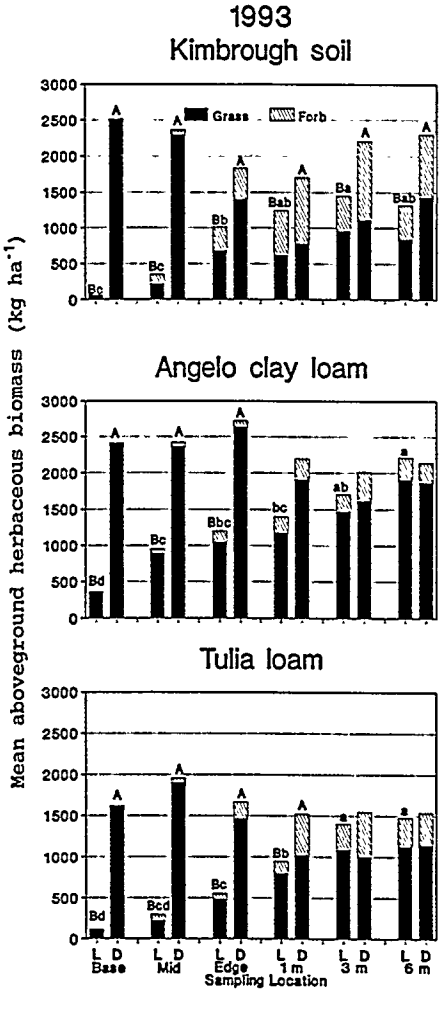


**Fig. 6. Mean grass and forb aboveground biomass (kg $ha^{-1}$) in 6 sampling locations around live (L) and dead (D) redberry junipers on 3 sites near San Angelo, Tex. in 1993. Means within a site and sampling location that subtend different uppercase letters are different ($P \leq 0.05$). Means within a site and treatment (live or dead) that subtend different lowercase letters are different ($P \leq 0.05$).**

shrub species beneath junipers has also been reported by Arnold (1964), Armentrout and Pieper (1988) and McPherson et al. (1988). Differences in understory composition in the zones around large redberry junipers suggests the tree influences had created microsites that could facilitate different successional pathways (Cattelino et al. 1979) among the zones surrounding redberry junipers.

The original grasslands that occupied our study sites as well as the current redberry juniper woodland communities represent stable states or seral stages (Archer 1989, Friedel 1991, Laycock 1991). Graminoid-driven succession predominated within the original grassland domain, characterized by low grazing pressure, high fire frequency and intensity, and low probability and rate of woody plant establishment. Heavy, continuous grazing of these areas by cattle, sheep, and goats during the late 1800's and early 1900's weakened the climax grasses, caused major changes in herbaceous species composition, reduced the frequency and intensity of fire, and thus facilitated the establishment of redberry juniper. These communities crossed the threshold from grasslands to juniper-dominated woodlands when sufficient numbers of junipers became established and reached reproductive maturity. Juniper-driven successional processes then began predominating, characterized by debilitation of understory herbaceous plants, a general reduction in understory diversity, density, basal area, and productivity, an influx of subsidiary species, further reduction in fire frequency and intensity, and a high incidence and rate of juniper seedling establishment. These juniper woodlands will not revert to grassland even if grazing is stopped, and furthermore, little or no improvement in range condition would occur if grazing were discontinued. Conversion of these juniper woodlands back to grasslands will require substantial initial intervention (reclamation) by the range manager, e.g., mechanical control methods or herbicides, to substantially reduce the juniper-driven successional processes. Reestablishment of steady state grasslands will require sustained intervention by the range manager, e.g., proper grazing management, periodic application of fire (Rasmussen et al. 1986), and periodic use of mechanical (Wiedemann and Cross 1981) or individual plant treatments (Ueckert and Whisenant 1982, Welch 1991) for maintenance control of redberry juniper.

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# Predicting flowering of 130 plants at 8 locations with temperature and daylength

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## Abstract

**An improved plant phenological method is needed to accurately predict flowering of a large array of plant species at locations with a wide range of latitude. Degree days or degree days times daylength cannot be used to accurately predict flowering of both early and late flowering species when grown at locations with wide range of latitude. Published flowering dates of 130 plant species from among 8 locations in central North America ranging in latitude from 39 to 50° N and longitude 84 to 108° W were used to develop a degree days times daylength factor to predict flowering dates. Plants flowering in late June flowered at the same time at all 8 locations regardless of latitude. Species flowering earlier than late June flowered earlier at southern locations than those at Treesbank, Manitoba. Species flowering after late June flowered later at southern locations than those at Treesbank. Flowering of 124 species divided among 8 locations was most accurately predicted by the accumulation of degree days (threshold=2° C) times daylength factor (1/(0.259-0.0140*daylength) from the first of December. This method slightly discounts daylength below 13 hours and greatly increased its weight for every hour over 13 hours. This method predicted flowering dates with a standard deviation of 0.1, 0.5, -1.7, 2.4, -0.1, 6.0, -1.8, and -1.1 days for Swift Current, Saskatchewan; Treesbank, Manitoba; Sidney, Mont.; Fargo, N.D.; Sauk and Dane Co., Wisc.; Wauseon, Ohio; and Manhattan, Kans.; respectively. Degree days or degree days times daylength had a standard deviation of 10 and 18 days in predicting flowering dates at Manhattan, Kans.**

**Key Words: degree days, flowering, modeling, phenology**

An improved plant phenological method is needed to accurately predict flowering date of a large array of plant species at locations with a wide range of latitudes. Hopkins' Law (Hopkins, 1938) states that "Other conditions being equal, the variation in the time of occurrence of a given periodical event in life activity in temperate North America is at the general average rate of 4 days to each 1 degree latitude, 5 degrees longitude, and 400 feet (122 meters) of altitude, later northward, eastward, and upward in spring and early summer, and the reverse in late summer and autumn". Caprio (1967) and Hopp and Blair (1973) found that the flowering of lilac (*Syringa vulgaris* L. and *S. persica* X *vulgaris* L.) at various locations in western, north central and north eastern United States did not follow Hopkins' Law.

The summation of positive temperatures (degree days) above a threshold temperature has been used to predict flowering dates (Lindsey and Newman 1956, Holmes and Robertson 1959, White 1979). Degree days often failed when applied in climatic areas that differed significantly from the locations where it was developed (Holmes and Robertson 1959). Degree days was inadequate to predict plant development or flowering date when crops were planted at different dates (Madariaga and Knott 1951) and locations (Magoon and Culpepper 1932, Moorman et al. 1990).

Nuttonson (1955) found that degree days times daylength was better than degree days alone in predicting development of winter and spring wheat (*Triticum aestivum* L.) at a wide range of latitudes in the United States and Russia. McMaster and Smika (1988) and others have also shown this or conflicting results. Recent models of winter cereal development are based upon rate of daylength change at the time of crop emergence (Baker et al. 1980, McMaster et al. 1991). In contrast, development of spring cereals was based upon daylength (not rate of change) at crop emergence (Wright and Hughes 1987). Robertson (1953 and 1968) and Wright and Hughes (1987) found that the development of wheat and barley (*Hordeum vulgare* L.) responded to daylength above some threshold depending upon growth stage rather than the simple relationship proposed by Nuttonson (1955).

The objective of this study was to develop a method to predict flowering dates of a large array of plant species at 8 locations ranging from 39 to 50° N latitude and 84 to 108° W longitude in central North America. Degree days or degree days times daylength cannot be used in plant growth models to predict plant development or flowering dates of plants at locations with a wide range of latitude.

## Materials and Methods

Published data from 8 locations (Swift Current, Saskatchewan [50.27° N 107.73° W]; Treesbank, Manitoba [49.7° N 99.6° W]; Sidney, Mont. [47.73° N 104.15° W]; Fargo, N.D. [46.9° N 96.8° W]; Sauk Co., Wisc. [43.6° N 89.67° W]; Dane Co., Wisc. [43.08° N 89.42° W]; Wauseon, Ohio [41.6° N 84.12° W]; and Manhattan, Kans. [39.18° N 96.57° W]) were used to test the accuracy of various methods of predicting flowering dates for a

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wide array of plant species. Mean flowering dates of 145 plant species near Swift Current (Budd and Campbell 1959), 400 species near Treesbank (160 km southeast of Brandon) (Criddle 1927), 170 species near Fargo (Stevens 1956), and yearly flowering dates of 53 species near Sidney (White 1979), 233 species in Sauk and Dane counties near Madison, (Leopold and Jones 1947), 161 species near Wauseon (Smith 1915), and 132 species near Manhattan (Hulbert 1963) were sorted to identify those species common at Treesbank and at any one of the other 7 locations. After updating plant names there were 64 plant species common between Treesbank and Swift Current and 22, 39, 41, 30, 24, and 17 plant species common between Treesbank and Sidney, Fargo, Sauk, Dane, Wauseon, and Manhattan, respectively (Table 1). Data included 8 species of trees, 12 shrubs, and 110 forbs for a total of 130 plant species. The forbs included 88 perennial, 9 biennial, and 13 annual species. At Swift Current, Treesbank, and Fargo where data were not available for individual years a species was used only when the mean flowering date was based on 3 or more years of data. Where yearly flowering dates were available at Sidney, Sauk, Dane, Wauseon, and Manhattan only flowering dates within a given 5-year period were used and only if flowering had been recorded for at least 3 of the 5 years.

Budd and Campbell (1959) defined flowering as the full opening of the petals to expose stamens and pistil. Multiflowering plants were considered flowering when first florets bloomed. Hulbert (1963) and Leopold and Jones (1947) reported flowering of trees when first pollen was shed as noted in Table 1. Stevens (1956) reported flowering when first pollen was shed for all plants. White (1979) reported flowering of forbs and shrubs when 10% of the plants within the study area had at least one flower. Criddle (1927) did not state how he determined first flowering.

Mean flowering date and summation of degree days or degree days times daylength factor at each location were restricted to the following 5-year periods: 1950 through 1954 for Swift Current, Fargo, and Manhattan, 1910 through 1914 for Treesbank, 1967 through 1971 for Sidney, 1941 through 1945 for Sauk and Dane, and 1891 through 1895 for Wauseon. It was assumed that any 5-year period within the data sets should accurately estimate the mean flowering date of a species. Too many species would have been eliminated if a longer period had been chosen. Linear and quadratic polynomial regressions were used to plot flowering dates of plants at Treesbank versus 7 other locations. Treesbank was chosen as the common location to compare all others to because its had flowering dates of the largest number of species that were common to all locations. If any other location had been used it would have decreased the number of species available for comparison. Each regression was significant at $P<0.05$ level.

Daily maximum and minimum air temperatures from first of December through last of September for the 5-year period selected for Swift Current airport, Brandon (closest weather station to Treesbank), Sidney, Fargo, Wisconsin Dell for Sauk, Madison for Dane, Wauseon, and Manhattan (town) were used to calculate degree days or degree days times daylength factor. Degree hours were accumulated every 0.1 hour from sunrise to sunset then divided by 10 and by daylength to put it on a daily bases. Air temperature every 0.1 hour was determined from maximum and minimum temperatures by de Wit (1978) method. Baker et al. (1988) found that the de Wit method was most accurate in estimating hourly air temperatures of the 3 methods tested. Daily sunrise and sunset at each location was calculated with a Hewlett-Packard time-shared BASIC computer program (36180 rev. A 3/72).

The method reported by Lindsey and Newman (1956) was used to determine which threshold temperature from -6 to 10° C (at 2° C interval) was optimum in predicting flowering dates at 5 locations (Sidney, Sauk, Dane, Wauseon, and Manhattan) where individual yearly flowering dates were available. The optimum threshold temperature was at the inflection point when the coefficient of variations were plotted for the various threshold temperatures (Lindsey and Newman 1956). A 4-year period was used at Sidney, Sauk, and Dane while a 5-year period was used at Wauseon and Manhattan.

The average number of degree days or degree days times daylength factor over 5 years was than calculated for each location for each day of the year. The mean flowering date for each species at each location was used to calculate the average (over 5 years) degree days or degree days times daylength factor that had been accumulated when each species flowered at each location.

The accuracy of each method in predicting flowering dates was evaluated by 2 methods. The first method determined accuracy by plotting the various mean (averaged over 5 years) degree days or degree days times daylength factor calculated for each species at each of the 7 locations against that calculated for Treesbank. A method was considered accurate if the variability around the linear model was small enough that I could accept the hypothesis of a 1 to 1 relationship of degree days or degree days times daylength factor required for each species to flower from the earliest to the latest flowering species. Because of the nature of the data sets from the 8 locations almost all of the usable information was required to develop the model, consequently validation will come from use of the model in future research.

The second method of determining accuracy was the standard deviation in days between mean flowering date and predicted flowering date. The variation of degree days or degree days times daylength factor between locations was not used to determine the accuracy of each method because of the large difference in the size of numbers between methods. The size of units also varied depending upon threshold temperature and weight given to daylength.

A common base unit was needed to compare how well each method accounted for variation in flowering dates between locations. Therefore, a normalizing procedure was used to convert the various methods of accumulated degree days or degree days times daylength factor to an appropriate calendar date for each species at each location. The mean unit over locations was used to calculate the calendar date that a method would predict flowering of each species at each location. The difference between the actual flowering date and predicted flowering date was used to calculate standard deviation by location. Thus the various methods of accumulating degree days or degree days times daylength factor were compared in plus or minus so many days. White (1979) used a similar method to compare the accuracy of various methods in predicting the flowering date of 53 species near Sidney, Mont., over a 4-year period.

## Results and Discussion

There was a straight line relationship between species

**Table 1. List of 130 plant species (alternate name in parenthesis), mean flowering date (month/day), years of record used to determine the best method to predict flowering dates at 8 location in central North America.**

| Species | Trees-bank | Swift Current | Sidney | Fargo | Sauk | Dane | Wauseon | Man-hattan |
|---|---|---|---|---|---|---|---|---|
| 1. *Acer negundo* L. | 5/1 (18) | . | . | . | . | 4/14(5) | 4/24(5) | 4/20(5) |
| 2. *Achillea millefolium* L. | 6/9 (12) | . | 6/22 | 6/16(4) | 6/2 (4) | 5/31(4) | 6/16(5) | . |
| 3. *Allium textile (reticulatum)* Nels & Macbr | 5/29(7) | 5/21(11) | 5/20 | 5/16(4) | . | . | . | . |
| 4. *Androsace occidentalis* Pursh | 4/24(16) | . | . | . | . | . | . | 4/6 (4) |
| 5. *Anemone canadensis* L. | 6/9 (12) | 6/12(9) | . | . | 6/1 (4) | . | . | . |
| 6. *Anemone cylindrica* Gray | 6/13(10) | . | . | . | 6/3 (4) | . | . | . |
| 7. *Anemone multifida* Poir. | 6/1 (8) | 5/29(5) | . | . | . | . | . | . |
| 8. *Antennaria microphylla* Rydb. | 6/13(9) | 5/29(9) | . | . | . | . | . | . |
| 9. *Apocynum androsaemifolium* L. | 6/22(9) | . | . | . | 6/28(4) | 6/26(3) | . | . |
| 10. *Aquilegia canadensis* L. | 6/5 (11) | . | . | . | 5/19(4) | 5/17(4) | 5/13(5) | 5/11 (5) |
| 11. *Arabis holboellii* Hornem. | 5/14(15) | 5/21(7) | 5/12 | . | . | . | . | . |
| 12. *Artemisia frigida* Willd. | 8/11(4) | 8/8 (4) | . | . | . | . | . | . |
| 13. *Aster commutatus (adsurgens)* Gray | 7/31(9) | 8/5 (7) | . | . | . | . | . | . |
| 14. *Aster laevis* L. | 7/22(12) | 8/14(6) | . | . | . | . | . | . |
| 15. *Aster novae-angliae* L. | 8/8 (9) | . | . | . | 8/21(4) | . | . | . |
| 16. *Aster simplex (paniculatus)* Willd. | 7/28(4) | . | . | 8/20(4) | . | . | . | . |
| 17. *Astragalus adsurgens (striatus)* Pallas | 6/18(13) | 6/27(6) | . | . | . | . | . | . |
| 18. *Astragalus agrestis (hypoglottis)* Dougl. ex Don | 5/21(16) | 6/2 (12) | . | . | . | . | . | . |
| 19. *Astragalus crassicarpus (caryocarpus)* Nutt. | 5/15(16) | . | . | . | . | . | . | 5/6 (4) |
| 20. *Astragalus flexuosus* Dougl. ex Don | 6/10(8) | 6/23(6) | . | . | . | . | . | . |
| 21. *Bidens cernua* L. | 8/6 (5) | 8/12(4) | . | . | 8/28(4) | . | . | . |
| 22. *Caltha palustris* L. | 5/7 (17) | . | . | . | 4/28(4) | 4/21(4) | . | . |
| 23. *Calystegia (Convolvulus) sepium* R. Br. | 6/29(8) | . | . | 6/25 | 6/17(4) | 6/17(3) | 6/17 (5) | . |
| 24. *Campanula rotundifolia* L. | 6/20(13) | 6/29(11) | . | . | 6/13(4) | . | . | . |
| 25. *Capsella bursa-pastoris* Medik. | 5/3 (6) | . | . | 5/1 (4) | 4/24(6) | . | 4/10(5) | 4/1 (5) |
| 26. *Cerastium arvense* L. | 5/11(19) | 5/25(13) | . | . | . | . | . | . |
| 27. *Cirsium undulatum* Spreng. | 7/10(7) | 7/9 (4) | 6/27 | 7/5 (4) | . | . | . | . |
| 28. *Comandra umbellata (richardsiana)* Nutt. | 5/24(16) | . | . | . | 5/20(4) | 5/8 (3) | . | . |
| 29. *Conyza (Erigeron) canadensis* Cronq. | 7/2 (5) | 7/29(5) | . | 7/13(4) | 7/31(4) | 7/24(3) | . | . |
| 30. *Cornus stolonifera* Michx. | 6/3 (15) | . | . | . | . | 5/12(4) | . | . |
| 31. *Corylus americana* Walter | 4/20(14) | . | . | . | 4/7 (4) | 4/1 (4) | 4/9 (5) | . |
| 32. *Cypripedium calceolus pubescens* Correll | 6/6 (14) | . | . | . | . | 5/22(5) | . | . |
| 33. *Draba reptans (caroliniana)* Fernald | 4/24(19) | . | . | . | 4/17(4) | . | . | . |
| 34. *Dracocephalum parviflorum* Nutt. | 6/11(10) | . | . | 6/22(4) | . | . | . | . |
| 35. *Echinacea (Brauneria) pallida* Nutt. | 7/5 (10) | . | 6/30 | . | . | . | . | . |
| 36. *Elaeagnus commutata (argentea)* Bernh. ex Rydb. | 6/1 (9) | 6/8 (10) | . | . | . | . | . | . |
| 37. *Ellisia nyctelea* L. | 6/3 (4) | . | . | 5/21(4) | . | . | . | 4/26(5) |
| 38. *Epilobium angustifolium* L. | 6/30(11) | 7/9 (6) | . | . | . | . | . | . |
| 39. *Erigeron glabellus (asper)* Nutt. | 6/2 (14) | 6/13(9) | . | . | . | . | . | . |
| 40. *Erigeron philadelphicus* L. | 6/10(12) | . | . | 6/8 (4) | . | . | 5/27(5) | . |
| 41. *Erigeron strigosus (ramosus)* Muhl. ex Willd. | 6/22(6) | . | 6/28 | . | 6/13(4) | . | 6/4 (5) | . |
| 42. *Erysimum asperum* DC. | 6/3 (15) | . | 5/20 | . | . | . | . | . |
| 43. *Erysimum inconspicuum (parviflorum)* Mcmil. | 6/8 (16) | 6/10(10) | . | . | . | . | . | . |
| 44. *Fragaria virginiana (glauca)* Duchesne | 5/12(17) | 5/25(8) | . | . | 5/12(4) | 5/8 (8) | . | . |
| 45. *Fraxinus pennyslvanica* Marshall | 5/21(3) | . | . | . | . | . | . | 4/15(5) |
| 46. *Gaillardia pulchella (aristata)* Foug. | 6/15(11) | 6/23(10) | . | . | . | . | . | . |
| 47. *Galium boreale* L. | 6/13(18) | 6/15(11) | . | . | 6/12(3) | 6/10(4) | . | . |
| 48. *Gaura coccinea* Nutt. ex Pursh | 6/10(4) | 6/17(10) | 6/8 | . | . | . | . | . |
| 49. *Geum triflorum* Pursh | 5/4 (21) | 5/13(13) | . | . | 5/5 (3) | . | . | . |
| 50. *Glycyrrhiza lepidota* Pursh | 6/30(10) | 7/14(5) | . | 6/21(4) | . | . | . | . |
| 51. *Grindelia squarrosa* Dunal | 7/25(8) | . | . | 7/28(4) | . | . | . | . |
| 52. *Helenium autumnale* L. | 7/19(5) | 8/2 (4) | . | . | . | . | . | . |
| 53. *Helianthemum canadense* Michx. | 7/9 (4) | . | . | . | . | 6/3 (3) | . | . |
| 54. *Helianthus maximiliani* Schrad. | 7/12(8) | . | . | 7/8 (4) | . | . | . | . |
| 55. *Helianthus petiolaris* Nutt. | 7/18(5) | . | . | 7/5 (4) | . | . | . | . |
| 56. *Heterotheca (Chrysopsis) villosa* Shinners | 6/15(13) | 7/7 (7) | 6/14 | . | . | . | . | . |
| 57. *Hypoxis hirsuta* Coville | 6/5 (3) | . | . | . | 5/31(4) | 5/31(3) | . | . |
| 58. *Lactuca canadensis* L. | 7/7 (5) | . | . | . | . | . | 7/23(5) | . |
| 59. *Lactuca pulchella* DC. | 7/4 (7) | . | 6/25 | 7/4 (4) | . | . | . | . |
| 60. *Lappula echinata* Gilib. | 6/13(7) | 6/28(5) | . | 5/30(4) | . | . | . | 5/10(4) |
| 61. *Liatris punctata* Hook. | 7/23(12) | 7/23(7) | 8/5 | . | . | . | . | . |
| 62. *Linum lewisii (perenne)* Pursh | 6/8 (12) | 6/5 (8) | 6/12 | . | . | . | . | . |
| 63. *Lithospermum canescens* Lehm. | 5/18(20) | . | . | . | 5/1 (4) | 5/3 (6) | 5/6 (5) | . |
| 64. *Lithospermum incisum (angustifolium)* Lehm. | 5/25(11) | 5/30(9) | . | . | . | 5/23(3) | . | 4/24(4) |
| 65. *Lobelia spicata* Lam. | 7/8 (4) | . | . | . | . | 6/12(3) | . | . |

**Table 1. Continued.**

| Species | Trees-bank | Swift Current | Sidney | Fargo | Sauk | Dane | Wauseon | Man-hattan |
|---|---|---|---|---|---|---|---|---|
| 66. *Lygodesmia juncea* Don ex Hook. | 7/8 (4) | 7/11(6) | 7/7 | 7/3 (3) | . | . | . | . |
| 67. *Lysimachia (Steironema) ciliata* L. | 6/27(9) | 7/16(4) | . | . | . | . | . | . |
| 68. *Maianthemum canadense (interius)* Desf. | 6/5 (9) | . | . | . | 6/3 (4) | . | . | . |
| 69. *Mirabilis (Oxybaphus) nyctaginea* Macmil. | 6/18(5) | . | . | 6/17(4) | . | . | . | 5/16(5) |
| 70. *Oenothera biennis (strigosa)* L. | 6/30(9) | 7/10(4) | . | 7/13(4) | 7/5 (4) | . | . | |
| 71. *Oenothera nuttallii (pallida)* Sweet | 7/4 (8) | 7/24(4) | . | 6/22(4) | . | . | . | . |
| 72. *Orthocarpus luteus* Nutt. | 7/7 (10) | 7/27(6) | . | . | . | . | . | . |
| 73. *Oxalis stricta* L. | 6/6 (5) | . | . | 6/9 (4) | 5/22(4) | 5/24(4) | 6/8 (5) | 5/7 (5) |
| 74. *Oxytropis lambertii* Pursh | 6/7 (12) | . | 5/22 | 6/3 (4) | . | . | . | . |
| 75. *Penstemon albidus* Nutt. | 6/7 (15) | 6/9 (11) | 6/3 | . | . | . | . | . |
| 76. *Penstemon gracilis* Nutt. | 6/17(10) | 6/26(10) | . | . | 6/4 (4) | . | . | . |
| 77. *Petalostemon candidus* Michx. | 6/29(9) | 7/12(6) | . | . | 7/12(4) | . | . | . |
| 78. *Petalostemon purpureus* Vent. | 7/5 (8) | 7/21(8) | 7/14 | . | 7/12(4) | . | . | . |
| 79. *Phlox hoodii* Richards. | 5/3 (5) | 4/30(13) | 4/26 | . | . | . | . | . |
| 80. *Plantago major* L. | 6/23(4) | . | . | 6/23(4) | . | . | 7/2 (5) | . |
| 81. *Polygonatum commutalum (canaliculatum)* Dietr. | 6/20(11) | . | . | . | . | . | 6/12(5) | . |
| 82. *Populus deltoides* Bartram (pollen) | 5/11(4) | . | . | . | . | 4/13(4) | 4/30(5) | . |
| 83. *Populus tremuloides* Loeve & Loeve (pollen) | 4/19(21) | . | . | . | 4/10(6) | 4/10(6) | 4/3 (5) | . |
| 84. *Potentilla anserina* L. | 6/1 (18) | 5/29(7) | . | . | . | . | . | . |
| 85. *Potentilla arguta* Pursh | 6/18(8) | 7/2 (7) | . | . | 6/7 (4) | . | . | . |
| 86. *Potentilla concinna* Richards. | 5/1 (13) | 5/7 (12) | . | . | . | . | . | . |
| 87. *Potentilla norvegica (monspeliensis)* L. | 6/18(6) | 7/12(3) | . | 6/19(4) | . | . | . | . |
| 88. *Potentilla pensylvanica (strigosa)* L. | 6/18(10) | 7/7 (5) | 6/23 | . | . | . | . | . |
| 89. *Prunus pensylvanica* L.F. | 5/17(20) | . | . | . | 5/5 (4) | 5/1 (4) | . | . |
| 90. *Prunus pumila (besseyi)* L. | 5/17(17) | . | . | . | 5/3 (4) | . | . | . |
| 91. *Prunus virginiana* L. | 5/28(16) | . | . | . | 5/3 (4) | 5/8 (4) | . | 5/11(4) |
| 92. *Psoralea argophylla* Pursh | 7/2 (7) | 7/13(8) | 7/4 | 6/29(4) | . | . | . | . |
| 93. *Psoralea esculenta* Pursh | 6/19(10) | . | 6/13 | . | . | . | . | . |
| 94. *Pulsatilla patens (wolfgangiana)* Mill. | 4/13(21) | 4/20(13) | . | . | 4/7 (4) | 4/10(8) | . | . |
| 95. *Quercus macrocarpa* Michx. | 5/27(19) | . | . | . | . | . | 5/15(5) | 4/30(5) |
| 96. *Ranunculus rhomboideus* Goldie | 4/20(19) | 5/3 (13) | . | . | . | . | . | . |
| 97. *Ranunculus sceleratus* L. | 6/3 (15) | . | . | 5/30(4) | . | . | . | . |
| 98. *Ratibida columnifera* Wooton & Standl. | 7/2 (9) | 7/13(8) | 7/7 | 7/4 (4) | . | . | . | . |
| 99. *Rosa blanda* var. *hispida* Ait. | 6/13(15) | . | . | . | 6/2 (4) | 6/1 (4) | . | . |
| 100. *Rudbeckia laciniata* L. | 7/13(6) | . | . | 7/26(4) | 7/19(4) | . | . | . |
| 101. *Rudbeckia serotina hirta* Nutt. non Sweet | 6/28(9) | . | . | 6/19(3) | 6/22(4) | 6/17(4) | 7/3 (5) | . |
| 102. *Rumex venosus* Pursh | 5/26(3) | . | . | . | . | . | . | 5/2 (5) |
| 103. *Sagittaria latifolia* Willd. | 7/14(4) | . | . | . | 7/27(3) | . | . | . |
| 104. *Salix discolor* Muhl. | 4/19(20) | . | . | . | . | 4/6 (7) | . | |
| 105. *Senecio canus* Hook. | 6/4 (7) | 6/9 (8) | . | . | . | . | . | . |
| 106. *Senecio plattensis* Nutt. | 6/4 (15) | . | . | . | . | . | . | 5/14(5) |
| 107. *Silene antirrhina* L. | 6/21(10) | . | . | 6/20(3) | . | . | . | . |
| 108. *Silene noctiflora* L. | 6/24(4) | . | . | 6/22(3) | . | . | . | . |
| 109. *Sisyrinchium angustifolium* Mill. | 5/25(11) | 6/8 (11) | . | . | . | . | . | . |
| 110. *Smilacina stellata* Desf. | 5/26(16) | 5/30(7) | . | . | 5/14(4) | 5/8 (5) | . | 4/30(5) |
| 111. *Solidago canadensis* L. | 7/17(11) | . | . | 8/8 (4) | . | . | . | . |
| 112. *Solidago missouriensis* Nutt. | 7/3 (5) | 7/20(5) | 7/30 | . | . | . | . | . |
| 113. *Solidago rigida* L. | 7/20(13) | 7/20(4) | . | 8/10(4) | 8/25(4) | 8/15(3) | . | . |
| 114. *Sphaeralcea (Malvastrum) coccinea* Rydb. | 6/7 (4) | 6/16(13) | 6/9 | . | . | . | . | . |
| 115. *Spiraea alba (salicifolia)* Du Roi | 6/28(10) | . | . | . | 7/8 (6) | . | . | . |
| 116. *Stachys palustris* L. | 6/29(8) | 7/17(5) | . | 7/1 (4) | . | . | . | . |
| 117. *Stellaria longipes* Goldie | 5/30(7) | 6/12(6) | . | . | . | . | . | . |
| 118. *Symphoricarpos occidentalis* Hook. | 6/25(10) | 7/3 (9) | 7/13 | 6/26(4) | . | . | . | . |
| 119. *Taraxacum officinale* Weber | 5/19(8) | 4/26(10) | 5/10 | 5/9 (4) | . | 4/17(5) | 4/26(5) | 3/17(4) |
| 120. *Thermopsis rhombifolia* Nutt. ex Richards. | 6/11(4) | 5/10(13) | . | . | . | . | . | . |
| 121. *Toxicodendron (Rhus) radicans* Kuntze | 6/16(8) | . | . | 6/17(4) | 6/12(4) | . | 6/19(5) | . |
| 122. *Ulmus americana* L. (pollen) | 4/28(14) | . | . | . | 4/14(4) | 4/5 (4) | 4/8 (5) | 3/9(5) |
| 123. *Viburnum lentago* L. | 6/9 (12) | . | . | . | 5/26(5) | . | . | . |
| 124. *Viburnum opulus (trilobum)* L. | 6/9 (11) | . | . | . | . | . | 5/27(5) | . |
| 125. *Vicia americana* Muhl. ex Willd. | 6/4 (16) | . | . | 5/31(4) | . | . | . | . |
| 126. *Vicia sparsifolia* Nutt. ex Torr. & Gray | 5/26(9) | 6/1 (10) | . | 6/1 (4) | . | . | . | . |
| 127. *Viola canadensis* L. | 5/17(16) | . | . | . | . | . | 5/10(5) | . |
| 128. *Viola conspersa* Reichenb. | 5/6 (21) | . | . | . | . | . | 5/4 (5) | . |
| 129. *Viola pedatifida* Don | 5/21(15) | 6/1 (3) | . | . | . | . | 5/1 (5) | . |
| 130. *Zizia aptera (cordata)* Fernald | 5/29(9) | 6/4 (10) | . | . | . | . | . | . |

flowered at Swift Current, Sidney, and Manhattan compared to when they flowered at Treesbank (Fig. 1). However, the relationship of flowering date at Fargo, Sauk, and Wauseon with those at Treesbank was curvilinear. The coefficient of determination ($r^2$) of flowering dates at Treesbank versus the other 7 locations was the lowest at Manhattan (0.84) and ranged from 0.90 to 0.96 at the other locations. These data showed that plants flowering in late June flowered at the same time regardless of latitude. Plants flowering at the other 6 locations before late June were earlier than those at Treesbank and those flowering after late June were later than those flowering at Treesbank. This relationship is similar to that predicted by Hopkins' Law (Hopkins 1938).

Flowering dates of 10 of the 130 species deviated more than 15 days from the regression line for a given location. The mean flowering date of only 3, 2, 0, 0, 3, 0, and 4 species at Swift Current, Sidney, Fargo, Sauk, Dane, Wauseon, and Manhattan, respectively, deviated more than 15 days. These deviations could have been caused by genotypes, different responses to daylength, and temperature at the various locations. These 10 species could have also been misnamed or subspecies.

*Taraxacum officinale* deviated from the regression line 20 to 30 days at Swift Current, Dane, and Manhattan. Because of this deviation *Taraxacum officinale* would not be a good index species for predicting development of other species. Later flowering species such as *Cirsium undulatum* at Sidney, *Helianthemum canadense* at Dane, *Lobelia spicata* at Dane, and *Solidago missouriensis* at Sidney all flowered more than 18 to 35 days off the regression line at one location. The early flowering species that deviated significantly from the regression line were *Acer negundo* at Manhattan, *Androsace occidentalis* at Manhattan, *Antennaria microphylla* at Swift Current, *Astragalus crassicarpus* at Manhattan, and *Thermopsis rhombifolia* at Swift Current. The remaining 124 species present at 2 or more locations were used to test the accuracy of various methods to predict flowering dates.

I tested 49, 87, 23, 18, and 37 species at Sidney, Sauk, Dane, Wauseon, and Manhattan to determine the optimum threshold temperature to predict flowering date with degree days by Lindsey and Newman (1956) method. Species at Sidney and Manhattan were divided into early and late flowering groups. Species at Sauk were divided into early, middle, and late flowering groups. Species at Dane and Wauseon were left in one group at each location. This method found that the optimum threshold temperature was 2° C for all locations except Sidney. Sidney's optimum threshold temperature was 3° C for both the early and late flowering groups. The optimum threshold temperature for both the early and late flowering groups at Manhattan was 2° C. The optimum threshold temperature for all 3 groups at Sauk was

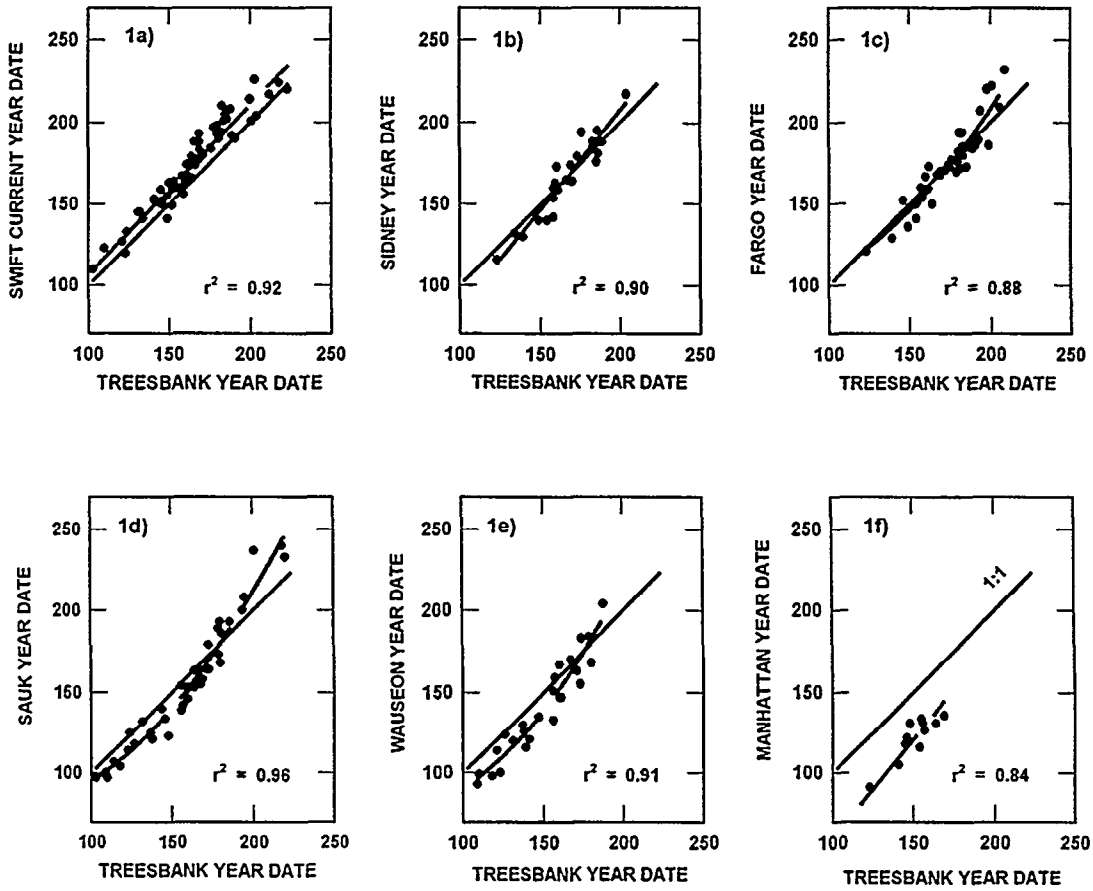


**Fig. 1. Relationship of year date (days from 1st of Jan.) that plants flowered at Treesbank, Manitoba versus Swift Current, Saskatchewan; Sidney, Mont.; Fargo, N. D.; Sauk Co., Wisc.; Wauseon, Ohio; and Manhattan, Kans.**

Table 2. Accuracy of degree days, degree days times daylength, and degree days times daylength factor (all threshold 2° C) in predicting the flowering date of 14 to 61 species at Treesbank versus 7 other locations.

| Location species | Equation | Degree days | Degree days times daylength | Degree days times day-length factor |
|---|---|---|---|---|
| Swift | Intercept | 31 | 604 | 1926 |
| Current | Slope | 0.93 | 0.93 | 0.95 |
| n=61 | $r^2$ | 0.92 | 0.92 | 0.92 |
| | Sd, days | 5.3 | 4.0 | 0.1 |
| Sidney | Intercept | -36 | -648 | -123 |
| n=23 | Slope | 1.24 | 1.21 | 1.05 |
| | $r^2$ | 0.88 | 0.88 | 0.87 |
| | Sd, days | -6.1 | -4.8 | -1.7 |
| Fargo | Intercept | -250 | -3265 | -2494 |
| n=40 | Slope | 1.32 | 1.27 | 1.05 |
| | $r^2$ | 0.87 | 0.87 | 0.88 |
| | Sd, days | 2.0 | 1.3 | 2.4 |
| Sauk | Intercept | -105 | -1672 | -1353 |
| n=39 | Slope | 1.52 | 1.43 | 1.10 |
| | $r^2$ | 0.93 | 0.93 | 0.94 |
| | Sd, days | -6.1 | -4.5 | -0.1 |
| Dane | Intercept | -141 | -2037 | -1626 |
| n=28 | Slope | 1.41 | 1.31 | 0.98 |
| | $r^2$ | 0.90 | 0.90 | 0.90 |
| | Sd, days | 2.9 | 3.7 | 6.0 |
| Wauseon | Intercept | -4 | -462 | 224 |
| n=25 | Slope | 1.52 | 1.41 | 1.02 |
| | $r^2$ | 0.89 | 0.88 | 0.88 |
| | Sd, days | -9.8 | -6.6 | -1.8 |
| Manhattan | Intercept | 255 | 2690 | 3608 |
| n=14 | Slope | 1.19 | 1.00 | 0.61 |
| | $r^2$ | 0.79 | 0.79 | 0.75 |
| | Sd, days | -18.4 | -10.2 | -1.1 |

2° C. Therefore 2° C was used as the threshold temperature for all species. White (1979) also found by a different method that 2° C was the optimum threshold temperature for early flowering species and 4° C for late flowering species.

The degree days (threshold 2° C) predicted flowering dates with a standard deviation of 2 to 18 days at the various locations (Table 2). Regression analysis showed that slope of accumulated degree days of when each species flowered varied from 0.92 to 1.52 depending upon the location.

Degree days (threshold 2° C) times daylength as suggested by Nuttonson (1955) was better than the degree days in predicting flowering dates. It's standard deviation was 1 to 8 days better than degree day only depending upon the location. Again there was not a 1 to 1 relationship between accumulated degree days times daylength of when each species flowered at Treesbank and any of the other 7 locations. Slopes ranged from 0.93 to 1.43 (Table 2).

The degree days (threshold 2° C) times daylength factor (1/(0.259 - 0.0140 * daylength) was by far the best method to predict flowering dates of 124 species divided among 8 locations. This daylength factor slightly discounted daylength below 13 hours and greatly increased its weight for every hour over 13 hours (Fig. 2). This method had a standard deviation of 3 to 9

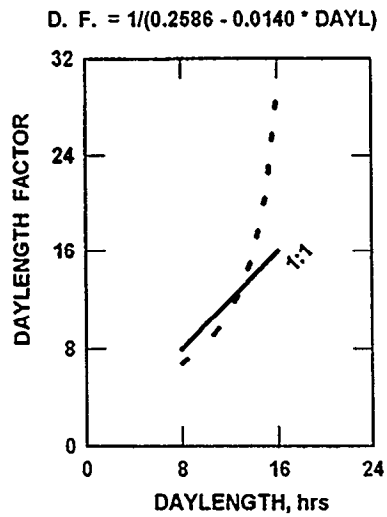


Fig. 2. Equation used to factor daylength (D. F.) to predict flowering of 124 plants divided among 8 locations in central North America.

days less than degree days times daylength at 5 of the 7 locations (Table 2). It had a standard deviation of 0 to 17 days better than degree days only at 6 of 7 locations. Regression analysis showed that slope of accumulated degree days times daylength factor of when each species flowered was nearly one at 6 of 7 locations thus the variability was small enough that I could accept the hypothesis of a 1 to 1 relationship of degree days times daylength factor accumulated at Treesbank versus any of the other locations (Fig. 3).

During the process of determining how to adjust daylength to predict flowering it became apparent that degree days times daylength factor had to be accumulated from the first of December in order to predict flowering dates at Manhattan. Accumulation of degree days or thermal units from the first of March worked well at Sidney, Mont. (White 1979). However, even accumulation of degree days times daylength factor from the first of January or later caused large errors in predicting flowering dates at Manhattan.

Degree days times daylength factor need to be calculated at least every hour from sunrise to sunset to accurately accumulate thermal units. Lindsey (1963) found that using only maximum and minimum temperatures with the degree days caused an 8 to 15% error in calculating degree days.

## Conclusions

The degree days times daylength factor accurately predicted flowering dates of 124 species among 8 locations ranging from 39 to 50° N latitude and 84 to 108° W longitude. The degree days and degree days times daylength could not be used to predict flowering dates of plants at widely ranging latitudes. Each hour of daylength above 13 hours had a larger effect on flowering than each hour under 13 hours. This accounts for why crops planted at different times of the year did not develop or mature with the same number of degree days. There was a 1:1 relationship between degree days times daylength factor required for plants to

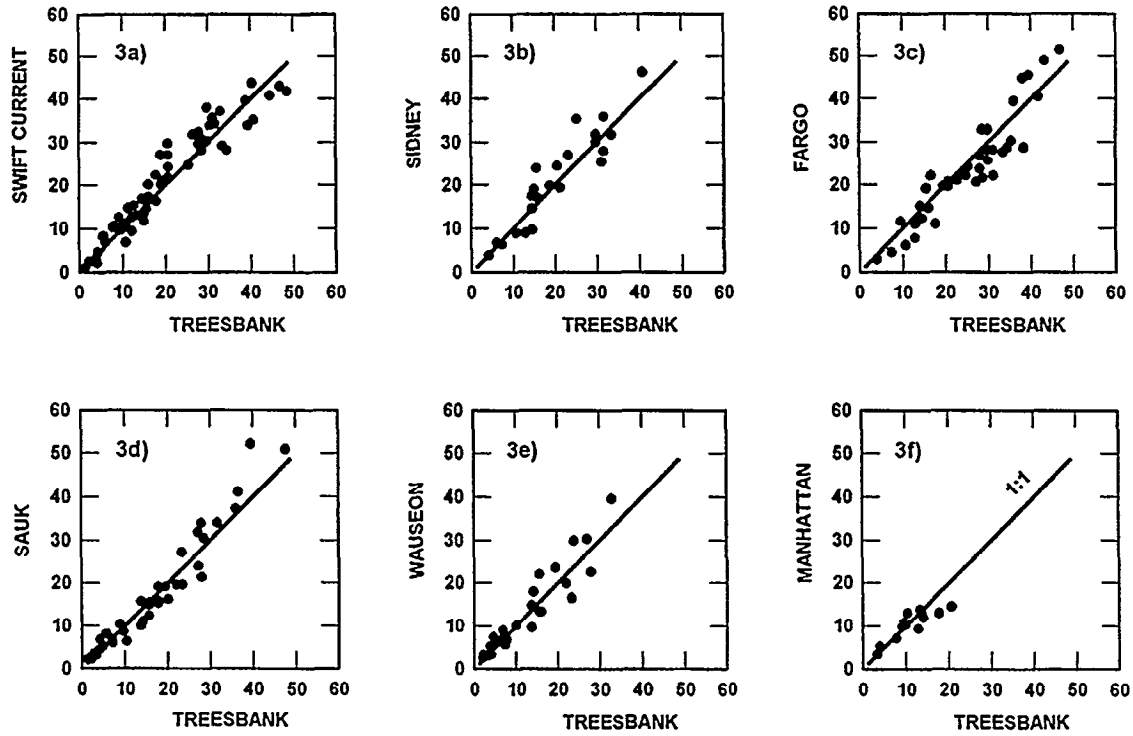


**Fig. 3. Relationship of degree days times daylength factor (1,000s) accumulated when plants flowered at Treesbank, Manitoba versus Swift Current, Saskatchewan; Sidney, Mont.; Fargo, N.D.; Sauk Co., Wisc.; Wauseon, Ohio; and Manhattan, Kans.**

flower at Treesbank versus 7 other locations with a wide range of latitude. This method accounted for why plants that flower in late June flower at all latitudes at the same time. It also accounted for why plants that flower before late June flower earlier at southern latitudes and why plants that flower after late June flower later at southern latitudes when compared to those at a northern location.

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# Impacts of defoliation on tiller production and survival in northern wheatgrass

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## Abstract

**Although northern wheatgrass (*Agropyron dasystachyum* (Hook.) Scribn.) is a dominant or co-dominant species that decreases under grazing in northern Mixed Prairie, little is known about its response to herbage removal at different times during the growing season. The objective of this research was to determine the effects of defoliation on the tiller production and survival of this native perennial on a clayey range site in mixed prairie in south-central Saskatchewan. Vegetation was subjected to a factorial experiment with an initial defoliation in early-May, June, July, or August and repeated at 2- or 6-week intervals until mid-September in the same plots for 3 years. An undefoliated control was also included. On average defoliation enhanced tillering (71%) and survival relative to the control, and tiller recruitment was greatest during June and September 1989. Generally tiller survival decreased as the date of emergence in the growing season was delayed. Numbers of tillers emerging was positively correlated with soil water (r=0.77). Some tillers of northern wheatgrass lived 5 years. The 2- and 6-week intervals of defoliation had little influence on tiller survival, but initiating defoliation near the time of tiller emergence reduced survival whereas delaying defoliation until August increased their survival. Increased tillering may be an adaptive feature enabling northern wheatgrass to tolerate defoliation by re-establishing lost photosynthetic area and maintaining or even increasing basal area. Thus, once released from grazing it may rapidly increase phytomass production in a relatively short time. Delaying grazing until August will maximize tiller survival of northern wheatgrass.**

**Keywords: *Agropyron dasytachyum* (Hook.) Scribn., grazing, Mixed Prairie, population dynamics, tillering, tiller demographics**

Tillering responses to defoliation in grasses are extremely complex. Herbage removal of little bluestem (*Schizachyrium scoparium* (Michx.) Nash) extended the period of tiller recruitment, but the total number of tillers was unaffected (Butler and Briske 1988). Defoliation may also reduce the senescence of shoots (Crawley 1983), and tillering can increase or decrease following defoliation (Archer and Detling 1984, Willms 1988, Willms and Fraser 1992). A single defoliation of northern wheatgrass (*Agropyron dasystachyum* (Hook.) Scribn.) reduced tillering in a greenhouse study (Li and Redmann 1992). Lauenroth et al. (1985) reported that intensity and frequency of defoliation interactively influenced tillering in western wheatgrass (*Agropyron smithii* Rydb.) with densities reduced by repeated and heavy defoliation. With frequent defoliation grasses may undergo changes towards prostrate ecotypes that have high potential for tillering (Painter and Detling 1981). This change in growth form may help plants escape or tolerate defoliation through rapid tillering and leaf growth.

Tillering is a key process in the maintenance of populations for northern wheatgrass because it is rhizomatous and seldom produces seeds. However, it is difficult to assess the effects of disturbance on the population dynamics of rhizomatous grasses unless the focus is placed on tillers. Detailed studies of tiller dynamics are useful in predicting outcomes of different management activities (Jones and Mott 1980).

The objective of this study was to examine the recruitment and survival of northern wheatgrass tillers on a northern Mixed Prairie over a 3-year period to test the hypothesis that multiple defoliation regimes do not alter tillering and survival in this rhizomatous perennial.

## Methods

### Study Site Description

Research was conducted at the Matador Research Station of the University of Saskatchewan, approximately 70 km north of Swift Current (50°42'N, 107°43'W, elev. 685 m). The site is located within a glacial lake plain near the northern edge of the mixed prairie in the northern Great Plains (Coupland 1950). Soils are Rego Brown and Calcareous Brown Series in the Sceptre Association of the Chernozemic Brown Subgroup (Aridic Borolls) (Coupland et al. 1974).

The study area is a clayey range site with northern and western wheatgrass potentially producing about 75% of the total phytomass (Coupland et al. 1974). Northern wheatgrass is clone-forming, with short slender rhizomes and clustered tillers. It is generally loosely to densely tufted, has intra- and extra-vaginal shoots, giving a tussock-like growth form. Several shoots may originate from one node.

Annual precipitation data were obtained from Beechy, Saskatchewan (50°46'N, 107°19'W, elev. 670 m) about 40 km northeast of the study site. Annual precipitation in 1988 was only

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70% of the 50-year mean of 373 mm, while precipitation in 1989 and 1990 was 106% and 113% of the long-term average.

### Experimental Design and Sampling Methods

The experiment was conducted from 1988 to 1990 in a pasture that had been heavily grazed during the summer in several previous years; ecological range condition was estimated as fair in 1986 and 1987 (J.T. Romo unpub. data) according to Abouguendia's (1990) classification. A 50 × 50-m exclosure was established and 8-clipping treatments with 4-initiation dates and 2 intervals, and an undefoliated control were replicated 4 times in a randomized-complete-block design. Plots were 5 × 6 m and a 1-m buffer was maintained on all sides. Plots were initially defoliated in early May, June, July, or August, and again at 2- or 6-week intervals until mid-September of each year. In the text May+2 implies the first defoliation was in May and again every 2 weeks through the summer, and so on. A Jari sickle-mower was used to mow plots to a 5-cm stubble, and all harvested plant material was removed. Treatments were repeated on the same plots each year.

A 10 × 10-cm permanent quadrat was randomly established in each plot in mid-May 1988 to monitor tiller demographics. All live tillers were counted in May 1988 when the study was begun, marked with a colored wire at their base and grouped as the mixed-age tillers because their ages were unknown. These permanent quadrats were revisited at 2 to 4-week intervals from May or June through September each year, and survival of previously marked tillers was recorded and new ones were tagged with wires of different colors. Tillers that emerged on the 2 observation dates in each month were grouped. The recruitment observations were terminated in July 1990, but survival was determined until June 1991.

Soil water was determined biweekly from May through September each year. Soils were collected in 2.5-cm cores at the 0-15-cm depth, weighed and dried at 80°C for 48 hours. Dry weights were determined and gravimetric water content was then calculated.

A test of homogeneity was used to analyze the recruitment of tillers in each month among treatments, and if Chi-square values were significant at $P \leq 0.05$, each treatment was tested against the control. Because the number of tillers varied among plots and treatments, survival was expressed as the ratio of living tillers at a given time to the initial number of tillers. Each year survival of tillers over the growing season and through the winter was compared among treatments in September and the following May or June. Hypotheses were tested by using Chi-square assuming equal survival among treatments for tillers emerging within a month. Survival in the control and all defoliation treatments were set equal to test defoliation effects. Survival in the 2- and 6-week intervals of defoliation were set equal and survival in the initial defoliation in May, June, July, and August were equalized. All possible, pairwise Chi-square comparisons were made at $P \leq 0.05$.

## Results

### Tiller Recruitment

With the exception of August and September 1988 (data not shown) when no tillers were produced, they were recruited throughout the study with most in June and September 1989 (Table 1). On average, defoliation increased tillering 71% more than the undefoliated control. Tiller recruitment in 1988 and 1990 was similar among treatments. In 1989, treatments of July+6 and August+6 produced 3- to 6-fold more tillers in May than the control, while in June every defoliation treatment except those initiated in June had twice as many new tillers as control. Greater than 2-fold more tillers were recruited in the July+2 and August+2 treatments than the control in September 1989.

Recruitment of tillers was positively correlated with soil water at 0-15 cm (Y=-25.7+1.62X, r=0.77, Y=tillers 0.04m$^{-2}$). Tiller recruitment was negatively correlated with mean daily air temperature (Y=43.9-1.71X, r=-0.43).

### Survival of the Mixed-age Tillers

Tiller survival in the control was significantly lower (60 to 67%) than the mean of defoliation treatments except in June 1991 when it was 63%, a difference that was not significant (Table 2). When defoliation was initiated in May, survival in September 1988 and May 1989 was lower than if defoliated later. Survival

**Table 1. The number of northern wheatgrass tillers recruited in 1988, 1989, and 1990. An initial defoliation was imposed in early May, June, July, or August and repeated at 2- or 6-week intervals in 1988, 1989, and 1990. Values for control are also presented.**

| | Defoliation Treatments | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| Month of Observation | May +2 | May +6 | Jun. +2 | Jun. +6 | Jul. +2 | Jul. +6 | Aug. +2 | Aug. +6 | Control |
| | Tillers 0.4m$^{-2}$ | | | | | | | | |
| 1988 | | | | | | | | | |
| Jun. | 7 | 2 | 3 | 2 | 7 | 9 | 6 | 6 | 0 |
| Jul. | 12 | 11 | 2 | 11 | 14 | 11 | 8 | 13 | 7 |
| 1989 | | | | | | | | | |
| May | 10 | 8 | 8 | 7 | 8 | 13* | 8 | 23* | 4 |
| Jun | 44* | 40* | 37 | 30 | 59* | 45* | 46* | 43* | 23 |
| Jul. | 7 | 0 | 7 | 6 | 5 | 6 | 3 | 3 | 3 |
| Aug. | 6 | 2 | 3 | 6 | 1 | 1 | 5 | 3 | 4 |
| Sep. | 20 | 14 | 22 | 14 | 30* | 25 | 29* | 23 | 13 |
| 1990 | | | | | | | | | |
| May | 9 | 2 | 6 | 5 | 2 | 5 | 6 | 7 | 4 |
| Jun. | 8 | 4 | 8 | 6 | 2 | 4 | 6 | 3 | 6 |
| Jul. | 2 | 5 | 3 | 8 | 2 | 2 | 2 | 0 | 1 |
| Total | 125* | 88 | 99* | 95* | 130* | 121* | 119* | 124* | 66 |

* Numbers within an observation data are significantly ($P \leq 0.05$) different from control.

Table 2. Mean survival of mixed aged tillers for northern wheatgrass marked in May 1988 and observed through 3 consecutive growing seasons and winters.

| Defoliation Treatment | Observation Date: Sep. 1988 | May 1989 | Sep. 1989 | May 1990 | Sep. 1990 | Jun. 1991 |
|---|---|---|---|---|---|---|
| | (%) | | | | | |
| Control | 54a[1] | 43a | 31a | 31a | 24a | 19a |
| Defoliation mean | 81b | 68b | 49b | 45b | 40b | 30a |
| May | 65a[2] | 46a | 38a | 37a | 33a | 26a |
| Jun. | 82ba[3] | 72ba | 46aa | 39aa | 37aa | 26aa |
| Jul. | 83baa[4] | 69baa | 47aaa | 43aaa | 36aaa | 28aaa |
| Aug. | 92bba | 84bbb | 65bbb | 61bbb | 55bbb | 40bba |
| 2-weeks | 83a[5] | 70a | 52a | 48a | 41a | 28a |
| 6-weeks | 80a | 66a | 47a | 42a | 40a | 32a |

[1]A similar letter within an observation date indicates that means are not significantly different ($P \geq 0.05$) between control and the defoliation treatments.
[2]A similar letter within an observation date indicates that means are not significantly different ($P \geq 0.05$) for all pairwise comparisons between months. First column of letters compares May to June, July, and August defoliations.
[3]Second column of letters compares June to July and August defoliations.
[4]Third column of letters compares July and August defoliations.
[5]A similar letter within an observation date indicates that means are not significantly different ($P \geq 0.05$) between 2- and 6-week intervals of defoliation.

Table 4. Mean survival of tillers for northern wheatgrass marked in July 1988 and observed through 3 consecutive growing seasons and winters.

| Defoliation Treatment | Observation Date: Sep. 1988 | May 1989 | Sep. 1989 | May 1990 | Sep. 1990 | Jun. 1991 |
|---|---|---|---|---|---|---|
| | (%) | | | | | |
| Control | 43a[1] | 43a | 43a | 43a | 14a | 14a |
| Defoliation mean | 74b | 52b | 38a | 36a | 33b | 24a |
| May | 59a[2] | 41a | 37a | 33a | 26a | 11a |
| Jun. | 69aa[3] | 38aa | 15ba | 15ba | 15aa | 15aa |
| Jul. | 80baa[4] | 60bba | 32aba | 32aba | 32aba | 28bba |
| Aug. | 90bbb | 67bba | 62bbb | 57bbb | 52bbb | 43bbb |
| 2-weeks | 75a[5] | 58a | 44a | 44a | 39a | 25a |
| 6-weeks | 76a | 48a | 34a | 30b | 28a | 24a |

[1]A similar letter within an observation data indicates that means are not significantly different ($P \geq 0.05$) between control and the defoliation treatments.
[2]A similar letter within an observation date indicates that means are not significantly different ($P \geq 0.05$) for all pairwise comparisons between months. First column of letters compares May to June, July and August defoliations.
[3]Second column of letters compares June to July and August defoliations.
[4]Third column of letters compares July and August defoliations.
[5]A similar letter within an observation date indicates that means are not significantly different ($P \geq 0.05$) between 2- and 6-week intervals of defoliation.

of tillers was similar when first defoliated in June or July, and delaying defoliation until August generally improved survival. With the exception of September 1988 and June 1991 tiller survival was greater in the August than the July defoliation treatment. Tiller survival was similar when defoliated at 2- or 6-week intervals, decreasing from 82% in September 1988 to 30% in June 1991.

### Survival of Tillers Produced in 1988

Since no tillers emerged in the control plots in June 1988, comparisons of survival were made only among the defoliation treatments on all dates. Survival was highest when initially defoliated in May (Table 3). None of the tillers produced in June 1988 and defoliated in June were living after September 1988. All tillers produced in June 1988 died by June 1991 if defoliated during July. Tillers defoliated in August had higher survival rates than those defoliated either in June or July. On average 39% of the tillers were living in the May and August defoliation treatments in June 1991. Survival of tillers was 33 to 50% less when defoliated every 6 weeks than biweekly except in September 1988 and June 1991 when it was similar.

With the exception of September 1989, May 1990, and June 1991 survival in control was 42 to 64% of the mean of defoliation treatments for tillers produced in July (Table 4). Survival of tillers was lowest in the May and June defoliation treatments after May 1989. Tiller survival was generally greatest when defoliation was delayed until August. Except in May 1989 survival was greater when first defoliated in August than July. After 3 years, survival was lowest when first defoliated in May or June and highest in August. Generally there were no differences between 2- or 6-week intervals of defoliation.

Table 3. Mean survival of tillers for northern wheatgrass marked in June 1988 and observed through 3 consecutive growing seasons and winters.

| Defoliation Treatment | Observation Date: Sep. 1988 | May 1989 | Sep. 1989 | May 1990 | Sep. 1990 | Jun. 1991 |
|---|---|---|---|---|---|---|
| | (%) | | | | | |
| Control | —[1] | — | — | — | — | — |
| Defoliation mean | 85 | 54 | 40 | 39 | 33 | 19 |
| May | 100a[2] | 100a | 78a | 78a | 67a | 44a |
| Jun. | 80ba[3] | 0ba | 0ba | 0ba | 0ba | 0ba |
| Jul. | 69baa[4] | 50bba | 25bba | 19bba | 13bba | 00baa |
| Aug. | 92bbb | 67bbb | 58bbb | 58bbb | 50bbb | 33bbb |
| 2-weeks | 87a[5] | 70a | 52a | 52a | 39a | 17a |
| 6-weeks | 79a | 47b | 32b | 26b | 26b | 21a |

[1]No tillers were produced in the control
[2]A similar letter within an observation date indicates that means are not significantly different ($P \geq 0.05$) for all pairwise comparisons between months. First column of letters compares May to June, July and August defoliations.
[3]Second column of letters compares June to July and August defoliations.
[4]Third column of letters compares July and August defoliations.
[5]A similar letter within an observation date indicates that means are not significantly different ($P \geq 0.05$) between 2- and 6-week intervals of defoliation.

Table 5. Mean survival of tillers for northern wheatgrass marked in May 1989 and observed through 2 consecutive growing seasons and winters.

| Defoliation Treatment | Observation Date: Sep. 1989 | May 1990 | Sep. 1990 | Jun. 1991 |
|---|---|---|---|---|
| | (%) | | | |
| Control | 100a[1] | 75a | 50a | 25a |
| Defoliation mean | 82b | 76a | 69b | 58b |
| May | 56a[2] | 50a | 50a | 33a |
| Jun. | 93ba[3] | 87ba | 67ba | 60ba |
| Jul. | 90baa[4] | 86baa | 81bba | 67baa |
| Aug. | 87baa | 77baa | 74baa | 65baa |
| 2-weeks | 85a[5] | 74a | 62a | 47a |
| 6-weeks | 80a | 78a | 75b | 65b |

[1]A similar letter within an observation date indicates that means are not significantly different ($P \geq 0.05$) between control and the defoliation treatments.
[2]A similar letter within an observation date indicates that means are not significantly different ($P \geq 0.05$) for all pairwise comparisons between months. First column of letters compares May to June, July and August defoliations.
[3]Second column of letters compares June to July and August defoliations.
[4]Third column of letters compares July and August defoliations.
[5]A similar letter within an observation date indicates that means are not significantly different ($P \geq 0.05$) between 2- and 6-week intervals of defoliation.

Table 6. Mean survival of tillers for northern wheatgrass marked in June 1989 and observed through 2 consecutive growing seasons and winters.

| Defoliation Treatment | Observation Date: Sep. 1989 | May 1990 | Sep. 1990 | Jun. 1991 |
|---|---|---|---|---|
| | (%) | | | |
| Control | 61a[1] | 57a | 48a | 43a |
| Defoliation mean | 83b | 75a | 61a | 46a |
| May | 83a[2] | 79a | 68a | 52a |
| Jun. | 84aa[3] | 76aa | 60aa | 42aa |
| Jul. | 85aaa[4] | 67aaa | 60aaa | 41aaa |
| Aug. | 79aaa | 61bba | 57aaa | 47aaa |
| 2-weeks | 83a[5] | 66a | 57a | 41a |
| 6-weeks | 82a | 75a | 66a | 51a |

[1]A similar letter within an observation date indicates that means are not significantly different ($P \geq 0.05$) between control and the defoliation treatments.
[2]A similar letter within an observation date indicates that means are not significantly different ($P \geq 0.05$) for all pairwise comparisons between months. First column of letters compares May to June, July and August defoliations.
[3]Second column of letters compares June to July and August defoliations.
[4]Third column of letters compares July and August defoliations.
[5]A similar letter within an observation date indicates that means are not significantly different ($P \geq 0.05$) between 2- and 6-week intervals of defoliation.

Table 8. Mean survival of tillers for northern wheatgrass marked in August 1989 through 2 consecutive growing seasons and winters.

| Defoliation Treatment | Observation Date: Sep. 1989 | May 1990 | Sep. 1990 | Jun. 1991 |
|---|---|---|---|---|
| | (%) | | | |
| Control | 100a[1] | 100a | 75a | 25a |
| Defoliation mean | 74b | 48b | 44b | 26a |
| May | 50a[2] | 38a | 38a | 25a |
| Jun. | 89ba[3] | 67ba | 56ba | 22aa |
| Jul. | 100bba[4] | 50aba | 50aaa | 50bba |
| Aug. | 75bbb | 38aba | 38aba | 25aab |
| 2-weeks | 75a[5] | 38a | 38a | 25a |
| 6-weeks | 92b | 83b | 75b | 42b |

[1]A similar letter within an observation date indicates that means are not significantly different ($P \geq 0.05$) between control and the defoliation treatments.
[2]A similar letter within an observation date indicates that means are not significantly different ($P \geq 0.05$) for all pairwise comparisons between months. First column of letters compares May to June, July and August defoliations.
[3]Second column of letters compares June to July and August defoliations.
[4]Third column of letters compares July and August defoliations.
[5]A similar letter within an observation date indicates that means are not significantly different ($P \geq 0.05$) between 2- and 6-week intervals of defoliation.

## Survival of Tillers Produced in 1989

As of September 1989 defoliation decreased tillers first marked in May 1989, but increased survival during September 1990 and June 1991 (Table 5). When initially defoliated in May tiller survival was only 52 to 67% of those defoliated during either June, July, or August. In September 1990 and June 1991 tiller survival was 21 to 38% greater when defoliated every 6 weeks than biweekly.

Survival of tillers produced in June 1989 was generally similar in the defoliation regimes and control, except in September 1989 when it was 26% lower in the control (Table 6). The initial month tillers were defoliated had no significant affect on tiller survival. Throughout the study survival of tillers produced in June 1989 was not significantly different in the 2- and 6-week intervals of defoliation.

All tillers produced in July 1989 died in the control, but 59% were living in the defoliation treatments in September 1989 (Table 7). Delaying defoliation until July or August increased tiller survival in September 1989. Delaying defoliation until tiller survival by 47 to 73% compared to defoliation in May, June or July the first 2 years. In September 1990 tiller survival in the June and August defoliation treatments was simliar, but survival of tiller was lower in the August than the July treatment. Except in June 1991 survival of tillers was greater in the August than the May treatment. Tiller survival was not significantly different when defoliated at 2- or 6-week intervals.

Relative to control survival of tillers produced in August 1989 was reduced 26% by defoliation in 1989 and 52 to 41% in May and September 1990, respectively (Table 8). With the exception of June 1991, tiller survival was less when first defoliated in May than in June. In September 1989 and June 1991 it was also greater when initially defoliated in July than in August. Survival averaged 26% among treatments in June 1991 with it being highest in the July defoliation. Nearly 50% fewer tillers lived when

Table 7. Mean survival of tillers for northern wheatgrass marked in July 1989 and observed through 2 consecutive growing seasons and winters.

| Defoliation Treatment | Observation Date: Sep. 1989 | May 1990 | Sep. 1990 | Jun. 1991 |
|---|---|---|---|---|
| | (%) | | | |
| Control | 00a[1] | 00a | 00a | 00a |
| Defoliation mean | 59b | 46b | 38b | 30b |
| May | 43a[2] | 43a | 29a | 29a |
| Jun. | 54aa[3] | 46aa | 38aa | 23aa |
| Jul. | 64baa[4] | 36aaa | 36aaa | 36aba |
| Aug. | 83bbb | 67bbb | 50bab | 33aaa |
| 2-weeks | 59a[5] | 50a | 41a | 32a |
| 6-weeks | 60a | 40a | 33a | 27a |

[1]A similar letter within an observation date indicates than means are not significantly different ($P \geq 0.05$) between control and the defoliation treatments.
[2]A similar letter within an observation date indicates that means are not significantly different ($P \geq 0.05$) for all pairwise comparisons between months. First column of letters compares May to June, July and August defoliations.
[3]Second column of letters compares June to July and August defoliations.
[4]Third column of letters compares July and August defoliations.
[5]A similar letter within an observation date indicates that means are not significantly different ($P \geq 0.05$) between 2- and 6-week intervals of defoliation.

Table 9. Mean survival of tillers for northern wheatgrass marked in September 1989 and observed through 2 consecutive growing seasons and winters.

| Defoliation Treatment | Observation Date: May 1990 | Sep. 1990 | Jun. 1991 |
|---|---|---|---|
| | (%) | | |
| Control | 92a[1] | 69a | 46a |
| Defoliation mean | 91a | 82b | 55a |
| May | 79a[2] | 74a | 47a |
| Jun. | 94ba[3] | 75aa | 39aa |
| Jul. | 87aaa[4] | 84aaa | 60aba |
| Aug. | 100bbb | 92bba | 67bba |
| 2-weeks | 88a[5] | 81a | 51a |
| 6-weeks | 95a | 84a | 61a |

[1]A similar letter within an observation date indicates that means aer not significantly different ($P \geq 0.05$) between control and the defoliation treatments.
[2]A similar letter within an observation date indicates that means are not significantly different ($P \geq 0.05$) for all pairwise comparisons between months. First column of letters compares May to June, July and August defoliations.
[3]Second column of letters compares June to July and August defoliations.
[4]Third column of letters compares July and August defoliations.
[5]A similar letter within an observation date indicates that means are not significantly different ($P \geq 0.05$) between 2- and 6 week intervals of defoliation.

Table 10. Mean survival of tillers for northern wheatgrass produced in May, June or July 1990 and observed through 1 growing season and winter.

| | Observation Date | | | | | |
|---|---|---|---|---|---|---|
| | May tillers | | Jun. tillers | | Jul. tillers | |
| Defoliation Treatment | Sep. 1990 | Jun. 1991 | Sep. 1990 | Jun. 1991 | Sep. 1990 | Jun. 1991 |
| | (%) | | | | | |
| Control | 75a[1] | 50a | 67a | 50a | 67a | 50a |
| Defoliation mean | 90b | 71b | 80b | 51a | 96b | 38a |
| May | 82a[2] | 73a | 75a | 42a | 100a | 57a |
| Jun. | 82aa[3] | 73aa | 93ba | 63ba | 91ba | 18ba |
| Jul. | 100bba[4] | 71aaa | 100bba | 33aba | 100aba | 50aba |
| Aug. | 100bba | 69aaa | 100bba | 44aba | 100aba | 50aba |
| 2-weeks | 87a[5] | 74a | 67a | 50a | 100a | 22a |
| 6-weeks | 95b | 68a | 100b | 53a | 93b | 47b |

[1]A similar letter within an observation date indicates that means are not significantly different ($P \geq 0.05$) between control and the defoliation treatments.
[2]A similar letter within an observation date indicates that means are not significantly different ($P \geq 0.05$) for all pairwise comparisons between months. First column of letters compares May to June, July and August defoliations.
[3]Second column of letters compares June to July and August defoliations.
[4]Third column of letters compares July and August defoliations.
[5]A similar letter within an observation date indicates that means are not significantly different ($P \geq 0.05$) between 2- and 6-week intervals of defoliation.

they received 2 rather than 6 weeks of rest between defoliation events.

Survival was similar in the defoliation treatments and control except in September 1990 when 16% fewer tillers were alive in the control (Table 9). More tillers survived when herbage was first removed in August than in May or June. Except for May 1990 tiller survival was equal in the July and August treatments. Rest periods between defoliation did not affect survival.

### Survival of Tillers Produced in 1990

In September 1990 survival of tillers produced in all months during 1990 was greater when defoliated than in control (Table 10). Defoliation increased survival of May 1990 tillers during June 1991, but herbage removal had no effect on tillers initiated in either June or July. Deferring defoliation until July or August improved survival in September 1990 for May tillers while survival of June tillers was poorest when first defoliated in May. Fewer July tillers survived in the June-initiated defoliation than when defoliated earlier or later. Winter survival for May tillers was similar among treatments whereas winter survival of tillers produced in June and defoliated that month was greater than if defoliated in May, July, or August. Survival of tillers produced in July was lowest when defoliated in June. Two- or 6-week defoliation had no consistent effect on tillers initiated in 1990.

## Discussion

Although a host of biotic and abiotic factors affect tiller production (Murphy and Briske 1992) recruitment of tillers in perennial grasses of temperate regions is most common in spring or fall (Butler and Briske 1988, Miller and Rose 1992). With the exception of August and September 1988, continuous recruitment of tillers was observed for northern wheatgrass, with most entering the population in June and September 1989. Maxwell (1977) also observed seasonal variation in northern wheatgrass tiller densities with most in May and least in August coinciding with peaks and minimums in precipitation and soil water. In the present study, tiller recruitment was also positively correlated with soil water. The absence of tillering in late summer and fall of 1988, and low recruitment in July and August of 1989 are attributed to dry conditions. Busso et al. (1989) also reported crested wheatgrass (*Agropyron desertorum* Fisch. ex Link) and bluebunch wheatgrass (*Pseudoroegneria spicata* (Pursh) A. Love; Syn: *Agropyron spicatum* Pursh) did not produce tillers in a dry autumn.

Relatively low tiller recruitment in the control was attributed to the population adjusting to the removal of grazing, modification of the microenvironment, and apical dominance in tillers that were not defoliated. When defoliation pressure is removed, plant size may increase through larger tillers instead of more tillers being produced (Peterson 1962, Milchunas et al. 1988). Because phytomass production in the control equaled that in the defoliation treatments (Zhang and Romo 1994) and tiller number was less in the control, response of tillers must have been one of increased size with protection.

The accumulation of litter in the control compared to the defoliation treatments (Zhang and Romo 1994) probably reduced radiation, light, and temperature at the soil surface, inhibiting initiation of new tillers (Ong et al. 1978). On the other hand, tillering can be enhanced by opening the canopy, increasing surplus energy and the amount of red light at the base of the plant (Deregibus et al. 1985, Casal et al. 1985) as shown for plains rough fescue (*Festuca hallii* Vasey Piper) and rough fescue (*Festuca campestris* Rydb.) (Willms et al. 1986). Alternatively, apical dominance in tillers that were not defoliated may have limited initiation of new tillers (Murphy and Briske 1992).

Greater tillering by northern wheatgrass with defoliation represents overcompensation in response to defoliation (McNaughton 1983), however, shoot phytomass showed equal compensation while root and crown phytomass were undercompensated (Zhang and Romo 1994). This decline in roots may reduce resource acquisition, competitive ability and productivity (Caldwell 1984). Plants that have a greater potential for tillering tend to prevail under grazing (Carman 1985). Increased tillering may enable northern wheatgrass to tolerate defoliation by re-establishing lost photosynthetic area and maintaining or increasing basal area.

Generally, tiller survival was similar in the 2 defoliation intervals, suggesting that the frequencies were not temporally segregated enough to induce differences in responses. Defoliation during emergence tended to reduce survival of new tillers. Initiating defoliation after tillers emerged was less detrimental to their survival than herbage removal before or during tiller emergence. There was also a trend of decreasing tiller survival as the date of emergence in the growing season was delayed. New tillers rely on parent tillers for nutrients and energy during emergence (Welker et al. 1985, 1987) and if parent plants are defoliated, the resources for developing tillers may diminish and their survival reduced (Jónsdóttir and Callaghan 1989). Thus, delaying defoliation probably enabled uninterrupted development of tillers. In contrast tillers may escape defoliation at early stages, however, the removal of herbage on parent tillers may decrease their survival because of reduced assimilate transfer.

Assuming the initial mix-aged tillers all emerged in the previous season, tillers of northern wheatgrass can live more than 4 years because about 25% were alive at the end of the study. Zhang (unpub. data) noted that some of the mixed-age tillers were still living after 5 years. Coupland and Abouguendia (1974)

reported that 29% of the tillers of northern and western wheatgrass lived 3 years while Maxwell (1977) noted that 21% lived at least 2 years. Tillers of western wheatgrass and several other mixed prairie grasses lived 2 to 3 years (White 1977).

### Management Implications

Northern wheatgrass tillers have potentially long lifespans, and this perennial responded to repeated defoliation by increased tillering and longevity relative to the control. This enhanced production and survival of tillers may enable northern wheatgrass to increase phytomass production in a relatively short time when grazing pressure is relieved. Increased tillering with repeated defoliation can potentially be exploited to increase tiller densities and speed recovery of deteriorated range. This proposition must, however, be tested on a small scale before it is extensively applied because this range type can be damaged quickly by repeated defoliation (Zhang and Romo 1994).

Initiating defoliation before or during tiller emergence reduced tiller survival while delaying defoliation until August increased their survival. Tillers produced early in the season tended to have greater longevity and survival than those emerging later. It may be important to insure the recruitment and survival of these longer-lived tillers for they may add stability to populations when recruitment is limited. Delaying grazing until August will maximize potential phytomass harvest (Zhang and Romo 1994) and tiller production and survival in this grassland.

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# Gas exchange and water relations of Lemmon's willow and Nebraska sedge

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## Abstract

**There is considerable interest in riparian zones in the western United States, yet little information is available on the autecology of plant species that dominate these areas. We measured gas exchange and xylem water potential of Nebraska sedge (*Carex nebrascensis* Dewey) and Lemmon's willow (*Salix lemonii* Bebb) growing in a streamside location in the northern Sierra Nevada over a 2 year period. Standing biomass of both species and leaf area index of Lemmon's willow was also determined. Rooting activity of Nebraska sedge was measured the second year of the study. Measurements were taken during 1988 and 1989 with growing season precipitation 46% and 110% of average, respectively. Photosynthesis was remarkably similar for the 2 species (10.9 and 11.1 μ moles $m^{-2}$ $second^{-1}$ for Nebraska sedge and Lemmon's willow, respectively) when averaged over all dates for the 2 years. However, the 2 species exhibited different seasonal and yearly patterns of photosynthesis. Nebraska sedge maintained higher rates of photosynthesis during the early portion of the growing season and Lemmon's willow had higher photosynthesis during mid to late summer. Mean seasonal rates of willow photosynthesis were higher than those of the sedge during the drought year, and the opposite was true during the average year. Yearly average photosynthesis varied more for the sedge than for the willow. However, mean seasonal photosynthesis rates for each species were higher in an average year compared to a drought year. Nebraska sedge almost always had more negative values of xylem water potential than Lemmon's willow (overall average was -2.6 MPa and -1.25 MPa for Nebraska sedge and Lemmon's willow, respectively). Trends in transpiration and conductance were similar among species, except that Nebraska sedge maintained higher rates than Lemmon's willow during the spring of 1989. Willow biomass was similar among years, but willow leaf area index and sedge biomass were slightly greater in the wet year (1989) compared to the dry year. Contrasting growth forms and morphology of the 2 species may help explain differences in gas exchange and xylem water potential. The ability of willows to tap groundwater and the concentration of sedge roots in the upper soil profile probably accounts for the differential response to drought.**

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**Key words: water stress, photosynthesis, riparian species**

Riparian zones have become a focal point in the management of rangelands. Information on classification and management responses of riparian ecosystems is beginning to accumulate. However, we know relatively little about physiological responses of riparian species, or the processes that control productivity and integrity of these ecosystems.

Willows (*Salix* spp.) and sedges (*Carex* spp.) are 2 of the most important genera in riparian communities in the western United States (Youngblood et al. 1985, Kovalchik 1987). These genera exist as co-dominants in many of the more mesic riparian communities. Previous research has demonstrated that *Carex*-dominated communities can have very high levels of root mass and root length densities, although the vast majority of roots are concentrated in the upper 20 or 30 cm of soil (Manning et al. 1989). The concentration of roots in the upper soil profile is typical of the fibrous rooted graminoids. Woody plants, such as *Salix* spp., generally are able to extend roots deeper into the soil, although we are not aware of any detailed information on *Salix* rooting patterns. A study which employed stable isotopes of water demonstrated that *Salix* depends heavily on groundwater (Busch et al. 1992).

If *Salix* and *Carex* occupy different below-ground niches, we predict that the patterns of gas exchange (transpiration and photosynthesis) and moisture stress (xylem potential) would also differ. Presumably, the shallower-rooted *Carex* plants will experience water-stress and limit gas exchange earlier in the growing season than the deeper-rooted *Salix*. The objective of this study was to compare seasonal patterns of gas exchange and moisture stress in Lemmon's willow (*Salix lemmonii* Bebb) and Nebraska sedge (*Carex nebrascensis* Dewey) growing together on a montane streamside site.

## Materials and Methods

### Study Area

The study was conducted during 1988 and 1989 on Freeman Creek in the northern Sierra Nevada near Davis Lake in Plumas County, Calif. The elevation is about 1,750 m and precipitation averages 96 cm with 85% occurring between October and April. Growing season precipitation measured about 10 km from the study site was 46% and 110% of average during 1988 and 1989, respectively. Downcutting had lowered the streambottom of

Freeman Creek to about 1.5 m below the stream terrace and the streambank-to-streambank cross-sectional width ranged from about 6 to 10 m. The woody vegetation was dominated by Lemmon's willow and herbaceous vegetation by Nebraska sedge. Other conspicuous species include Baltic rush (*Juncus balticus* Willd.) tufted hairgrass (*Deschampsia cespitosa* (L.) Beauv.), Beckwith clover (*Trifolium beckwithii* S. Watson), and lodgepole pine (*Pinus contorta* Loudon ssp. *murrayana* (Grev. and Balf.) Critchf). Nomenclature follows Hickman (1993).

### Gas Exchange and Xylem Water Potential

Photosynthesis, transpiration, leaf temperature, and stomatal conductance were measured with an LI-6200 portable photosynthesis system (LI-COR, Inc., Lincoln, Neb.)[1] equipped with 0.25-L leaf chamber. Immediately after the gas exchange measurements, the leaves were excised and placed in a pressure chamber (3000 Series, Soil-Moisture Equip. Corp., Santa Barbara, Calif.) to determine xylem water potential. Leaves were placed on moist paper towels and returned to the laboratory for measurement of leaf area with a LI-3000 area meter (LI-COR, Inc, Lincoln, Neb.).

Sampling of leaves was conducted in 6 contiguous 3 × 3 m blocks. Each block contained both species. In each block, 1 set of measurements was taken on fully developed leaves of Nebraska sedge and Lemmon's willow during early afternoon. Plants within each block were selected at random. We used contiguous blocks on a stretch of stream to limit the environmental variation during the measurement period. A complete set of measurements could be taken in a 2 to 3 hour period. We measured leaves exposed to full sunlight; in the case of the willows, the leaves were in the upper 1/3 of the canopy and near the end of the branches. Mature willows with heights ranging from 1.5 to 2 m were sampled. Measurements were taken on 12 dates during late May to late September, 1988; and 13 dates during mid-April to late September, 1989.

### Plant Standing Crop and Soil Parameters

Biomass of willows and sedges was determined in early September of both years. One 33.5 × 33.5 cm plot per block was clipped for Nebraska sedge standing crop. Nebraska sedge made up nearly 100% of the herbaceous standing crop within the sampling locations. Three branches of Lemmon's willow per block were cut at ground level and transported to the laboratory. A subsample of leaves was scanned for area with a LI-3000 area meter (LI-COR, Lincoln, Neb.), dried at 60° C for 96 hours and weighed. The remaining leaves were separated from the branches. Leaf and branch material were dried at 60° C for a week and weighed. Leaf mass, specific leaf area, and average canopy diameter were used to calculate leaf area index of the willows. The leaf area index calculation for willow is leaf area per unit of canopy area; thus, values are not representative of willow leaf area indexes in the community as a whole, rather they represent leaf area index above the ground area occupied by willow canopies. The number of nodes with green leaves remaining on lateral branches in early and late September was determined as an index of leaf senescence.

Rooting activity was assessed using Pyrex® minirhizotron tubes in conjunction with a root periscope. The procedure and equipment used was similar to that described by Karl and Doescher (1991), except that minirhizotron tubes were inserted 30° from vertical, and the bottom was sealed with a rubber stopper and epoxy. Bands of 2 cm width were marked on the tubes at 10 cm intervals. The center of the bands were at 5, 15, 25, 35, 45, 55, and 65 cm from the soil surface. Total number of root intersections in the 2 cm bands were counted and values are presented as root number $cm^{-2}$. These values provide an index of rooting activity. Three tubes were buried along the sampling transect during September 1988 in areas dominated by sedge and measurements taken on 5 dates during 1989.

Soil temperature (0-12 cm) was recorded at 3 locations during each measurement date with an integrating temperature probe. Pairs of gypsum blocks (Beckman Corp. Palo Alto, Calif.) were buried at 10 and 40 cm soil depths at 3 locations along the sampling transect to assess soil moisture.

### Experimental Design and Data Analysis

The study was arranged as a complete block, with 3 × 3 m macroplots as blocks. Each block contained Lemmon's willow and Nebraska sedge, and the 2 species were handled as treatments. Analyses were conducted using the General Linear Model (GLM) procedure in SAS (SAS 1985). The 2 years were analyzed separately. When species by sampling date interactions were significant for a variable, the data were analyzed within each sampling date. Unless otherwise stated, statistical significance was assessed at the $p<0.05$ level.

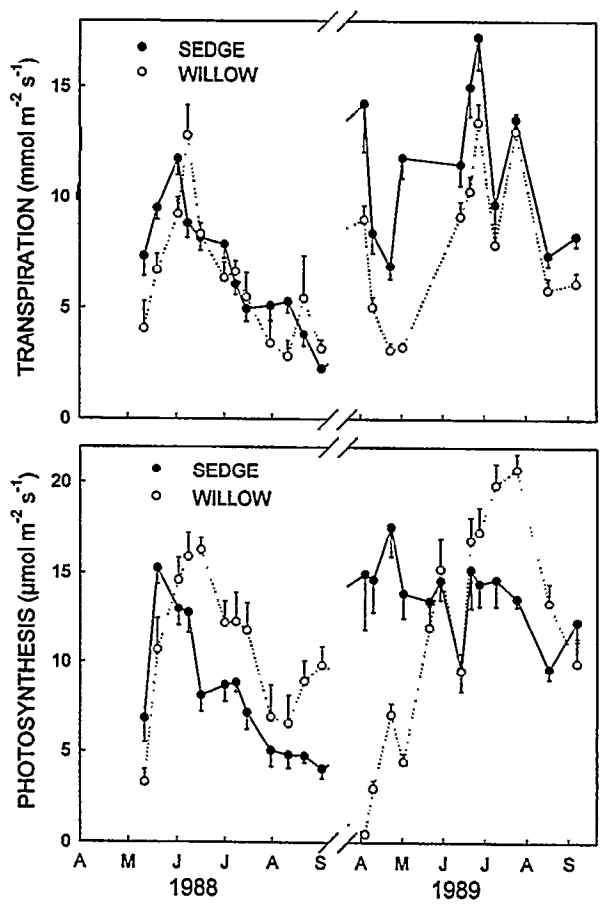


**Fig. 1. Seasonal trends in photosynthesis and transpiration of Nebraska sedge and Lemmon's willow (mean ± 1 standard error).**

[1]Mention of tradename does not indicate endorsement by USDA.

## Results

Seasonal trends in photosynthesis and transpiration are presented in Fig. 1. The interaction of species and date was significant ($p<0.02$) for both parameters during each of the 2 years. Analysis of species differences at each sampling date helped explain the nature of the interactions. During 1988, photosynthesis was significantly higher for willow as compared with sedge from mid June to the end of July, and from late August through September. Differences between species were not significant in late May or early August. Photosynthesis was significantly lower for willow compared with sedge in the spring (April to mid-May) of 1989, significantly higher for willow during mid summer (July through August), and similar among species in September. In general, transpiration rates were similar for the 2 species during 1988. Conversely, during the wetter 1989, transpiration rates for sedge were significantly higher on all dates, except mid August and September.

Seasonal trends in conductance and xylem water potential are presented in Fig. 2. There were significant species by sampling date interactions for both variables. The nature of the interaction for conductance appeared to be higher values for the sedge compared to the willow during the first 4 sampling dates, and similar values during subsequent sampling dates. When the data were analyzed at each sampling date, xylem water potential was significantly different on all sampling dates, except early June 1988, and one date each in May, June, August, and September 1989. The sedge consistently had lower xylem water potential (i.e. greater stress) than did the willow. This was particularly evident during the summer of 1988.

Biomass, leaf area, and average seasonal photosynthesis values appear in Table 1. Biomass of willow is presented on a per plant basis and biomass of sedge is on a ground area basis. Willow biomass was similar each year, but during the wetter year (1989) a greater proportion of mass was allocated to leaves, and thus leaf area index was greater. Sedge biomass was greater during the average precipitation year (1989) compared to the drought year (1988). Willow maintained a higher seasonal average photosynthesis than sedge during the drought year, but the opposite was true during the average precipitation year.

Soil temperature ranged from 10 to 20°C (Fig. 3). Soil moisture reflected the differences in average precipitation during the 2 years. Below average precipitation in 1988 resulted in low soil water potential by early August; whereas, soil moisture remained high during the entire 1989 growing season (Fig. 3). The onset of senescence also varied by year. The initial yellowing of willow leaves was observed on 11 August in 1988 compared to 8 September in 1989. By the first week of October, green leaves were no longer present during either year. The number of nodes with green leaves was 56% and 54% on 16 September and 28 September 1988, respectively, and 56% on 28 September 1989.

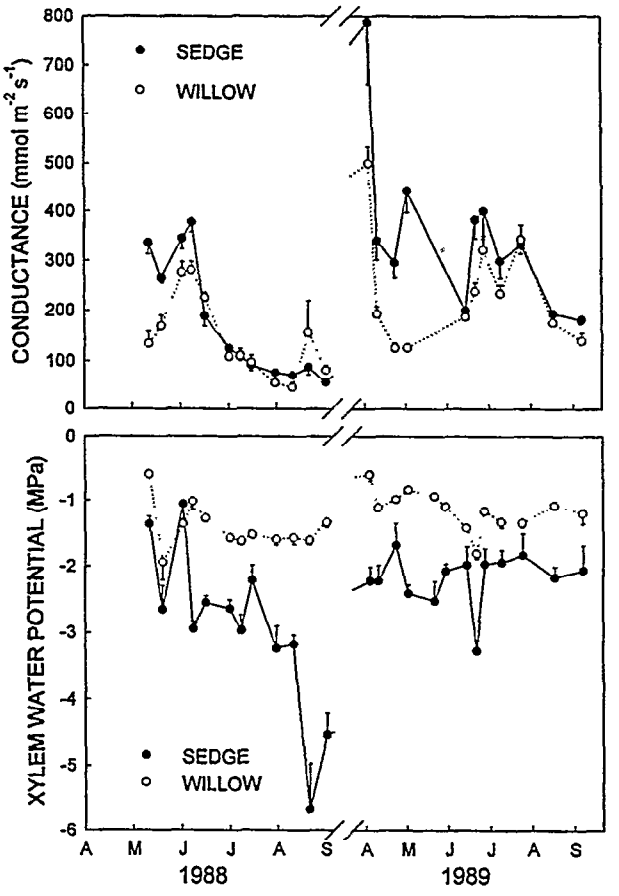


**Fig. 2. Seasonal trends in xylem water potential and conductance of Nebraska sedge and Lemmon's willow (mean ± 1 standard error).**

Rooting activity of Nebraska sedge peaked in mid July for the upper 4 soil depths (Fig. 4). However, below 40 cm there was relatively little activity during any of the measurement dates. We observed that rooting activity was minimal in the water table. Active rooting in the upper 40 cm did not occur until the water table dropped below that point.

**Table 1. Plant mass, leaf area, and mean seasonal photosynthesis (PS) for Lemmon's willow and Nebraska sedge. Branch number and total weight of Lemmon's willow are on a per plant basis. Percentage of branch and leaf are on a mass basis, specific leaf area (SLA) is area of leaf per unit mass, and leaf area index (LAI) is leaf area of willow projected against ground area below the willow canopy (n=6).**

| | Lemmon's willow | | | | | | | Nebraska sedge | |
|---|---|---|---|---|---|---|---|---|---|
| Year | Branch Number | Total dry weight | Branch | Leaf | SLA | LAI | Seasonal PS | Biomass | Seasonal PS |
| | | (kg/plant) | (%) | (%) | (cm$^2$/g) | | (μ moles m$^{-2}$ second$^{-1}$) | (g/m$^2$) | (μ moles m$^{-2}$ second$^{-1}$) |
| 1988 | 41.8 ± 4.41 | 6.2 ± 2.4 | 86.5 | 13.5 | 85.3 ± 4.0 | 4.1 | 10.8 | 152.5 ± 50.6 | 8.1 |
| 1989 | 42.2 ± 4.6 | 6.2 ± 2.7 | 82.0 | 18.0 | 81.0 ± 7.3 | 5.1 | 11.5 | 202.5 ± 28.2 | 13.7 |

[1]Mean ± standard deviation

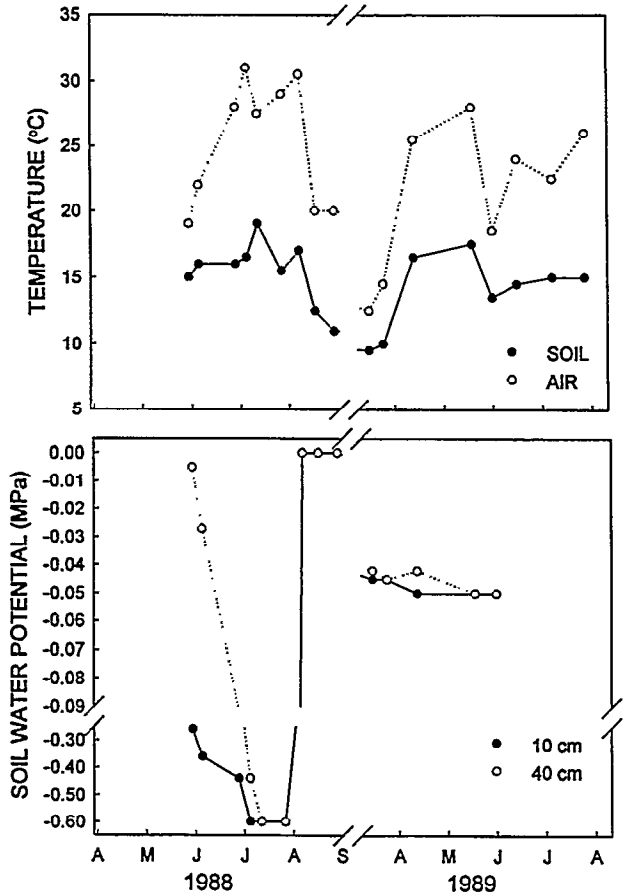


**Fig. 3. Midday soil water potential, soil temperature and air temperature for the study area on Freeman Creek near Portola, Calif.**

## Discussion

The 2 species studied have different growth forms and thus differences in physiological response might also be expected. The seasonal pattern of photosynthesis did vary between species. Lemmon's willow leaves did not reach maximum photosynthetic values until mid-summer (Fig. 1). During 1989 the leaves were 1 to 2 cm long when we initiated measurements and averaged 4.4 cm by 13 June when photosynthesis increased to more than 10° (μ moles $m^{-2}$ $second^{-1}$). Thus, there would appear to be sufficient leaf material early in the season for Lemmon's willow to achieve reasonably high photosynthesis. Conductance was sufficient (Fig. 2) during this period such that stomatal closure did not appear to limit photosynthesis of willow during the early growth phase. Midday soil and air temperatures (Fig 3.) during the study did not appear low enough to limit photosynthesis. Anderson and McNaughton (1973) found that transpiration and photosynthesis of several willow species were not affected when soil temperature was reduced from 20°C to 3°C. In the present study, soil temperature was well above 3°C during all measurement dates.

Nebraska sedge maintained higher photosynthesis than Lemmon's willow early in the growing season, but had lower photosynthesis during the latter part of the season. The 2 species also exhibited very different yearly responses. During the drought year (1988), Lemmon's willow maintained higher seasonal average photosynthesis than Nebraska sedge, whereas the opposite ranking occurred during the average year (Table 1). The explanation presumably lies in the rooting habits of the 2 species. Nebraska sedge tends to concentrate rooting activity in the upper 40 cm of the soil profile (Fig. 4, Manning et al. 1989), whereas, willows are able to use groundwater (Busch et al. 1992). Thus, during drought years when surface soil moisture was limiting (Fig. 4), the sedge would be at a disadvantage compared with willows. Over the 2-year period, mean photosynthetic rates for the 2 species were remarkably similar (10.9 and 11.1 μ moles $m^{-2}$ $second^{-1}$ for Nebraska sedge and Lemmon's willow, respectively). Although the mean photosynthetic rate was similar, the seasonal and yearly patterns of photosynthesis were very different between species.

Probably the most striking difference between the 2 species was in xylem water potential. Lemmon's willow had less negative values of xylem water potential than Nebraska sedge during all measurement dates and did not exhibit the seasonal trend evident in Nebraska sedge during the drought year. When averaged over the season, Nebraska sedge has xylem water potential values that were twice as negative (-3.0 and -2.2 MPa for 1988 and 1989, respectively) as those of Lemmon's willow (-1.4 and -1.1 MPa for 1988 and 1989, respectively). Young et al. (1985) measured xylem water potential for several species of *Salix* in Wyoming and also found minimum values in the range of -1.0 to -2.0 MPa. In contrast, transpiration and conductance were similar for the 2 species, except that Nebraska sedge tended to have higher early season values compared with Lemmon's willow. Thus, Lemmon's willow maintained water flow to leaves and exhibited less "water stress" (as inferred from xylem water potential) than Nebraska sedge.

Many of the seasonal differences in water relations between the 2 species can probably be explained by belowground structures. Nebraska sedge has a very profuse rooting habit with about 99% of the root length in small (<1 mm) roots (Manning et al. 1989). We could not find any detailed root observations for willows; however, woody species tend to have a larger proportion of roots

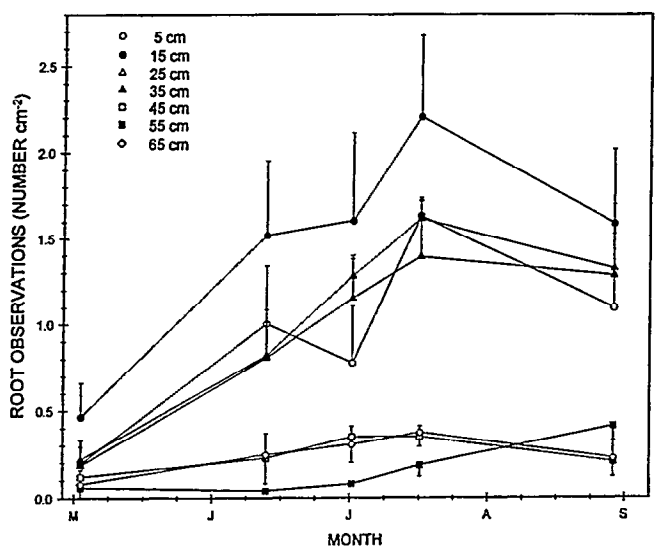


**Fig. 4. Seasonal trend in rooting activity of Nebraska sedge during 1989 (mean ± standard error, n=3).**

in the > 1 mm size classes. Strong and LaRoi (1983) found that only 5% of the root mass of aspen was in the <2 mm size class. In general, the fibrous root system of Nebraska sedge should be efficient at extracting moisture from the upper portions of the soil profile. On the other hand, the large diameter woody roots of Lemmon's willow should be more efficient than Nebraska sedge at transporting water from the water table to transpiring leaves.

It appears that Nebraska sedge concentrates roots in the upper soil profile as evidenced by rooting activity (Fig. 4) and previously published data on root biomass and root length density (Manning et al. 1989). In a Nebraska sedge community, Manning et al. (1989) found that 85% of the root length between 0-40 cm was concentrated in the upper 20 cm of the soil profile. We found the greatest number of active roots at 15 cm with little rooting activity below 40 cm. We also noted that active root growth did not occur directly in the water table. Root growth occurred at depths above the water table. Kawase (1981) cited decreased root growth as one of the responses plants typically exhibit during waterlogged conditions. The mid-summer peak for rooting activity suggests riparian species may be out-of-phase with upland sagebrush steppe communities in timing of root growth. In general, rooting activity of perennial upland species peaks in late spring or early summer when soil water is available (Richards 1984, Harris 1977, Fernandez and Caldwell 1975). Riparian graminoid species may have delayed root growth until soils are not saturated or the water table recedes.

Peak standing biomass of willow was similar during the 2 year period, however, a greater proportion of biomass was allocated to leaves during the average precipitation year compared to the dry year (Table 1). The greater allocation to leaves explains the higher leaf area index of willow during 1989 compared to 1988. We did not measure leaf area index of sedge, but the higher biomass (which is almost entirely leaf material) suggests leaf area index was also higher in 1989 as compared with 1988. The decrease in leaf area of Lemmon's willow and biomass of Nebraska sedge in the dry vs. average precipitation year was very similar (24% and 25%, respectively). However, as previously mentioned, the seasonal photosynthesis of Nebraska sedge was reduced to a greater extent by drought than that of Lemmon's willow (41% and 6% reduction, respectively).

Seasonal differences between Lemmon's willow and Nebraska sedge existed for photosynthesis, transpiration, conductance, and xylem water potential. These trends could be explained by yearly changes in precipitation, and by morphological and physiological differences between the 2 species. The willow achieved greater maximum photosynthesis than the sedge during both dry and normal years, while it maintained similar or slightly lower rates of transpiration and conductance. However, average photosynthetic rate over the 2 year study period was very similar between species. Similar rates of transpiration between the 2 species, yet higher (less negative) xylem water potential for the willow suggest that willow had lower resistance to water movement than sedge. During the year of below average precipitation, willow had a higher than average photosynthesis throughout the growing season. The ability of willow to tap the water table may explain its ability to maintain photosynthesis during summer drought.

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# Genetic variation and inheritance characteristics for carbon isotope discrimination in alfalfa

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## Abstract

**The negative correlation between carbon isotope discrimination (Δ) and water-use efficiency in $C_3$ species, including alfalfa (*Medicago sativa* L.), suggests that Δ might be useful in the selection of alfalfa cultivars that use water more efficiently. We initiated field experiments with alfalfa in northern Utah to determine genetic variation for Δ within representative breeding populations, the effect of drought on Δ, magnitudes of heritability for Δ, genetic regulation of Δ, and how Δ differs among plant parts. In an experiment conducted under a rainout shelter facility equipped with a line-source sprinkler system, genetic variability for Δ was not detected in 15 clones each from the NC-83-1 germplasm and 'Spredor 2' cultivar. In another experiment with 25 clones from the NC-83-1 germplasm, there was significant ($P<0.01$) genetic variation for Δ with a range of 1.6 per mil (‰), and broad-sense heritabilities exceeded 0.80. In a field trial with 78 cultivars and elite breeding lines, significant genetic variation for Δ was observed, although the range for Δ was only 0.8‰. We also detected significant genetic variation for Δ in a diallel experiment with 196 crosses from 14 parent clones from NC-83-1. Furthermore, general combining ability was significant, but specific combining ability and reciprocal effects were not, indicating that standard breeding techniques could be used to alter Δ response in alfalfa. Plant parts differed significantly for Δ with stems having the lowest value (18.7‰) followed by the entire shoot (19.0‰), upper leaves (19.4‰), and bottom leaves (20.2‰). The lack of significant statistical interactions among plant parts suggested that any plant part could be sampled to determine Δ. The results from these experiments indicated that promise exists for using Δ to improve water-use efficiency in alfalfa; however, use of more diverse germplasm may be necessary to expand opportunities for selection in North American alfalfa germplasm.**

**Key Words: *Medicago sativa*, carbon isotope ratio, water-use efficiency, transpiration efficiency**

Alfalfa (*Medicago sativa* L.) is the world's most important forage crop (Barnes et al. 1988) and is the only forage known to have been cultivated before recorded history (Michaud et al. 1988). Alfalfa is a widely adapted perennial legume that provides a high-quality forage, fixes atmospheric nitrogen, exhibits rapid growth after defoliation, and survives in dry, high-temperature environments. It persists well on rangelands once it is established (Miles 1969, Wilton et al. 1978, Rumbaugh and Pedersen 1979) and naturally reseeds itself on sites that receive as little as 280 mm annual precipitation (Rumbaugh 1982). Alfalfa is capable of fixing nitrogen on semiarid rangelands (Johnson and Rumbaugh 1981) and increases the forage and protein yields of associated crested wheatgrass [*Agropyron cristatum* (L.) Gaertner] (Rumbaugh et al. 1982). Because of its many attributes, alfalfa is recommended more frequently for range improvement projects than any other legume species (Rumbaugh and Townsend 1985).

Alfalfa is able to survive on semiarid rangelands probably because of its extensive root system and its ability to become semi-dormant during severe, prolonged periods of drought. Even so, alfalfa water use is considered relatively extravagant because its seasonal evapotranspiration is large compared to other crops (Sheaffer et al. 1988). However, early in the 1900s, Briggs and Shantz (1914) reported that alfalfa cultivars differed in their water-use efficiency or transpiration efficiency (amount of dry matter produced per unit of transpiration). Cole et al. (1970) also found significant differences in water-use efficiency among 5 cultivars and 2 experimental lines of alfalfa. Greater variation in water-use efficiency was detected within cultivars than among cultivars, which suggested that efficient genotypes could be used as germplasm to improve water utilization.

Despite the apparent variability for water-use efficiency in alfalfa, cultivars have not been specifically developed for high water-use efficiency. This probably is due to the lack of practical techniques for screening large breeding populations for water-use efficiency. Techniques such as gas exchange procedures can rapidly assess relationships between $CO_2$ uptake and water loss, but these are instantaneous values that may not reflect integrated responses throughout the growing season. Pot-weighing techniques reliably evaluate water-use efficiency, but cannot accommodate the large number of breeding lines typically required in plant improvement programs.

One promising technique for indirectly evaluating water-use efficiency in $C_3$ species involves analysis of the stable carbon isotope composition ($^{12}C$ and $^{13}C$) in plant tissues (Ehleringer et al. 1993). Farquhar et al. (1982) and Farquhar and Richards (1984) theorized that $^{13}C$ discrimination (Δ) should be negatively related to water-use efficiency because Δ and water-use efficiency are independently associated with leaf intercellular $CO_2$ concentration. This negative association between Δ and water-use efficien-

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cy has been confirmed for many $C_3$ crop species (Farquhar et al. 1989) and various cool-season grasses (Johnson and Asay 1993). Selection for low Δ has been proposed as a method to indirectly estimate long-term water-use efficiency and to select for improved water-use efficiency in breeding programs for $C_3$ crop species. Johnson and Tieszen (1994) reported a significant negative association between Δ and water-use efficiency in alfalfa and found that Δ differed significantly among 18 alfalfa accessions. Their results suggested that Δ could be used to evaluate water-use efficiency in alfalfa.

Additional background information about Δ and its inheritance is required before Δ can be effectively utilized in alfalfa improvement programs. Accordingly, we designed a series of 5 experiments to determine genetic variation for Δ in representative alfalfa breeding populations, the effect of drought on Δ, magnitudes of heritability for Δ, genetic regulation of Δ, and how Δ differs in various plant parts of alfalfa.

## Materials and Methods

### Rainout Shelter Experiments

Thirty randomly selected clones of alfalfa [15 clones each from the broad-based NC-83-1 germplasm (Kehr et al. 1975) and the cultivar 'Spredor 2'] were vegetatively propagated in a greenhouse during the winter of 1984-85 and transplanted in May 1985 to the Utah State University Evans Farm, approximately 2 km south of Logan, Utah. The soil at the site is a Nibley silty clay loam (fine, mixed, mesic Aquic Argiustoll). The site is equipped with an automated rainout shelter facility (modified after Upchurch et al. 1983) that automatically moves over the plot area when it rains or snows and excludes precipitation from the plot area. After the precipitation event, the shelter is automatically moved from the plots, exposing the plot area to ambient environmental conditions. A line-source sprinkler system (Hanks et al. 1976) specifically designed for a 10-m by 47-m plot area (Willardson et al. 1987) was used in the rainout shelter to control water application to the plot area. Water application was uniform along the length of the sprinkler line, but was high adjacent to the line and decreased to near 0 at about 5 m perpendicular from the sprinkler line. Consequently, this system exposed plants to a gradient of water application in a field environment.

Individual plots were established perpendicular to the line-source sprinkler system and were comprised of 1 row of 14 propagules of a single clone or genotype. Propagules were spaced at 30 cm within a row, and rows were 60 cm apart. Propagules on each end of the rows were designated as border plants. Although a total of 6 water treatment levels were defined (1 = wettest, 6 = driest) with 2 propagules/clone contained in each level, only 3 water levels were used in this study (1, 3, and 5). The plots were arranged in a modified split-plot design with the 30 clones as whole plots and the 6 water levels as subplots. The design was replicated 4 times, twice on each side of the line-source irrigation pipe. For this study only 2 replications on 1 side of the irrigation pipe were sampled.

During the establishment year (1985), plots were irrigated uniformly as required for optimum growth. Plots were hand clipped 3 times (June, July, and August) in 1985. In 1986 plots were irrigated with the line-source system from April through October. A total of 1, 24, and 52 cm of irrigation water were applied to the 3 water levels that were sampled.

Plants were hand clipped to a 6-cm stubble height on 10-11 June, 14-15 July, and 21-22 August in 1986. Samples were dried at 70°C in a forced-air oven to obtain plant dry weights. The largest, most fully expanded leaves in the upper 15 cm of the canopy of each plant were removed from the shoots and ground to pass a 1-mm screen. Samples were analyzed for carbon isotope composition on a dual-inlet, double-collector gas isotope mass spectrometer following complete sample combustion. The carbon isotope ratio was calculated by comparing the $^{13}C$ to $^{12}C$ composition of the sample relative to the Pee Dee belemnite standard. These carbon isotope ratios were used to calculate Δ using a value of -8‰ for the carbon isotope ratio for air (Mook et al. 1983), as described by Farquhar et al. (1989).

Data were analyzed using a split-split plot analysis following the procedures recommended by Hanks et al. (1980) for line-source irrigation experiments. Water levels were considered as fixed variables, and harvest/year and clones were considered as random variables. Approximate F tests were required in the combined analysis of variance.

### Genetic Variability Experiment

Twenty-five plants were randomly selected within a field plot of NC-83-1 alfalfa (Kehr et al. 1975). Multiple stem cuttings were obtained from each plant during May 1985 and were grown in pots in the greenhouse. On 20 August 1986, these clonal propagules of the 25 lines were transplanted to the Utah State University Evans Experimental Farm. Plots consisted of individual propagules spaced 0.5 m apart within a row and 1 m between rows. The plot was bordered on all sides by other NC-83-1 clonal propagules. The experimental design was a randomized complete block with 5 replications; however, only 3 replications were sampled in the second year of the study. Plots were hand clipped to a 6-cm stubble height 3 times each growing season (June, July, and Sept.) and were not irrigated after the year of establishment. In 1988 (20-21 July) and 1989 (31 July-1 Aug.), the largest, most fully expanded leaves in the upper 15 cm of the canopy of each plant were removed from the shoots, dried at 70°C in a forced-air oven to a constant weight, and ground to pass through a 1-mm screen.

After determination of Δ (described above), data were subjected to analysis of variance. Broad-sense heritability values were computed on a mean basis as the ratio $\sigma_c^2/\sigma^2_{\overline{ph}}$ where $\sigma_c^2$ is the variance component arising from differences among clones, and $\sigma^2_{\overline{ph}}$ is the phenotypic variance among the clones or the variance of a clonal mean. In the computation of variance components, clones and years were considered as random variables. Approximate F-tests were required in analyses combined across years.

### Alfalfa Variety Trial

This experiment was conducted in conjunction with an irrigated alfalfa trial that was established near Morgan, Utah. On 30 April and 1 May 1981 a total of 90 alfalfa cultivars or elite breeding lines were seeded in 5-row plots (6.1 m length) with 15.2 cm spacing between rows. The experimental design was a randomized complete block with 4 replications. The soil is a Yeates Hollow loam series, which is classified as a clayey-skeletal, montmorillonitic, frigid typic Argixeroll. This trial was part of a collaborating farmer's field, which was subjected to a 3-cut, 30-

35 day harvest schedule. The farmer sprinkler irrigated on a 10-14 day rotation depending on water availability. On 17 July 1986 the second crop was harvested with a plot harvester at the late-bud/early flower stage. Shoots were randomly selected from the harvested material from 78 of the cultivars or elite breeding lines in the trial. The samples were dried at 70°C in a forced-air oven to constant weight. The largest, most fully expanded leaves in the upper 15 cm of the canopy of each plant were removed from the shoots and ground to pass through a 1-mm screen. Because the farmer inadvertently harvested a portion of the trial prior to our sampling, the fourth replication was not available for 11 of the 78 entries. After determination of Δ, data were subjected to analysis of variance procedures using the General Linear Model (GLM) statistical package for unbalanced data (SAS Institut., Gary, N.C.).

### Diallel Experiment

All 196 possible mating combinations (including self and reciprocal crosses) were made among 14 alfalfa plants selected at random from the NC-83-1 breeding population (Kehr et al. 1975). Seed from each cross was germinated, and seedlings were grown in a soil-peatmoss mixture (3:1) in cone-shaped plastic containers (21 cm length × 4 cm diameter at the top). The greenhouse regime was 30/15°C day/night temperature, natural daylength (ranging from 8 to 14 hours), and a daily watering schedule. Six replications of single plants from each cross were transplanted to a field location near Logan, Utah, on 9 May 1985 (approximately 140 days after germination). The experimental design was a randomized complete block with 1-m spacing between plants. Only 3 replicates were sampled for this study. The plants were allowed 1 year for establishment, and no irrigation was applied after the establishment year. The first growth of the established plants was clipped and discarded in mid-June 1986. On 16-18 July 1986, the largest, most fully expanded leaves in the upper 15 cm of the canopy of each plant were removed from the shoots, dried at 70°C in a forced-air oven to constant weight, and ground to pass a 1-mm screen. After Δ determination, combining ability effects for Δ were calculated according to method I, model II (random model) of Griffing (1956). General and specific combining abilities were calculated according to method II, model I (fixed model) of Griffing (1956).

### Plant Part Experiment

Two clones of alfalfa from the broad-based NC-83-1 germplasm and 2 clones from the cultivar 'Spredor 2,' which appeared to exhibit different (though not statistically different) Δ responses, were used in this experiment. These 4 clones were included in the 30 clones evaluated in the rainout shelter experiment, and the same plots described above for that study were used in this experiment. Four replications and 2 water levels (1 and 5) were sampled. In 1992 irrigation water was applied to the plots from April through October; 121 cm of water were applied for water level 1 and 17 cm for water level 5.

Plants were clipped to a 6-cm stubble height on 4-5 June 1992, and clippings were discarded. On 21-22 July 1992 plants were harvested at a 6-cm stubble height and separated into upper leaves, lower leaves, and stems. In addition, some shoot samples were kept intact to obtain an overall Δ for the entire shoot. Samples were dried at 70°C in a forced-air oven to constant weight and ground to pass through a 1-mm screen. After determination of Δ (described above) for various plant conponents, data were analyzed using a split-split plot analysis of variance.

## Results and Discussion

### Rainout Shelter Experiment

The 30 clones of alfalfa did not differ significantly for Δ, either when data from each harvest were analyzed separately or when data were combined across harvests (Table 1). In comparing the 15 clones of the NC-83-1 population to the 15 clones from the 'Spredor 2' cultivar, the 2 populations differed ($P<0.05$) only for Harvest 1 (data not shown). No population differences were observed for the second or third harvests or in the combined analysis of the data. These results indicated that the clones used in our experiment, which came from NC-83-1 germplasm and 'Spredor 2', did not exhibit consistent, reproducible differences in Δ. The NC-83-1 germplasm (Kehr et al. 1975) is particularly broad based with one of its main sources from 94 cultivars, including experimental synthetics, breeding populations, and released germplasms adapted to the northern USA, and the other primary source consisting of 36 foreign plant introductions. Because alfalfa is a heterogenic, cross-pollinated species, considerable genetic variation typically is observed for most morphological and physiological characteristics and would have been expected for Δ, particularly among the clones from the NC-83-1 germplasm.

**Table 1. Degrees of freedom (df) and significance levels for the sources of variation for Δ in the split-plot ANOVA for individual harvests and combined data for the rainout shelter experiment.**

| | | Harvest dates | | | |
|---|---|---|---|---|---|
| Source | df | 6/86 | 7/86 | 8/86 | Combined |
| Clones (C) | 29 | NS | NS | NS | NS |
| Water level (W) | 2 | NV† | NV | NV | NV |
| C × W | 58 | ** | NS | NS | NS |
| Harvests (H) | 2 | | | | ** |
| C × H | 58 | | | | ** |
| W × H | 4 | | | | ** |
| C × W × H | 116 | | | | NS |

** NS Significant at the 0.01 level of probability and not significant, respectively.
† NV = No valid F-test for water levels.

Although the F-test for water levels was not strictly valid because water treatments were not randomly placed along the line-source water application gradient, Δ differed markedly across water levels and was greatest in the highest water level and lowest in the drought treatment. The clone by water level interaction was significant for the first harvest, but not for the second or third harvests or in the combined analysis across harvests. Values of Δ differed by harvest: Harvest 2 > Harvest 3 > Harvest 1. The significant clone by harvest interaction indicated that the Δ response of clones was not consistent between harvests. The water level by harvest interaction also was statistically significant.

### Genetic Variability Experiment

The 25 clones from the NC-83-1 population evaluated in this experiment differed significantly ($P<0.01$) in their Δ response in 1988, 1989, and in the combined analysis across years (Table 2). The overall mean for Δ was lower ($P<0.05$) in 1988 than in 1989,

Table 2. Summary of 1988 and 1989 Δ data from 25 clones of NC-83-1 alfalfa grown near Logan, Utah.

| Statistic | Harvest year 1988 | 1989 | Combined |
|---|---|---|---|
| | | (‰) | |
| Mean | 19.5 | 20.0 | 19.7 |
| Range | | | |
| Minimum | 18.9 | 19.2 | 19.1 |
| Maximum | 20.4 | 21.1 | 20.7 |
| Variance component† | 0.15** | 0.18** | 0.15** |
| Heritability‡ | 0.86 | 0.82 | 0.81 |
| Coefficient of variation (%) | 1.8 | 1.7 | 1.0 |

**Mean square from which variance component was computed was significant at $P<0.01$.
†Variance component among clonal lines ($\sigma_c^2$).
‡Heritability computed in the broad sense (H) and on a mean basis, with 5 replicates in 1988, 3 replicates in 1989, and 3 replicates in the combined analysis.

and the range in Δ was greater in 1989 (1.9‰) than in 1988 (1.5‰). Broad-sense heritabilities (the proportion of total phenotypic variance attributable to genotypic differences) were relatively high (> 0.80) and consistent between years. These high broad-sense heritabilities are consistent with those previously reported for wheat (*Triticum aestivum* L.) (Condon et al. 1987), peanut (*Arachis hypogoea* L.) (Hubick et al. 1988), crested wheatgrass (*Agropyron desertorum* [Fischer ex Link] Schultes) (Johnson et al. 1990), cowpea (*Vigna unguiculata* [L.] Walp.) (Hall et al. 1990), and barley (*Hordeum vulgare* L.) (Acevedo 1993). Coefficients of variation were always less than 2%, reflecting high precision in Δ determinations.

The significant ($P<0.05$) year by clone interaction in this experiment (data not shown) suggests that caution should be used when combining Δ data across years. Nevertheless the correlation between years for Δ values was significant and positive (r = 0.80**, df = 73, $P<0.01$), indicating that clones performed quite consistently from 1 year to the next. This clonal consistency also is evident in the rankings of clones in each year. Eight of the 10 clones with the lowest Δ values in 1988 also were lowest in 1989; 9 out of the 10 clones with the highest Δ values were common to both years. This consistency in the performance of alfalfa clones across years or environments also was observed by Morgan et al. (1993) and Johnson and Tieszen (1994) and in cool-season perennial forage grasses by Read et al. (1992), Johnson (1993), and Johnson et al. (1993).

## Alfalfa Variety Trial

The 78 alfalfa varieties evaluated in northern Utah differed significantly ($P<0.01$) in their Δ response. However, the overall mean for Δ was 20.9‰ with a range of only 0.8‰, from 20.4‰ for 'Haymaker' to 21.2‰ for 'Deseret' (Table 3). This was a surprisingly narrow range of Δ in this large group of 78 U.S cultivars. Johnson and Tieszen (1994) found a range of 1.4‰ among 18 alfalfa accessions from around the world that were grown in irrigated and dryland field environments in southeastern Washington, although they did not detect significant differences among the 4 U.S. alfalfa cultivars included in their study. Our range in Δ also was smaller than the 1.1 to 1.5‰ range for 11 clones of yellow-flowered alfalfa (*Medicago sativa* subsp. *falcata* [L.] Arcang.) grown in northern Colorado (Morgan et al. 1993). Based on our results and those of Johnson and Tieszen (1994), variability for Δ apparently is limited among U.S. alfalfa cultivars. Given the greater variation observed for Δ in alfalfa accessions from the U.S. National Plant Germplasm System (Johnson and Tieszen 1994, Morgan et al. 1993), breeding programs interested in selection of alfalfa genotypes with low Δ may have to be selected from alfalfa accessions from plant introductions rather than U.S. cultivars. Alternatively, the range of Δ values among our 78 alfalfa cultivars may have been greater if plants had been grown under water-limited conditions, as observed in clones of crested wheatgrass (Read et al. 1991, 1992).

Values of Δ were very reproducible across replications in our experiment, as evidenced by the overall coefficient of variation for Δ of less than 1%. Similar to the results of Morgan et al. (1993), values of Δ were not related to green forage yield (r = -0.10).

Table 3. Alfalfa cultivars and advanced breeding lines evaluated forΔ in irrigated trial conducted at Morgan, Utah. Cultivars or lines are in descending order of Δ with Deseret having Δ = 21.2‰ and Haymaker having Δ = 20.4‰ (n = 3 or 4).

| | | | |
|---|---|---|---|
| Deseret | Valor | Hay Future† | AS-67† |
| Pacer | WL-309† | Hay Future | Agate |
| C/W 67 | Coop. F24OA | Ranger | Dawson |
| Wash. Syn. I | Vernal | Resist. II | Pi 545 |
| 20-30 | Lahonton | Apollo | Gladiator |
| WL 312† | Action | AS-13 | ATC |
| WL-310 | AS-49 | Super 721 | AS-67 |
| AS-49R | Classic | Kanza | C/W 8642 |
| WL-318† | WL-309 | C/W 634 | Blazer |
| Thor | Tempo | Pi 532 | Hi-phy |
| Anchor | WL-318 | C/W 62 | Riley |
| Vangard† | Vangard | ATRA 55 | WL 315 |
| Washoe | Anchor† | AS-13† | Phytor |
| Citation | AS-49R† | WL 220 | SC400A |
| Pi 581 | AS-63 | Baker | C/W 637 |
| Nev. Syn. XX | Weevlchek | WL 316 | RS-209† |
| 919 (20) | WL 314 | Pi 524 | Spredor 2 |
| Trident | WL 312 | Pacer† | Haymaker |
| Cascade | C/W 69 | 6-7730 | |
| Valor† | 167 | Apollo† | |

† Denotes pelleted seed.

## Diallel Experiment

Values of Δ differed significantly ($P<0.01$) among the 196 lines evaluated in this experiment (Table 4). Progeny means from the 14 parents ranged from 20.2 to 20.8‰, whereas the range for Δ was expectedly greater among the individual crosses (19.8 to 21.4‰). General combining ability was significant ($P<0.01$), while specific combining ability and reciprocal effects were not.

Table 4. Degrees of freedom (df) and mean squares with indicated significance levels for the sources of variation from the analysis of variance for Δ in the NC-83-1 diallel experiment.

| Source | df | Mean square |
|---|---|---|
| Crosses | 195 | 0.38** |
| General combining ability | 13 | 2.11** |
| Specific combining ability | 91 | 0.24 |
| Reciprocal | 91 | 0.26 |
| Error | 392 | 0.23 |

** Significant at $P<0.01$.

The significant mean square for general combining ability indicated that additive genetic variance among the parents was important in regulating Δ response in this population of alfalfa. The nonsignificant mean square for specific combining ability indicated that non-additive genetic variance, such as dominance or epistasis, was not important for Δ response. The nonsignificant reciprocal effect indicated that nonnuclear DNA did not contribute to the genetic regulation of Δ response. Broad-sense heritabilities of the half-sib families of the 14 clones serving as the female parent were 0.86, suggesting that the Δ response in this population of alfalfa is very amenable to selection.

Few experiments have used diallel analysis to evaluate inheritance characteristics of Δ in plants. However, White (1993) crossed 8 parents of common bean (*Phaseolus vulgaris* L.) in a diallel without reciprocals and evaluated the $F_2$ and $F_3$ populations for leaf Δ. Mean squares for general combining ability were generally larger than those for specific combining ability, suggesting that additive gene action also was important in common bean. Similar conclusions concerning inheritance of Δ were reached by Ehdaie et al. (1993) in wheat where significant additive variation was present for Δ. They concluded that Δ is a complex trait that is quantitatively inherited. Hall et al. (1993) compared $F_1$ hybrids from reciprocal crosses and parents of cowpea and found that differences in Δ involved nuclear rather than maternal inheritance. Read et al. (1993) found that narrow-sense (realized) heritabilities for Δ in crested wheatgrass exceeded 0.75 and that correlations between progeny means for Δ and means of the corresponding midparents were significant. The results of our present experiment along with these other inheritance studies suggest that Δ can be effectively manipulated through standard breeding techniques that typically are used for other quantitatively inherited traits. However, a more genetically diverse collection of alfalfa genotypes than the 14 NC-83-1 parents used in our experiment probably would be necessary.

### Plant Part Experiment

Significant differences ($P<0.01$) were detected among clones and plant parts in this experiment (Table 5), which we expected because the 4 clones were selected for their divergent Δ values. Stems had the lowest Δ followed by the entire shoot, upper leaves, and bottom leaves (Fig. 1). The Δ values for the entire shoot were between those for the leaves and stems, but were closest to Δ values of the stem, probably reflecting the large proportion of stem in the whole plant sample. The lower leaves developed during the early, cool portion of the growing season whereas the upper leaves grew during the hot, dry part of the growing season. Presumably, stomata were more open during the development of the lower canopy leaves than those in the upper canopy, resulting in a greater Δ in the lower leaves. Besides environmental effects, variation in Δ among various plant parts may also be due to differences in diffusional constraints (Farquhar et al. 1989), chemical composition (O'Leary 1981), ratio of assimilation rate to $CO_2$ diffusive conductance (Farquhar et al. 1989), photosynthetic metabolism (Wirth et al. 1977), and anatomical characteristics (Araus et al. 1992).

**Table 5. Degrees of freedom (df) and mean squares with indicated significance levels for the sources of variation from the analysis of variance for Δ in the plant part experiment.**

| Source | df | Mean square |
|---|---|---|
| Entry (E) | 3 | 3.82** |
| Water level (W) | 1 | 92.49 NV† |
| E × W | 3 | 0.41 |
| Plant part (P) | 3 | 11.69** |
| E × P | 9 | 0.22 |
| W × P | 3 | 0.12 |
| E × W × P | 9 | 0.06 |

** Significant at the 0.01 level of probability.
† NV = No valid F-test for water levels.

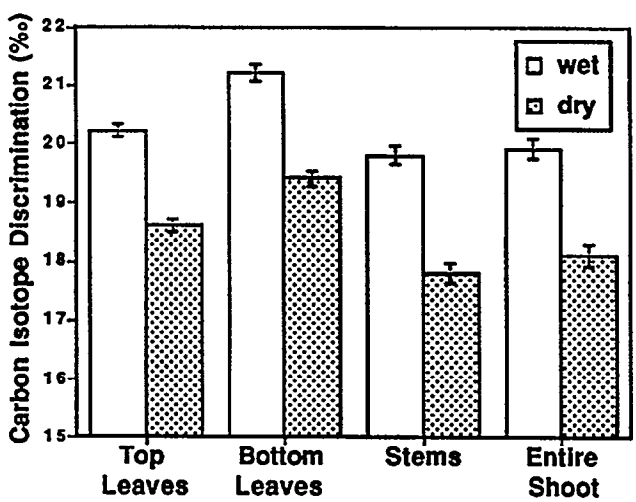


**Fig. 1. Carbon isotope discrimination (Δ) of top leaves, bottom leaves, stems, and entire shoot for 4 alfalfa clones grown under 2 water levels in rainout-sheltered plots (n = 4).**

Even though the comparison between water levels is not strictly valid because water treatments were not randomly placed, drought markedly decreased Δ values for all plant parts (Fig. 1). This agrees with results for alfalfa (Morgan et al. 1993, Johnson and Tieszen 1994) and many other species where drought typically reduces Δ because of lowered stomatal conductance, and for some species, a concomitant decline in photosynthetic capacity (Farquhar et al. 1989, Hall et al. 1990, Johnson et al. 1990, White 1993). Although plant parts differed in Δ, the clone by plant part and water level by plant part interactions were not significant. This indicated that even though the magnitude of Δ differed among the various plant parts, the relative Δ response was similar across clones or water levels. This suggests that any of the 3 plant parts or the entire shoot could be used to characterize Δ in alfalfa clones. Given the time and labor required to separate individual plant parts, the entire shoot may be the fastest and most economical sample to obtain and analyze for Δ in alfalfa breeding programs.

In summary, except for the rainout shelter experiment, our series of experiments showed that genetic variation for Δ existed within alfalfa and that broad-sense heritabilities for Δ exceeded 0.80. The narrow range of Δ values observed among the 78 U.S. cultivars grown under irrigation suggested that it may be necessary to use alfalfa plant introductions from the U. S. National Plant Germplasm System to increase diversity in Δ response. The results of the diallel experiment showed that additive genetic variance among parents was important in the inheritance of Δ and that it should be possible to effectively manipulate Δ response in alfalfa through standard breeding techniques. Although plant

parts differed in Δ, similarities in Δ response in plant parts across clones or water levels suggested that any plant part could be used consistently to characterize Δ in alfalfa breeding programs. Our results suggest that Δ may be a beneficial criterion for breeding and selecting alfalfa cultivars that use water efficiently under water-limited conditions. However, additional data concerning the physiological basis of Δ response, relationship of Δ to plant water status, and association between Δ and forage yield in alfalfa are required to document that selection for low Δ would lead to significant gains in water-use efficiency in alfalfa.

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# Near infrared reflectance spectroscopy estimation of $^{13}C$ discrimination in forages

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## Abstract

**Forage improvement programs often select for increased crude protein and dry matter digestibility. Additionally, breeding programs may be interested in selecting for enhanced transpiration efficiency or water use-efficiency. Forage crude protein and dry matter digestibility are commonly determined by near infrared reflectance spectroscopy (NIRS), whereas water use-efficiency is estimated from $^{13}C$ discrimination ($\Delta$) values obtained from isotope-ratioing mass spectrometers. If NIRS could predict $\Delta$, then W could be determined simultaneously with quality components at a much lower cost. To test this possibility, leaf samples of alfalfa (*Medicago sativa* L.) and several cool-season perennial grasses were analyzed with a dual-inlet, double collector gas isotope mass spectrometer, and values of $\Delta$ were calculated. Subsamples were scanned with monochromators that collected spectra from 400 to 2,500 nm or 1,100 to 2,500 nm, and absorption data were regressed with values of $\Delta$. Standard errors of calibration for regressing $\Delta$ with NIRS absorption values were higher for grasses than for alfalfa. Coefficients of variation for all validation sample sets used for prediction of $\Delta$ by NIRS were less than 3%, and NIRS correctly identified 77 to 82% of the samples with the lowest $\Delta$ values as determined by mass spectrometer analysis. This level of predictability may be acceptable for identification of genotypes with high water use-efficiency during the early phases of forage improvement programs.**

**Key Words: spectral analysis, range grasses, crested wheatgrass, creeping foxtail, alfalfa, Russian wildrye, water-use efficiency**

Farquhar et al. (1982) proposed that variation in $^{13}C$ discrimination ($\Delta$) in $C_3$ plants depends on the ratio of leaf intercellular $CO_2$ concentration ($C_i$) to ambient $CO_2$ concentration ($C_a$), which is related to transpiration efficiency or water-use efficiency (amount dry matter produced per unit of water transpired). Johnson et al. (1993) and Johnson and Asay (1993) reviewed the use of $\Delta$ for determining water use-efficiency in cool-season forage grasses. Because a leaf incorporates carbon through time via photosynthesis, measurement of $\Delta$ integrates $C_i/C_a$ which means $\Delta$ provides a potential means to select forage breeding populations with improved water use-efficiency (Johnson et al. 1990). Carbon isotope composition of plant tissues, from which $\Delta$ is determined, is typically analyzed with an isotope-ratioing mass spectrometer (Tieszen et al. 1983), which is expensive to purchase, operate, and maintain.

Near infrared reflectance spectroscopy (NIRS) is a rapid, precise, and nondestructive analysis method that measures moisture, oil, and protein concentration in grains (Hrushka and Norris, 1982). In addition, forage quality characteristics such as crude protein, acid and neutral detergent fiber, lignin, and in vitro dry matter disappearance have been successfully predicted by NIRS (Marten et al., 1983; Norris et al., 1976). This method has been certified by the Association of Official Analytical Chemists (AOAC) for the measurement of moisture, crude protein, and acid detergent fiber in forages (AOAC, 1990). As a result, NIRS is routinely used to evaluate forage quality characteristics in plant improvement programs.

When Okano et al. (1983) evaluated the potential of infrared absorption spectrometry for determining $^{13}C$ atom %, results were within 95 to 97% of the values obtained by mass spectrometry, and the relative standard deviation was less than 3%. They showed that infrared spectrometry could distinguish differences [about 14 per mil (‰)] in $^{13}C$ abundance between $C_3$ and $C_4$ plants. This suggests that spectrophotometric techniques might be useful in predicting $\Delta$. This study was initiated to determine if NIRS can be reliably used to estimate $\Delta$ in a variety of forage species and genotypes.

## Materials and Methods

### Samples

The samples consisted of recently, fully expanded leaves of 30 alfalfa genotypes from 2 cultivars grown in Utah and 5 alfalfa cultivars grown in New Mexico, all under line-source sprinkler systems (Hanks et al. 1976). Alfalfa herbage was sampled from 4 cultivars grown under uniform rainfed conditions in South Dakota. In addition, flag leaves of 14 accessions from 9 Triticeae grass species were sampled from nurseries in Utah, Idaho, and Montana. We also harvested forage from 9 genotypes of crested wheatgrass [*Agropyron desertorum* (Fisch. ex Link) Schult.] grown in the greenhouse and 150 genotypes of creeping foxtail (*Alopecurus arundinaceus* Poiret) grown in South Dakota. Combinations of replicates, soil-water levels, and harvests pro-

Mention of a trade name does not imply an endorsement or recommendation by the USDA, Utah State University, or South Dakota State University over similar companies or products not mentioned.

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vided a total of 229 alfalfa and 358 grass samples. The Utah and New Mexico alfalfa and the greenhouse crested wheatgrass samples were dried at 70° C, whereas the South Dakota creeping foxtail and alfalfa and Triticeae grass samples were dried at 37° C. All samples were ground using a cyclone mill with a 1-mm screen.

**Carbon Isotope Analysis**

Ground samples (ca. 2 mg) were loaded into tin vessels and combusted in a C and N analyzer (Carlo Erba NA-1500; Fisons Instruments, Valencia, Calif.). The $CO_2$ and $N_2$ gases were separated at 50° C on a chromatographic column monitored by a thermal conductivity detector. The $CO_2$ gas from the C and N analyzer was trapped, cryogenically purified, and analyzed for $\sigma^{13}C$ (the ratio of $^{13}C/^{12}C$ relative to that of a Pee Dee Belemnite standard) using an isotopic ratioing mass spectrometer (SIRA 10; Fisons Instruments, Valencia, Calif.). Laboratory precision for σ13C exceeded 0.1 ‰. Standards 21 and 22 (NIST) were used routinely to verify accuracy of the working standards. The $\sigma^{13}C$ values were converted to Δ values as described by Farquhar et al. (1989), assuming a $\sigma^{13}C$ value for ambient air of -8.0 ‰ on the PDB scale (Mook et al. 1983). The Utah and New Mexico alfalfa and Triticeae grass samples were analyzed for Δ using similar procedures described above, except that the mass spectrometer was a Micromass 602E (VG Isotech, Middlewich, England) (Tieszen et al. 1983).

**Near Infrared Determinations**

Alfalfa and creeping foxtail samples from South Dakota were scanned with a scanning monochromator instrument (Model 5000, NIRSystems, Inc., Silver Spring, Md.) that collected spectra from 1,100 to 2,500 nm in 2 nm increments, whereas the remaining sample sets were scanned with a Model 6500 scanning monochromator that collected spectra from 400 to 2,500 nm in 2 nm increments. Both instruments used ISI software (Infrasoft International, Port Matilda, Penn.) to collect spectral data, develop calibration equations, and evaluate performance of calibration equations.

All 55 alfalfa and 137 creeping foxtail samples from South Dakota were identified for Δ analysis using the programs CENTER and SELECT (Shenk and Westerhaus, 1991), which are used to reduce the number of samples needed for calibration development. In theory, the CENTER program ranks samples in a file according to their Mahalanobis distance from the average spectrum of the file. This allows for the identification of samples that do not fit the population being examined. The SELECT program uses the "nearest neighbor" approach by examining the spectra of all samples and identifies groups or neighbors (similar to clustering). The program then selects a sample from each neighborhood for analysis by conventional laboratory procedures. This reduces the number of samples needed for chemical analyses by eliminating redundant samples.

The CENTER or SELECT programs were not used for the other sample sets because these samples all had been previously analyzed for Δ. The following sample sets were each split into 2 subgroups with the samples from 1 subgroup used for calibration and the other subgroup samples used for validation: New Mexico alfalfa samples; combined Utah and New Mexico alfalfa sample sets; greenhouse crested wheatgrass samples; combined Triticeae grass and greenhouse crested wheatgrass grass sample sets; and combined Utah and New Mexico alfalfa plus Triticeae grass and greenhouse crested wheatgrass grass sample sets. Spectral data from the foxtail and South Dakota alfalfa samples could not be combined with other studies because the spectra were obtained with different NIRS instruments.

Reflectance spectra for each wavelength were regressed with Δ values for the calibration samples from each sample set using a program that develops multiple regression equations utilizing methods similar to SAS® program PROC REG with the STEPWISE selection method. The program solves a regression equation in the form of:

$$Y = B_0 \pm B_1X_1 \pm B_2X_2 \pm B_3X_3 .... \quad (1)$$

where Y is Δ predicted by NIRS; $X_1$, $X_2$, and $X_3$ are absorption measurements or derivatives at wavelengths $\lambda_1$, $\lambda_2$, and $\lambda_3$, respectively; $B_0$ is the regression constant; and $B_1$, $B_2$, and $B_3$ are partial regression coefficients. Standard error of calibration (SEC) was calculated to assist in selection of the equation that best fit the Δ data:

$$SEC = [\Sigma(X_i-Y_j)^2/(N-p-1)]^{.5} \quad (2)$$

where $X_i$ is the value determined by conventional analytical methods, $Y_j$ is the predicted value from NIRS, N is the number of samples, and p is the number of dependent variables (wavelengths) in the calibration equation. The multiple coefficient of determination ($R^2$) and an F statistic (similar to the PROC REG SAS® procedure) also were used in selecting the best-fit equation. All F values for each independent variable in the equation had to be greater than 10 to be considered for the final equation.

Each of the calibration equations developed for each sample set were then tested (or validated) with a group of samples from the same sample set. None of the samples used in calibration development were used for validation. The standard error of prediction (SEP) was used to determine regression equation performance:

$$SEP = [\Sigma(X_i-Y_j)^2/(N-1)]^{.5} \quad (3)$$

where $X_i$, $Y_j$, and N are as previously defined (except that $X_i$ and $Y_j$ are from different populations). In addition, bias (mean reference analysis values minus mean NIRS-derived values), and a simple coefficient of determination ($r^2$) were used to evaluate regression equation performance. The SEP is also synonymous with √MSE, where MSE = mean square error. Coefficients of variation (CV) were also computed to compare results across the different sample sets:

$$CV = [\sqrt{MSE}/mean]*100) \quad (4)$$

where mean equals the NIRS predicted mean Δ for that particular sample set.

## Results and Discussion

Table 1 shows the total number of samples in each sample set and the number of samples used for calibration and validation. Grass samples generally had higher mean Δ values and higher standard deviations than did alfalfa samples.

The standard errors of calibration (SEC), which includes errors associated with both chemical analyses and regression, were lower for alfalfa than grass samples (Table 2). The South Dakota sample set had the lowest SEC compared to the other alfalfa sets,

Table 1. Mean, range, and standard deviation (SD) of carbon isotope discrimination (Δ) for forage samples from various studies.

| Sample Set | n[1] | Δ Mean | Δ Range | Δ SD |
|---|---|---|---|---|
| Alfalfa | | ‰ | --‰-- | |
| Utah (Ut.) | 58 (58,0) | 18.5 | 17.1-20.5 | 0.7 |
| New Mexico (N.M.) | 116 (50,66) | 18.8 | 17.2-20.1 | 0.7 |
| UT & NM combined | 174 (60,114) | 18.7 | 17.1-20.5 | 0.7 |
| South Dakota | 55 (55,0) | 19.9 | 18.8-20.5 | 0.4 |
| Grasses | | | | |
| Triticeae grasses (TG) | 78 (78,0) | 20.2 | 17.3-21.8 | 0.9 |
| Greenhouse crested wheatgrass (GCW) | 106 (50,56) | 23.1 | 19.9-24.8 | 1.2 |
| TG & GCW combined | 184 (52,132) | 21.6 | 17.3-24.8 | 1.8 |
| Creeping foxtail | 137 (137,0) | 19.4 | 17.3-21.2 | 0.7 |
| Combined alfalfa and grass | | | | |
| Ut. & N.M. alfalfa & TG & GCW grasses | 358 (127,231) | 20.3 | 17.1-24.8 | 2 |

[1] Number outside of parentheses is total number of samples in sample set; numbers in parentheses indicate the number of samples used for calibration and validation procedures, respectively, for a particular sample set.

which reflects the lower standard deviation obtained for the Δ values from the South Dakota set (Table 1). When the Utah and New Mexico alfalfa sample sets were combined into 1 group, the SEC increased and $R^2$ decreased compared to the individual sample sets (Table 2). Use of $R^2$ in NIRS regression development to determine accuracy can be misleading because this value can be affected by weak relationships between dependent and independent variables and/or minimal variation of the independent variables (Windham et al., 1989). Therefore, $R^2$ values must be interpreted with caution. The same logic applies during the validation process to the statistic, $r^2$.

Partial-least-squares (PLS) regression analysis also was performed with these sample sets and produced no differences in equation performance compared to STEPWISE procedures (data not shown). Wavelengths used for regression analysis are listed (Table 2) in decreasing order of F value. Wavelengths were not consistently selected among the sample sets.

Figures 1a and 1b show the validation statistics and prediction equation with resulting regression lines for the individual New Mexico and the combined Utah and New Mexico alfalfa sample sets. The standard error of prediction (√MSE) estimates how well the calibration equation will perform on similar samples (error of

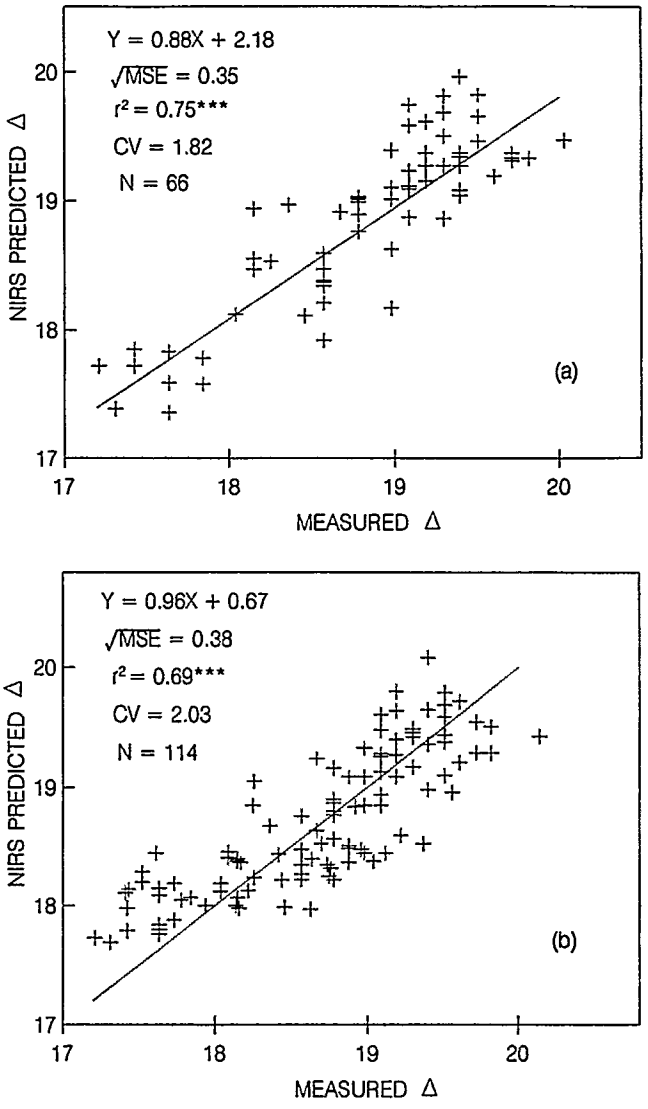
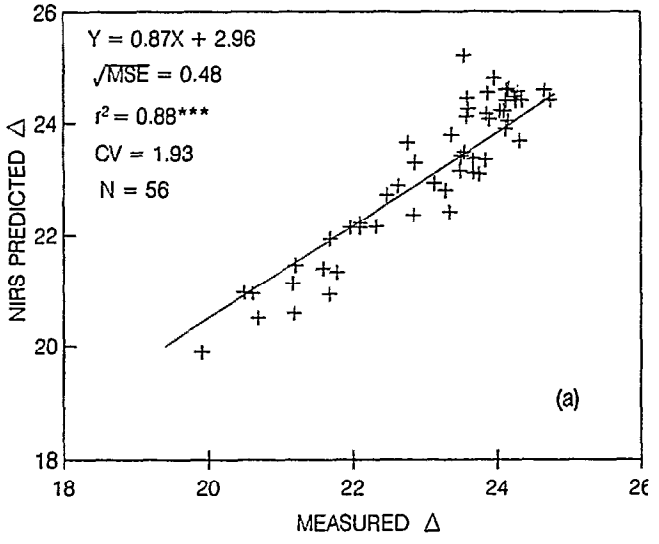



Fig. 1. Relationship between D predicted by NIRS and Δ measured by mass spectrometry (√MSE=standard error of prediction, $r^2$=simple coefficient of determination, CV=coefficient of variation, and N=number of samples). (a) New Mexico alfalfa (N.M). samples used for validation. (b) Combined Utah and New Mexico alfalfa samples (Ut. & N.M.) used for validation.

Table 2. Near infrared reflectance calibration statistics for determining carbon isotope discrimination (Δ).

| Sample Set | n[1] | SEC | $R^2$ | Math[2] | Wavelengths[3] |
|---|---|---|---|---|---|
| Alfalfa | | | | | ----------nm---------- |
| Utah (Ut.) | 58 | 0.30 | 0.80 | 1, 5, 5,1 | 2384,480,2264,1652,2032,2336 |
| New Mexico (N.M.) | 50 | 0.29 | 0.83 | 1, 5, 5,1 | 1724,1436 |
| Ut & N.M. combined | 60 | 0.40 | 0.66 | 2,10,10,1 | 2192,2392,2312 |
| South Dakota | 55 | 0.19 | 0.76 | 2,10,10,1 | 2236,2068,1228,2364,1708 |
| Grasses | | | | | |
| Triticeae grasses (TG) | 78 | 0.52 | 0.60 | 2,10,10,1 | 1372,1276,2144 |
| Greenhouse crested wheatgrass (GCW) | 50 | 0.56 | 0.80 | 1,10,10,1 | 2208,2448,2264,1476,1252 |
| TG & GCW combined | 52 | 0.61 | 0.89 | 1, 5, 5,1 | 464,1164,1180,1716 |
| Creeping foxtail | 137 | 0.44 | 0.61 | 2,10,10,1 | 1508,1652,1604,1476,1868,1700 |
| Combined alfalfa and grass | | | | | |
| Ut. & N.M. alfalfa & TG & GCW grasses | 127 | 0.55 | 0.93 | 1, 5, 5,1 | 2352,1460,2360,1772,2264,2336 |

[1] n = number of samples; SEC = standard error of calibration for Δ (‰); and $R^2$ = Multiple coefficient of determination.



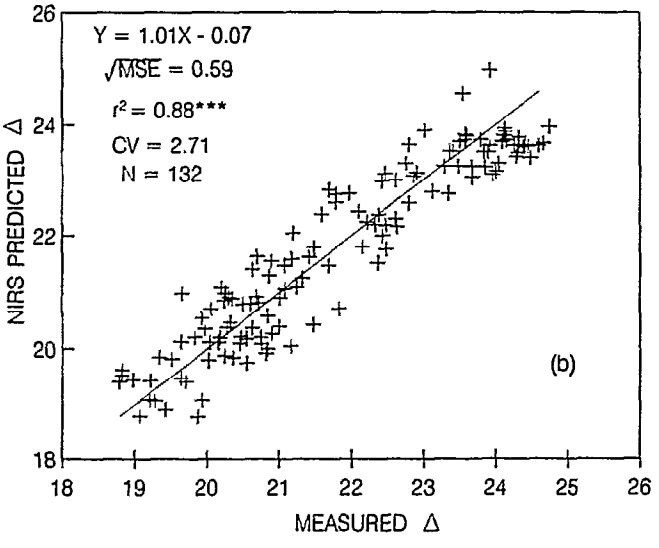




**Fig. 2. Relationship between Δ predicted by NIRS and Δ measured by mass spectrometry (√MSE=standard error of prediction, r²=simple coefficient of determination, CV=coefficient of variation, and N=number of samples). (a) Greenhouse crested wheatgrass (GCW) samples used for validation. (b) Combined Triticeae (TG) and greenhouse crested wheatgrass grass samples (TG & GCW) used for validation.**

prediction). Coefficients of variation (CV) were computed to compare validation errors across sample sets because magnitudes of Δ varied among sample sets. Values of Δ predicted by NIRS agreed quite well with actual Δ values for the New Mexico alfalfa samples ($r^2$=0.75***, CV=1.82, √MSE=0.35) (Fig. 1a). When the New Mexico and Utah sample sets were combined, NIRS did not predict Δ as well ($r^2$=0.69***, CV=2.03) even though the standard errors of prediction were similar.

The SEC values were similar among individual grass sample sets and the combined Triticeae grass and greenhouse crested wheatgrass sample set (Table 2). The $R^2$ values for the Triticeae grass and creeping foxtail sample sets were somewhat lower than the other sample sets. Values of Δ were predicted very well by NIRS for the greenhouse crested wheatgrass sample set (Fig. 2a). Combining the Triticeae grass sample set with the greenhouse

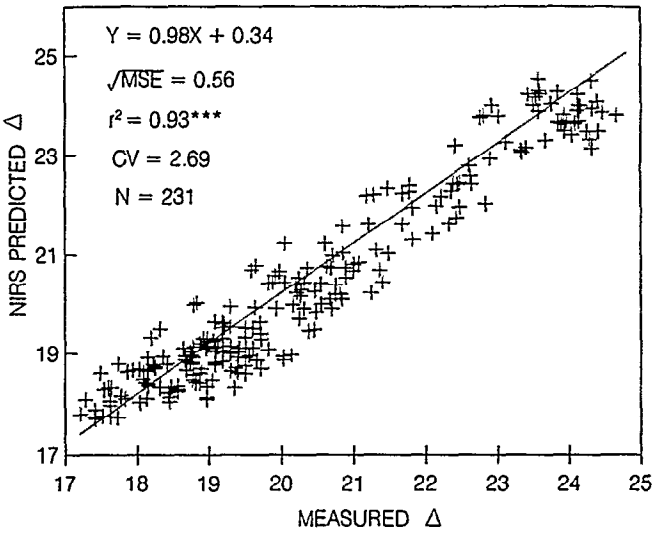



**Fig. 3. Relationship between Δ predicted by NIRS and Δ measured by mass spectrometry (√MSE=standard error of prediction, r²=simple coefficient of determination, CV=coefficient of variation, and N=number of samples). Data points represent a combination of Utah and New Mexico alfalfa samples and Triticeae and greenhouse crested wheatgrass samples (Ut. & N.M. alfalfa & TG & GCW grass) used for validation.**

crested wheatgrass sample set increased the standard error and coefficient of variation compared to the greenhouse crested wheatgrass sample set (Fig. 2b), whereas the $r^2$ remained the same.

The $R^2$ for the combined sample set (Utah and New Mexico alfalfa, plus Triticeae grass and greenhouse crested wheatgrass grass) was 0.93 with an SEC of 0.55 (Table 2). The increased $R^2$ in this combined sample set was probably caused by the greater diversity in spectra and Δ values than for the individual sample sets. The standard error of prediction and coefficient of variation for this combined sample set (Fig. 3) were similar to the combined Triticeae grass and greenhouse crested wheatgrass sample set (Fig. 2b).

The standard errors of prediction in this study were similar to those reported by Okano et al (1983). The coefficient of variations for our studies were less than 3%, which is comparable to results reported by Mayland et al. (1993). They found a significant relationship between ash concentration and Δ in genotypes of crested wheatgrass (r = 0.69). Windham et al. (1991) reported that NIRS could be used to measure ash in forage, esophageal, and fecal samples. They also noted that ash concentration in their samples was related to spectral peaks of silicon dioxide. Clark et al. (1989) reported, however, that elemental silica estimations with NIRS were variable (coefficient of variations ranged from 11 to 33%) in alfalfa, crested wheatgrass, and tall fescue (*Festuca arundinacea* Schreb.).

In breeding programs for forage grasses, NIRS sometimes is used to identify breeding lines with high forage quality (Starr et al. 1981). Because the entire spectral scan is stored in the computer, breeding lines could be identified simultaneously for both forage quality and high water-use efficiency (low Δ) using proper calibration equations. For the 5 sample sets used for validation (Figs. 1-3), we identified 20% of the samples in each set that NIRS predicted would have low Δ values, and compared these

samples with actual Δ values determined by mass spectrometer analysis. We found that NIRS analysis agreed with between 77 and 82% of the reference values for these samples. In the early stages of a breeding program where the number of samples and costs prohibit analyses of Δ by mass spectrometry, this level of predictability may be acceptable. At more advanced phases of a breeding program, however, where there may be few samples and accurate Δ analysis is required, this level of predictability may not be acceptable.

In summary, NIRS may be useful in predicting Δ in both grass and alfalfa samples. This ability may be related to ash concentration (Mayland et al. 1993, Windham et al. 1991). Results from our study indicate that coefficient of variations for NIRS estimation of Δ generally are quite low and are only slightly higher than coefficient of variations obtained with an isotope ratioing mass spectrometer. Also, the NIRS method requires less time for analysis, costs less to purchase or maintain, and does not require technicians with considerable training and expertise in chemistry. As a result, for some applications, NIRS may be a suitable alternative for determining Δ.

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# Supplement and forage effects on fecal output estimates from an intra-ruminal marker device

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## Abstract

**Three experiments were conducted to evaluate effects of supplemental protein and forage on marker estimated fecal output using an intraruminal continuous release marker device in grazing steers. In experiment 1, twelve steers were assigned to 3 treatments and fecal collections were made during a 6-day period in December 1990 and again in February 1991. Treatments were: 1) range forage only, 2) range forage + 0.32 kg protein/day from a 70% soybean meal - 30% wheat pellet, and 3) range forage + 0.32 kg crude protein/day from 15.1% meadow hay. Fecal output estimates derived from the marker device were similar ($P>0.10$) for all treatments and both periods. Fecal estimates derived from the marker device were greater ($P<0.01$) than fecal output from total fecal collection (3.5 kg/day vs 2.7 kg/day); the correlation between estimates from fecal collection and the marker device was 0.85. In experiment 2, ten steers were assigned to treatments 1 and 2 of experiment 1 during December 1991. Fecal output derived from the marker device was similar ($P>0.10$) for the 2 supplement treatments. Fecal output estimates were greater ($P<0.10$) for the marker device than fecal collection (1.80 kg/day vs 11.63 kg/day); the correlation between estimates from the marker device and total collection was 0.94. In experiment 3, fecal output was derived from the marker device during three 5-day collection periods. Steers grazed upland range in July (green immature forage) and September (cured mature forage) and grazed subirrigated meadow (immature regrowth) in October. Fecal output estimates from the marker device were different ($P<0.05$) between collection periods, (e.g., forage sources). When compared to total fecal collection, the marker device underestimated fecal output on range in July ($P<0.01$, 2.1 kg/day vs 2.5 kg/day) and on meadow in October ($P<0.01$, 2.6 kg/day vs 3.5 kg/day). Correlations between the marker device and fecal collection were 0.93 in July and 0.99 in October, respectively. Estimates from the marker device and total fecal collection were similar ($P>0.10$; $r = 0.93$) on range in September. Protein supplements had no effect on fecal estimates derived from chromic oxide released from a marker device, but the marker estimates were affected by forage source. Correlation between fecal collection and the marker method is high; however, total fecal collection should be used to correct fecal output derived by the marker device for each forage source.**

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**Key Words: beef cattle, rangeland, pasture, intake, chromic oxide**

Estimates of fecal output and forage indigestibility have traditionally been used to predict intake in grazing ruminants. Therefore, an accurate estimate of fecal output is important. Chromic oxide has been a popular marker to estimate fecal output (Raleigh et al. 1980). Chromium has been mordanted to fiber (Uden et al. 1980), impregnated in paper (Kiesling et al. 1969), mixed in supplement (Hopper et al. 1978), and contained in a gelatin capsule (Prigge et al. 1981). The most recent and promising form of administration is the intra-ruminal controlled marker release device (Adams et al. 1991). The marker device has considerable potential for grazing animal research. It reduces labor associated with daily dosing and total fecal collection, allowing more animals to be used, which should increase accuracy and reduce variation.

The marker release rate associated with the device appears to be somewhat variable (Adams et al. 1991) and research with sheep indicates it may be affected by diet (Parker et al. 1989) or supplementation in confined sheep (Hatfield et al. 1991). Our objective was to determine if marker estimated fecal output, using the marker release device in cattle, was affected by forage type or protein supplementation in a grazing situation.

## Methods and Materials

Three experiments were conducted on range or subirrigated meadow. The range is generally a choppy sandhill site. Dominant grass species were blue grama [*Bouteloua gracilis* (H.B.K.) Lag. ex Giffiths], little bluestem [*Schizachyrium scoparium* (Michx.) Nash], prairie sandreed [*Calamovilfa longifolia* (Hook). Scribn.], sand bluestem (*Andropogon hallii* Hack.), switchgrass (*Panicum virgatum* L.), sandlovegrass [*Eragrostis trichodes* (Nutt.) Wood], and indiangrass [*Sorghastrum nutans* (L.) Nash]. Common forbs and shrubs included western ragweed (*Ambrosia psilostrachya* Dc.) and leadplant [*Amorpha canescens* (Nutt.) Pursh]. Subirrigated meadow soils were classified as Gannett-Loup fine sandy loam (coarse-loamy, mixed mesic Typic Haplaquoll). Dominant meadow vegetation was smooth bromegrass (*Bromus inermis* Leyss.) redtop (*Agrostis stolonifera* L.), timothy (*Phleum pratense* L.), slender wheatgrass [*Agropyron trachycaulum* (Link) Malte], quackgrass [*A. repens* (L.) Beauv.], Kentucky bluegrass (*Poa pratensis* L.), prairie cordgrass (*Spartina pectina-*

*ta* Link), and several species of sedges (*Carex* spp.), and rushes (*Juncus* spp. and *Eleocharis* spp.). Less abundant grass species were big bluestem (*Andropogon gerardii* Vitman), indiangrass [*Sorghastrum nutans* (L.) Nash], and switchgrass (*Panicum virgatum* L.). Legumes were a minor component of the vegetation.

In experiment 1, twelve steers (4 steers/treatment, average body wt = 273 kg) grazing winter range were randomly allotted to 3 treatments: 1) no supplement, 2) 1.2 kg•steer$^{-1}$•day$^{-1}$ of a 70% soybean meal:30% wheat pellet (37% crude protein), or 3) 2.2 kg•steer$^{-1}$•day$^{-1}$ of meadow hay supplement (15.1% crude protein). All steers were orally dosed with an intraruminal continuous marker release device[1] 5 days before 6-day fecal collection period. Total fecal collections were made using fecal collection bags and a once daily rectal grab sample of feces (300-500 g) was collected. Once daily sampling with the release device was considered sufficient based on fecal excretion pattern of chromium and of chromic oxide release rate from the marker release device reported in other studies (Ellis et al. 1981, 1982; Furnival et al. 1990a, 1990b; Brandyberry et al. 1991). The first collection period was 10 December through 15 December 1990, while the second collection was 5 February through 13 February 1991. Both collections were made in the same pasture of native Sandhills range at the Gudmundsen Sandhills Laboratory near Whitman, Nebr. At 0700 each morning, rectal grab samples were taken for chromium analysis and fecal bags were emptied, mixed, and subsampled for organic matter analysis. Fecal output from total collection and the marker device were compared with a split-split-split plot design. Supplement treatments were the main plot, collection periods were the subplot, day was the sub-sub plot, and fecal output from total collection and the marker device were the sub-sub-sub plot. Main plot was tested by steer(treatment), subplot by steer(treatment × period), sub-sub plot by steer × period × day (treatment), sub-sub-sub plot by the residual.

In experiment 2, ten steers (average body wt = 230 kg) grazing winter range (same site as in experiment 1) were randomly allotted to 2 treatments (5 steers/treatment): 1) no supplement and 2) 1.2•steer$^{-1}$•day$^{-1}$ of a 70% soybean meal:30% wheat pellet (37% crude protein). All steers were orally dosed with a marker release device 5 days before a 5-day fecal collection period. Rectal grab samples were taken for chromium analysis and total fecal collections were made as in experiment 1. Fecal collection began 11 December and ended 16 December 1991. Fecal output from fecal collection and from the marker device were compared with a split-split plot design. Supplement treatments were the main plot, day was the subplot, and fecal output from total collection and the marker device were the sub-sub plot. Main plot was tested by steer(treatment) and subplot by steer × day(treatment), and the sub-sub plot by the residual.

In experiment 3, eight nonsupplemented steers (average body wt = 400 kg) grazing Sandhills range or subirrigated meadow were orally dosed with a marker release device as in experiment 1 for three 5-day fecal collection periods. The 3 collection periods provided diets with different plants or maturity and different chemical composition (Table 1). Rectal grab samples were taken for chromium analysis and total fecal collections were made as in experiment 1 except that fecal bags were also emptied, mixed, and subsampled in the evenings, as well as mornings. The first collection was 9 July through 13 July 1991 on native summer Sandhills range. The second collection was 17 September through 21 September 1991 in the same pasture as the first collection when the forage was more mature. The third collection was 21 October through 26 October 1991 on subirrigated meadow. Fecal output from fecal collection bags and from the marker device were compared in a split-split plot design. Collection periods (i.e. source of forage) were the main plot, day was the subplot, and fecal output from total collection and the marker device were the sub-sub plot. Main plot was tested with steer(period), the sub plot by steer × day(period), and the sub-sub plot by the residual. Simple correlations between fecal output from total fecal collection and the marker device were determined in each experiment.

**Table 1. Neutral detergent fiber (NDF), acid detergent fiber (ADF), and crude protein (CP) content of meadow and range diets from 3 experiments.**

| | Forage | CP | NDF | ADF |
|---|---|---|---|---|
| | | ---- % of organic matter ---- | | |
| Experiment 1 | | | | |
| December 1990 | Range | 4.6 | 68.5 | 45.6 |
| February 1991 | Range | 6.8 | 64.9 | 49.5 |
| Experiment 2 | | | | |
| December 1991 | Range | 4.5 | 71.5 | 46.3 |
| Experiment 3 | | | | |
| July 1991 | Range | 8.2 | 67.4 | 39.5 |
| September 1991 | Range | 7.3 | 64.2 | 43.8 |
| October 1991 | Meadow | 11.2 | 51.7 | 42.5 |

One day during each fecal collection period of experiments 1, 2, and 3 forage diets were collected during a 30-45 minute grazing period from 8 esophageally-fistulated cows. Fecal samples were dried at 60° C and fistula-forage samples were freeze dried and ground in a Wiley Mill to pass a 1-mm screen. Fecal grab samples were prepared for chromium analysis as described by Williams et al. (1962) and chromium concentration as determined by atomic absorption spectroscopy. Dry matter and ash of fecal and fistula forage samples were determined by standard procedures (AOAC 1984). Extrusa samples were also analyzed for crude protein (AOAC 1984) and neutral detergent fiber (Goering and Van Soest 1970). Fecal output was determined by dividing the daily release of chromium of the marker release device (provided by the manufacturer) by the concentration of chromium in the feces.

## Results and Discussion

In experiment 1, the supplement treatment × period and day × supplement treatment interactions were nonsignificant ($P>0.10$). Daily fecal output estimates from total fecal collection and the marker device varied ($P<0.10$), but were consistently higher for the marker device than total fecal collection (Fig. 1). The correlation between the marker device and fecal collection methods was 0.85. Fecal output estimates averaged across 6-day collection periods from the marker device were similar ($P>0.10$) for supplement treatments and periods of December and February. The fecal output estimated by the marker device (3.49 kg/day) was higher ($P<0.01$) than that from total fecal collection (2.70 kg/day).

In experiment 2, day effects were significant ($P<0.10$), and the

[1]Captec Chrome manufactured by Captec Pty. Ltd., Australia, distributed internationally by Nufarm limited, Manu Street Otahunu, P.O. Box 22-407, Auckland 6, New Zealand.

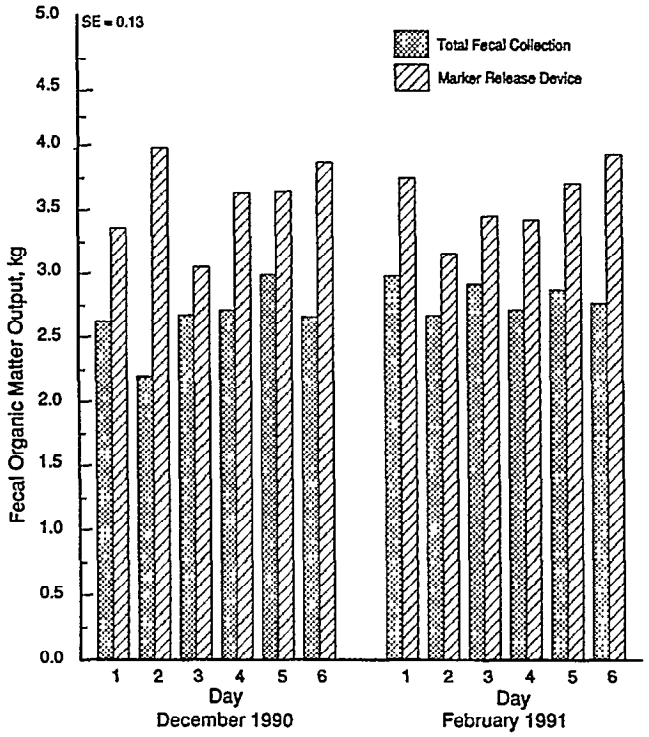


**Fig. 1. Daily organic matter fecal output and standard error (SE) estimated by total fecal collection and a continual marker release device from steers on 3 supplement treatments grazing Sandhills winter range during 2 collection periods in December and February (Experiment 1). Day effects were significant ($P<0.10$). Fecal output from marker release device was greater ($P<0.01$) than total fecal collection. Supplement, period, and supplement ÷ period interaction were not significant ($P>0.10$).**

day × supplement treatment interaction was non-significant ($P>0.10$). Fecal output estimates derived from the marker device (average of 5 days) were similar ($P>0.10$) for supplemented and non-supplemented steers. Fecal output estimated by the marker device (1.80 kg/day) was greater ($P<0.10$) than but highly correlated (r= 0.94) with that from total fecal collection (1.63 kg/day; Fig. 2).

In sheep trials, with a smaller but similar marker release device, Hatfield et al. (1991) found that supplemental barley affected fecal output estimates from the marker device in confinement, but not under grazing. For winter grazing trials, a need for multiple day sampling and adjustment of fecal output by total fecal collection are needed, but protein supplement effects on fecal output estimates appear to be insignificant.

In experiment 3, fecal collections were to be emptied once each 24 hours. However, after 24 hours on day one of fecal collections on range forage in July, fecal output was greater than collection bags would hold. Therefore, fecal bags were emptied at 12-hour intervals during experiment 3. Day one of July range data was not used in analysis.

In experiment 3, the day of collection × forage source interaction was significant ($P<0.01$). Fecal output by the marker device was lower ($P<0.01$) on native range in July (r=0.93) and on meadow in October (r= 0.99; Figs. 3 and 4) than total fecal collection. Total fecal output estimates from the marker device were similar ($P>0.10$) to estimates from total fecal collection on native

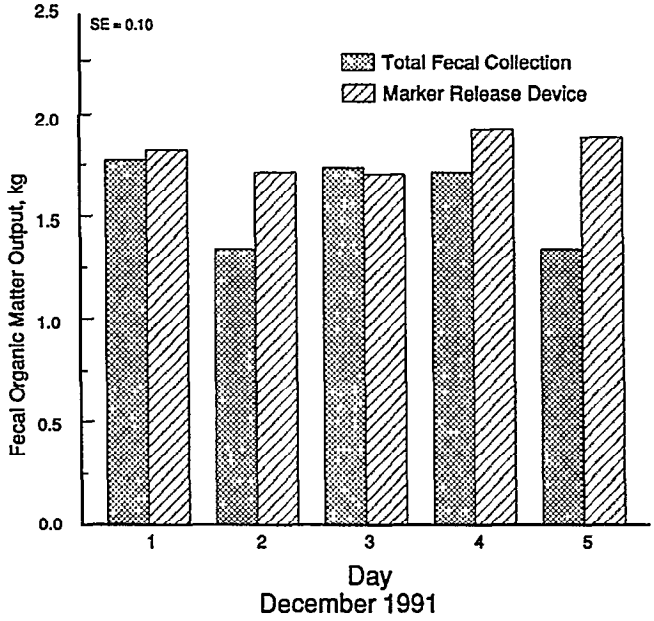


**Fig. 2. Daily organic matter fecal output and standard error (SE) estimated by total fecal collection and a continuous marker release device from steers on 2 supplement treatments grazing Sandhills winter range during December (Experiment 2). Day effects were significant ($P<0.10$). Fecal output from total fecal collection and marker release device differed ($P<0.10$).**

range in September (r=0.87). As in experiment 1, fecal output varied by day ($P<0.01$). During July and October experiments,

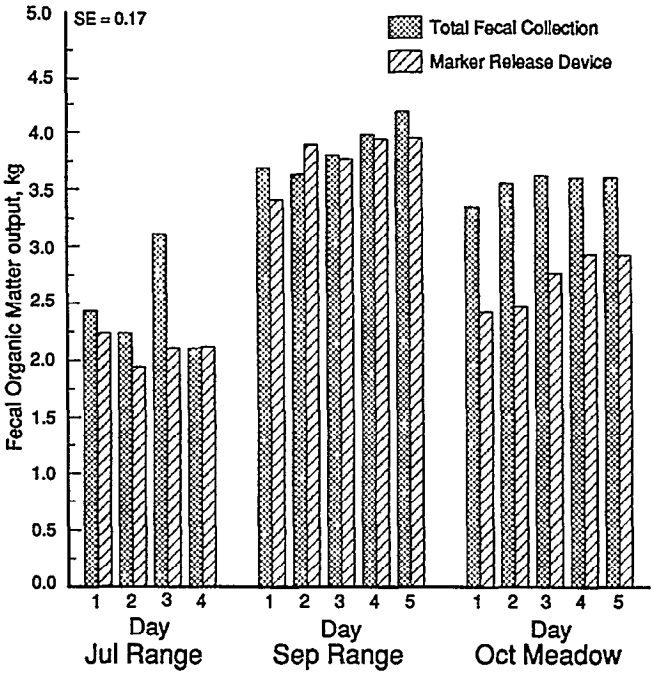


**Fig. 3. Daily organic matter fecal output and standard error (SE) estimated by total fecal collection and a continuous release marker device from steers grazing Sandhills range or subirrigated meadow during 4- 5-day collection periods (Experiment 3). Day × periods effect were significant ($P<0.01$).**

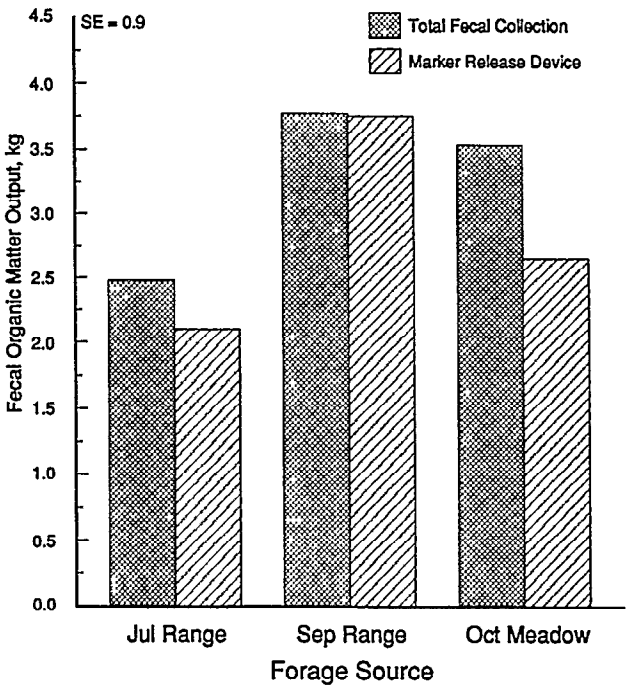


**Fig. 4. The effects of forage source on fecal output and standard error (SE) estimates from a continuous marker release device and total fecal collection averaged across 4- or 5-day collection periods (Experiment 3). Fecal output from a total fecal collection was greater ($P<0.01$) than fecal output from marker device for Jul. range and Oct. meadow. Fecal output for Sept. range was similar ($P>0.10$) for total fecal collection and marker device.**

daily fecal output was consistently lower for the maker device than for fecal collection (Fig. 3).

Our results are consistent with other studies. Using a smaller marker device in sheep fed 3 different forage diets in confinement, Parker et al. (1989) found small but significant differences in release of Cr between the 3 diets. Adams et al. (1991) observed differences between fecal output estimated by the marker device and total fecal collection for steers on native range, but found no differences between marker device estimates and total fecal collection in steers grazing fall wheatgrass pasture. In a confinement study with cattle, Pinchak and Hutcheson (1992) found that fecal estimates were similar for prairie hay and alfalfa hay. The results of experiment 3 indicate that changing forage source during the growing season necessitates comparing fecal output from the marker device to total fecal collection on a subset of animals for each grazing period or source of forage. Fecal output estimates by the marker device for experiments 1, 2, and 3 were corrected by multiplying fecal output from the marker device by a correction factor; the correction factor was fecal output from the marker device ÷ fecal output from total fecal collection. When the corrected fecal output estimates from the marker device were compared to total fecal collection by the statistical models described for each experiment in the materials and methods, no differences were detected ($P>0.10$) between the marker device and total fecal collection.

## Conclusions

For grazing cattle, we concluded that estimates of fecal output from the marker device were not influenced by supplementing winter range with protein. Estimates of fecal output by the marker device were affected by forage source (i.e., plant maturity, composition, etc.). We recommend that for each manufacturer's production batch of marker release devices and for each set of forage conditions the fecal output estimates from the marker device be corrected by total fecal collection and that multiple day collection be utilized. This conclusion is in agreement with recommendations by other researchers (Pinchak and Hutcheson 1992, Adams et al. 1991). If corrections are made for variation in manufacturers' batches and for forage conditions, the marker device for cattle appears to be a reliable method for obtaining estimates of fecal output in grazing trails.

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# Amino acid concentrations in seed of preferred forages of bobwhites

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## Abstract

**Nutritional factors have been hypothesized to regulate gallinaceous bird populations such as the Northern Bobwhite (*Colinus virginianus*). Although protein is considered one of the most important and limiting nutrient categories in wild animal populations, we lack a complete understanding of the availability of essential amino acids in foodstuff protein. Seed grains comprise a major component of the annual diet of bobwhites throughout its geographic range. We investigated the concentration of 17 amino acids in seed of 4 highly preferred forages of bobwhites from central Oklahoma. The total nitrogen content of seed was composed of 28-43% nonamino nitrogen of limited nutritional value. We provide evidence that crude protein may grossly over estimate true protein. Amino acid content of forages in lieu of crude protein may better describe the nutritional ecology of quail and other gallinaceous birds and provide new insights into the role of nutrition in regulating animal populations.**

**Key Words: *Colinus virginianus*, crude protein, nonamino nitrogen, nutrition**

Seed grains comprise a major component of the annual diet of bobwhite quail throughout its geographic range (Bookhout 1958, Robel and Slade 1965). Bobwhites show a distinct preference for seeds of wooly croton (*Croton capitatus* Michx.), common sunflower (*Helianthus annuus* L.), Florida paspalum (*Paspalum floridanum* Michx.), and western ragweed (*Ambrosia psilostachya* DC.) in rangelands of central Oklahoma (Baumgartner et al. 1952, Wiseman 1977, Rollins 1980, Tobler and Lewis 1981). Management practices have been developed to increase forage availability and diet quality for Northern Bobwhites (*Colinus virginianus*) (Wiseman and Lewis 1981, Webb and Guthery 1982). Although considerable efforts have been devoted to documenting crude protein in foods (Nestler et al. 1945, Newlon et al. 1964) and diets (Wood et al. 1986) of Northern Bobwhites, no attempts to document true protein concentration of food proteins and diets of bobwhites or other gallinaceous birds exist to our knowledge.

White (1978) proposed that available nitrogenous nutrients were the most limiting environmental resource to wild herbivore populations. Scarce quantities of digestible protein in plant material, high nitrogen requirements for reproduction, differential forage selectivity by individuals, and high juvenile mortality rates were offered as strong supporting evidence by White (1978). Because proteins vary considerably in amino acid composition, they also vary greatly in their nutritive quality. As a result, crude protein contents of diets may provide a poor index of protein quality (Sedinger 1984). Sedinger's (1984) analysis of amino acid concentrations in a variety of tundra plants used by geese indicated that crude protein determinations can overestimate true protein content by 22-52%. Many agricultural cereal grains and legumes also are poor sources of amino acids despite a high concentration of crude protein (Deyoe and Shellenberger 1965, Hang et al. 1980). We hypothesize that similar discrepancies exist with foods utilized by bobwhites, especially, given the high concentrations of nonamino nitrogen constituents found in many cultivated and weed seed grains (VanEtten et al. 1967, Holt and Sosulski 1981).

Although protein is thought to be one of the most important and limiting nutrients in wild populations, we unfortunately lack a complete understanding of its essential components, namely the amounts of essential amino acids. We choose to examine the quality of protein in seed from 4 ubiquitous plant species that are highly preferred and consumed in large amounts by bobwhites (Wood et al. 1986). Our primary objective was to document the amino acid composition in seed collected from central Oklahoma. We hypothesize that crude protein determinations may greatly overestimate true protein content of seed utilized by bobwhites.

## Methods

We examined seed of wooly croton, common sunflower, Florida paspalum, and western ragweed for variation in the quality of protein by profiling concentrations of their respective amino acids on the Cross Timbers Experimental Range, Payne County, Oklahoma (36°2' to 36°4'N, 97°9' to 97°11'W) located in the cross timbers land resource area (Garrison et al. 1977).

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Vegetation on the study area is similar to that of other areas in the cross timbers and is dominated by post oak (*Quercus stellata* Wang.) and black-jack oak (*Quercus marilandica* Muenchh.) in the overstory with interspersed tallgrass prairie (Ewing et al. 1984). Detailed descriptions of the study area have been previously published (Engle et al. 1991, Lochmiller et al. 1991, Stritzke et al. 1991).

All mature seeds of each species were harvested from approximately 100 plants on each of 4 different 32-ha sample plots from 13 September to 25 October 1990. Seeds of each species were pooled ($n = 1$) within each sample plot before laboratory analysis.

Seeds were separated from other plant material, cleaned by sieving, and composited by species and habitat type before further processing. Approximately 5-g subsamples were dried by lyophilization and ground to a fine powder using a micro-grinding mill. Fat content was assessed by ether-extraction using a Soxhlet apparatus (AOAC 1984). Total nitrogen was determined by micro-Kjeldahl analysis and converted to crude protein by multiplying the percent nitrogen by 6.25 (AOAC 1984).

Fat-extracted seed samples amounting to approximately 40 mg of protein were weighed into 25 × 150 mm glass tubes with teflon caps and hydrolyzed in 15 ml 6 N HCl under a nitrogen blanket at 110° C for 24 hours. One ml of the hydrolyzed sample was filtered through a 0.45-µm syringe filter[1]. Amino acids in the hydrolysates were precolumn derivatized with phenylisothiocynate and separated on a PICO:TAG reverse-phase column[2] (Cohen 1988). Derivatized amino acids were detected on-line spectrophotometrically and measured by comparing the area under the sample peak against that of an amino acid standard solution (Pierce H standard, Sigma Chemical) of known concentration. Concentrations of 17 individual amino acids were determined using high pressure liquid chromatography (HPLC). Tryptophan, an essential amino acid comprising about <1.0% of the total dry mass of seeds (Harrold and Nalewaja 1977), was destroyed by acid hydrolysis and therefore not measured. A casein reference protein[3] of known amino acid composition was hydrolyzed and analyzed along with seed samples. Sulfur-containing amino acid loss during acid hydrolysis (Spindler et al. 1984, Elkin and Griffith 1985) averaged 15% for methionine and 35% for cystine. Therefore methionine and cystine concentrations recovered were adjusted upward by 15 and 35% respectively. Amino acid concentrations were recorded as a relative proportion of the total amino acid content and on a dry mass basis.

Nonamino nitrogen concentrations in seed were a measure of the difference between amino acid nitrogen (HPLC analysis) and the total nitrogen (Kjeldahl analysis) contents. Nonamino nitrogen was assumed to be all nitrogen not incorporated into one of the amino acids recovered (HPLC analysis) and was assumed to be made up of a diverse group of compounds (Bell 1963, Synge 1963, Maynard et al. 1979). Unlike other measures of non-protein nitrogen (Holt and Sosulski 1981), we did not include free amino acids (those amino acids not bound to protein) that were recovered during HPLC analysis. Crude protein estimates were corrected (true protein + free amino acids) for nonamino nitrogen concentrations.

Differences in percent fat, crude protein, nonamino nitrogen, and amino acid concentration among plant species were tested by analysis of variance (PROC ANOVA, SAS 1988). We used the least significant differences test to isolate significant differences among means in the presence of a significant F-test ($P<0.05$).

[1]Acrodisc CRPTF, FIsher Scientific, Plano, Tex.
[2]Waters, Milford, Mass.
[3]Bovine milk, no. C-0376, Sigma Chem. Co., St. Louis Mo.

## Results

Variation in concentration of individual amino acids within a plant species was greater when expressed on a percent dry mass basis than relative percent of the total amino acid pool due to variation in percent crude protein (see SE in Tables 1 and 2). Crude protein differed ($P<0.01$) among all plant species and ranged from 5.1% for Florida paspalum to 16.3% for wooly croton (Table 1). Differences were also noted for concentration of fat among plant species ($P<0.01$); fat was lower in Florida paspalum than in other species and lower in western ragweed than in common sunflower.

Methionine and cystine were the least concentrated amino acids among seed species. Amino acid concentrations (% dry mass basis) ranged from 1.823 for glutamic acid to 0.011 for cystine. Amino acids were classified as essential or nonessential according to the NRC (1984) requirements. All essential and nonessential amino acids differed ($P<0.05$) among plant species when expressed as a relative percent of the total amino acid content (Table 1). This indicated that the quality of proteins as measured by the essential amino acid composition varied considerably among species. Differences in amino acids among plant species when expressed on a dry mass basis were less apparent (Table 2).

Whether the observed levels of the essential amino acids are adequate in meeting adult maintenance requirements can not be adequately determined because requirements for the nutrients have not been specifically determined for bobwhite quail. However, requirement information has been provided for a relat-

**Table 1. Mean ($n = 5$) percent fat, crude protein, and amino acid composition of wooly croton, Florida paspalum, western ragweed, common sunflower, and casein. Amino acids expressed as a percent of total amino acid.**

| Amino Acid | Croton | Paspalum | Ragweed | Sunflower | SE | Casein[1] |
|---|---|---|---|---|---|---|
| Fat % | 18.08$^{ab}$ | 0.60$^{c}$ | 14.73$^{b}$ | 20.14$^{a}$ | 1.88 | |
| Crude Protein % | 16.27$^{a}$ | 5.07$^{d}$ | 9.17$^{c}$ | 13.83$^{b}$ | 0.02 | 83.00 |
| Essential Amino Acids | | | | | | |
| Arginine | 9.47$^{a}$ | 3.66$^{c}$ | 6.72$^{b}$ | 6.28$^{b}$ | 0.31 | 3.94 |
| Histidine | 2.57$^{a}$ | 1.60$^{c}$ | 2.05$^{b}$ | 1.88$^{b}$ | 0.02 | 2.43 |
| Isoleucine | 4.93$^{a}$ | 4.30$^{b}$ | 4.78$^{a}$ | 4.92$^{a}$ | 0.02 | 4.82 |
| Leucine | 6.32$^{c}$ | 8.94$^{a}$ | 7.06$^{b}$ | 6.79$^{b}$ | 0.07 | 9.64 |
| Lysine | 4.69$^{a}$ | 3.53$^{b}$ | 4.31$^{ab}$ | 4.56$^{a}$ | 0.34 | 9.07 |
| Methionine | 1.32$^{a}$ | 0.71$^{b}$ | 0.53$^{b}$ | 0.84$^{b}$ | 0.04 | 2.69 |
| Phenylalanine | 4.08$^{b}$ | 5.32$^{a}$ | 3.85$^{b}$ | 3.88$^{b}$ | 0.14 | 4.32 |
| Threonine | 3.73$^{b}$ | 4.26$^{a}$ | 4.06$^{a}$ | 3.68$^{b}$ | 0.05 | 4.03 |
| Valine | 7.28$^{a}$ | 6.40$^{b}$ | 5.93$^{c}$ | 6.55$^{b}$ | 0.08 | 6.15 |
| Nonessential Amino Acids | | | | | | |
| Alanine | 6.91$^{b}$ | 12.98$^{a}$ | 6.79$^{b}$ | 6.75$^{b}$ | 0.21 | 3.27 |
| Aspartic acid | 11.10$^{a}$ | 8.86$^{b}$ | 10.83$^{a}$ | 10.08$^{ab}$ | 0.68 | 9.08 |
| Cystine | 0.34a | 0.13b | 0.33a | 0.15b | 0.01 | 0.00 |
| Glutamic acid | 14.70$^{b}$ | 15.72$^{b}$ | 19.28$^{a}$ | 18.88$^{a}$ | 1.33 | 19.29 |
| Glycine | 10.61$^{ab}$ | 7.09$^{c}$ | 9.48$^{b}$ | 11.87$^{a}$ | 0.88 | 2.37 |
| Proline | 5.61$^{c}$ | 8.20$^{a}$ | 6.48$^{b}$ | 6.29$^{b}$ | 0.11 | 9.08 |
| Serine | 3.94b | 5.83a | 6.00a | 4.48b | 0.46 | 5.09 |
| Tyrosine | 2.46a | 2.47ab | 1.52c | 2.12b | 0.05 | 4.74 |
| Total | 100.06 | 100.00 | 100.00 | 100.00 | | 100.01 |

[1]Reference protein ($n = 1$).
[a-c]Row means with same letters were not different ($P > 0.05$).

Table 2. Mean ($n$ = 5) amino acid composition of wooly croton, Florida paspalum, western ragweed, common sunflower, and casein. Amino acids expressed as a percent of dry mass basis.

| Amino Acid | Croton | Paspalum | Ragweed | Sunflower | SE | Casein[1] |
|---|---|---|---|---|---|---|
| Essential Amino Acids | | | | | | |
| Arginine | 1.285[a] | 0.223[b] | 0.690[b] | 0.717[b] | 0.278 | 0.374 |
| Histidine | 0.306[a] | 0.086[b] | 0.186[b] | 0.189[b] | 0.036 | 0.231 |
| Isoleucine | 0.497[a] | 0.197[b] | 0.366[ab] | 0.419[a] | 0.107 | 0.458 |
| Leucine | 0.637 | 0.408 | 0.545 | 0.580 | 0.148 | 0.916 |
| Lysine | 0.519[a] | 0.182[b] | 0.375[a] | 0.432[a] | 0.081 | 0.862 |
| Methionine | 0.162[a] | 0.037[b] | 0.047[b] | 0.081[ab] | 0.016 | 0.256 |
| Phenylalanine | 0.519 | 0.306 | 0.374 | 0.418 | 0.121 | 0.4103 |
| Threonine | 0.346 | 0.178 | 0.286 | 0.286 | 0.065 | 0.383 |
| Valine | 0.658[a] | 0.262[b] | 0.406[ab] | 0.497[ab] | 0.144 | 0.584 |
| Nonessential Amino Acids | | | | | | |
| Alanine | 0.473 | 0.399 | 0.356 | 0.392 | 0.116 | 0.234 |
| Aspartic acid | 1.121[a] | 0.412[b] | 0.842[a] | 0.866[a] | 0.216 | 0.863 |
| Cystine | 0.065[a] | 0.011[b] | 0.047[ab] | 0.026[b] | 0.001 | 0.00 |
| Glutamic acid | 1.673[a] | 0.805[b] | 1.682[a] | 1.823[a] | 0.465 | 1.833 |
| Glycine | 0.605[a] | 0.186[b] | 0.416[a] | 0.573[a] | 0.120 | 0.225 |
| Proline | 0.496 | 0.330 | 0.438 | 0.472 | 0.117 | 0.863 |
| Serine | 0.330 | 0.214 | 0.375 | 0.313 | 0.103 | 0.484 |
| Tyrosine | 0.346[a] | 0.157[b] | 0.165[b] | 0.249[ab] | 0.048 | 0.450 |
| Total | 10.10 | 4.39 | 7.60 | 8.33 | | 9.50 |

[1]Reference protein ($n$ = 5).
[ab]Row means with same letters were not different ($P$ > 0.05).

ed species the Japanese quail (NRC 1984). These requirements may be used for making general comparisons for adequacy of seeds meeting bobwhite quail requirements. Based on these comparisons it appears all seeds were deficient in the sulfur-containing amino acids with deficiencies for adult maintenance ranging from 45.9 to 88.6%.

Comparisons of the total nitrogen content (Kjeldahl analysis) to the amino acid nitrogen content (HPLC analysis) reveal that a substantial quantity of nitrogen was contained in nonamino nitrogen constituents (Table 3). Mean nonamino nitrogen values ranged from 27.74% for western ragweed to 47.56% for common sunflower, but were not different ($P$>0.05) among plant species. Crude protein concentrations adjusted for nonamino nitrogen yielded estimates of protein content well below crude protein. The calculated average conversion factor for adjusting Kjeldahl nitrogen values to more accurately reflect actual protein concentration was 3.96, compared with the standard of 6.25.

## Discussion

The nutritive value of nonamino nitrogen-containing compounds to quail is not entirely clear. Traditionally, nutritionists have used the rule-of-thumb of assigning half the nutritional value of protein nitrogen to nonamino nitrogen (Synge 1963). However, this is inconsistent because it apparently assumes the presence of nutritionally relevant free amino acids such as glycine, alanine, serine, glutamine, and others in the nonamino nitrogen category. We did not include these free amino acids as part of the nonamino nitrogen pool since they were measured (HPLC) as part of the total amino acid pool. The nonamino nitrogen can be used for synthesis of nonessential amino acids when essential amino acid requirements are met and crude protein

Table 3. Measure of total nitrogen (determined by Kjeldhal analysis) and amino nitrogen (HPLC amino acid analysis) in 4 important seed grains in the diet of bobwhites. The percentage of the total nitrogen pool recovered as amino nitrogen was calculated by difference and reported as nonamino nitrogen (% NAN). Correction factors for converting total nitrogen determinations (by Kjeldhal analysis) to protein estimates are provided.

| Plant | Kjeldhal Nitrogen | Amino Acid Nitrogen | NAN | Correction Factor | Adjusted CP |
|---|---|---|---|---|---|
| | (mg N/g DW) | (mg N/g DW) | (%) | | |
| Croton | 26.04±0.92 | 14.92±2.99 | 42.69±6.15 | 3.58 | 9.32±1.88 |
| Paspalum | 8.11±0.46 | 5.76±0.45 | 28.98±1.89 | 4.44 | 3.60±0.28 |
| Ragweed | 14.67±1.15 | 10.60±0.84 | 7.74±4.80 | 4.52 | 6.63±0.52 |
| Sunflower | 22.12±1.30 | 11.60±1.61 | 47.56±2.51 | 3.28 | 7.25±0.99 |

[1]Acrodisc CRPTF, Fisher Scientific, Plano, Tex.
[2]Waters, Milford, Mass.
[3]Bovine milk, no. C-0376, Sigma Chem. Co., St. Louis, Mo.

intake is low.

Conversion of Kjeldahl nitrogen to crude protein based on the traditional conversion factor of 6.25 appears to greatly overestimate the amount of true protein present in wild seed grains. The average conversion factor for adjusting Kjeldahl nitrogen determinations to reflect true protein concentration in our study was 3.96.

Digestibility of dietary protein is another important factor that can drastically influence protein requirements and the ability of certain protein sources to meet these requirements (Owens and Pettigrew 1989). Digestibilities of seed from many wild plant species used by bobwhites range from 40 to 90% (Robel et al. 1979). Both nonamino nitrogen and protein digestibility undoubtedly act in concert to reduce the overall nutritional value of nitrogen and distort the usefulness of crude protein as a measure for determining the adequacy of foods in meeting daily protein requirements.

A solution to the problems associated with assessing protein quality in diets is to compare essential amino acid composition of foods to dietary requirements. Dietary protein and essential amino acid requirements are usually determined experimentally using purified protein sources to formulate rations (with amino acid supplements) with a known essential amino acid composition (Allen and Young 1980, Serafin 1982). Nonamino nitrogen composition in purified protein sources, such as isolated soybean meal protein or casein, would normally be low compared to the whole food source (Bell 1963). Given the large and highly variable concentrations of nonamino nitrogen in wild seed grains compared to purified protein sources and specific dietary requirements for essential amino acids, profiles of concentrations of essential amino acids would provide a more accurate determination of forage quality.

These results highlight important concerns in the use of measures such as crude protein to assess the nutritional quality of common Northern Bobwhite foods, as well as foods of other gallinaceous birds. Because animals have dietary requirements for individual amino acids rather than protein, protein estimates should probably be used as an index of nutritive quality only and not used to assess the ability of particular forages or diets to meet nutrient intake requirements of birds. Failure of previous studies (Roseberry and Klimstra 1984) to find any significant relationships between dietary protein estimates and various intrinsic characteristics of populations (e.g., density, survival rates,

recruitment rates) could have been due in part to the inherent inaccuracies associated with measures of crude protein.

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# Spotted knapweed seed viability after passing through sheep and mule deer

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## Abstract

**Spotted knapweed (*Centaurea maculosa* Lam.), an introduced perennial plant, has invaded large areas of rangeland in the northwestern United States. Grazing animals may disseminate the weed by transporting seeds in their digestive system and depositing them in their feces. In this study percent viability and emergence of spotted knapweed seeds that passed through mule deer (*Odocoileus hemionus hemionus*) and sheep (*Ovis aries*) were determined. Percent viability included seeds that germinated and seeds that tested positive with tetrazolium. In the first trial, we pulse dosed 3 mule deer and 4 ewes with 5,000 spotted knapweed seeds each. Seed recovered from manure collected daily for 10 days after dosing was tested for percent viability. We recovered 11% of the knapweed seeds from the 3 mule deer, and 4% from the sheep. Based on high variability in (0 to 26%) percent viability of recovered seed, we thought that our drying the manure at 50°C may have killed some of the spotted knapweed embryos. To determine if drying at 50°C affected viability, we pulse dosed 4 rams with 5,000 spotted knapweed seeds each in a second trial. One subsample of manure was washed the same day to recover seeds and then dried at 35°C, a second subsample was dried at 50°C, washed, and then dried at 35°C. We recovered 17% of the spotted knapweed seeds from the 4 rams. No viable seeds were recovered from manure heated at 50°C, and no viable seeds were recovered more than 2 days after dosing. Percent viability of seeds recovered from manure dried at 35°C ranged from 0 to 22%. In both trials, percent viability of recovered seeds was lower compared with seeds that did not pass through animals. Sheep and mule deer can ingest, transport, and disseminate viable seeds of spotted knapweed in their feces.**

Key Words: *Centaurea maculosa,* weed, seed, rangeland, dispersal

Spotted knapweed (*Centaurea maculosa* Lam.) is a perennial plant introduced from Europe that has infested over 2.9 million ha in 9 states and 2 Canadian provinces in western North America (Lacey 1989). Although this noxious weed can be controlled with chemicals, widespread use of herbicides may be undesirable or infeasible over vast areas of native rangeland (Griffith and Lacey 1991). Weed scientists and land managers now recommend an integrated weed management approach, which includes grazing when and where appropriate to control noxious range weeds. Grazing weeds with livestock is appealing because it provides weed control and income to the landowner.

Seeds of many forage plants are consumed by grazing animals. While seeds can be destroyed by mastication and digestion (Atkeson et al. 1934, Thill et al. 1986), some pass through grazing animals. Using livestock to introduce desirable forage seed to new areas, or areas inaccessible to conventional seeding equipment has been recommended (Dore and Raymond 1942, Archer and Pyke 1991, Gardener et al. 1993), however, dispersing weed seed with livestock would be undesirable (Harmon and Keim 1934, Heady 1954, Lehrer and Tisdale 1956, Piggin 1978, Lacey et al. 1992).

Our objective was to determine if sheep (*Ovis aries*) and mule deer (*Odocoileus hemionus hemionus*) could disseminate spotted knapweed seed. Specifically we determined 1) seed passage, 2) percent viability of spotted knapweed seed after passing through digestive tracts, and 3) emergence of passed seed.

## Materials and Methods

### Trial 1

We collected mature spotted knapweed seeds at an infested site near Bozeman, Mont. Ten lots of 1,000 seeds were weighed to determine the mean weight of 5,000 seeds (8.38 g). Eight lots of 8.38 g of seed were placed into vials. Four tame mule deer and 4 sheep were penned individually at Utah State University. One deer was unable to adjust to the small pen and was removed from the study. Animals were fed 70 g rolled barley and alfalfa pellets ad libitum daily during the trial, beginning 7 days before they were pulse dosed with 8.38 g of spotted knapweed seeds mixed with the barley. A small amount of molasses was added to bind the knapweed seeds to the barley. Each animal was observed to ensure that all spotted knapweed seeds were consumed. Manure was collected from each animal, and oven-dried at 50°C daily for 10 days after dosing. After drying, manure samples were trans-

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ported to Montana State University. Some samples contained enough moisture to support active fungal growth when the samples arrived in Bozeman, thus all samples were redried at 50°C for 24 to 48 hours.

Each manure sample was thoroughly mixed, weighed and divided in half. One half was passed through a roller mill to crush pellets, washed through #10 (2 mm) and #30 (0.58 mm) sieves, and dried at 37°C. Spotted knapweed seeds were hand collected, counted and compared with unfed seeds for percent viability.

Two small subsamples (approximately 35 g) were taken from the second half of each manure sample and weighed. One subsample was placed on the surface of moist potting soil in a small flat. The second subsample was lightly crushed with a mortar and pestle, to simulate decomposing manure, before it was placed on potting soil. Ten controls were prepared at the same time, each with 40 unfed seeds placed on moist potting soil. All flats were randomly located in a greenhouse and misted daily for 5 weeks. Seedlings that emerged were counted and removed. To encourage additional germination, these flats were then placed in a vernalization chamber and moist stratified (4°C, 12 hours light/dark) for 10 weeks. After stratification, flats were returned to the greenhouse and misted daily for 10 weeks. Seedlings that emerged were counted and removed.

### Trial 2

Results from Trial 1 indicated that oven drying at 50°C may have affected the viability of some of the spotted knapweed embryos. A second trial was conducted to determine the effect of oven drying at 50°C on percent viability of spotted knapweed seeds after dosing and then passing through sheep. Spotted knapweed seeds were collected from the same area as for Trial 1 near Bozeman, Mont. All herbaceous material was removed and 10 lots of 500 seeds were weighed to estimate the weight of 5,000 seeds (8.68 g). Four lots of this weight were separated.

Four 2-year old Rambouillet rams were penned individually at the O.O. Thomas Nutrition Center at Montana State University. Animals were fed 2.5 kg of alfalfa pellets and 70 g cracked barley daily during the trial, beginning 1 week before they were pulse dosed with 8.68 g of spotted knapweed seeds bound with molasses to the barley. After dosing, manure was collected daily for the next 10 days. The manure was separated into 4 subsamples and weighed daily. One subsample was washed over sieves as described above, and immediately oven-dried at 35°C. The second subsample was first oven-dried at 50°C, washed over sieves, and then oven-dried at 35°C. Seeds recovered from the first 2 subsamples were tested for percent viability. The third subsample was oven dried and reweighed to determine moisture content of the fresh manure. To determine seedling emergence, the fourth subsample was placed directly on moist potting soil in a greenhouse and misted daily for 1 month. Five controls were established at the same time as these subsamples. In each control, 40 spotted knapweed seeds were placed directly on moist potting soil and misted daily. In this trial, no seedlings emerged from the manure samples after 1 month so the experiment was terminated.

### Percent Viability

Seeds were soaked in 10% (v/v) chlorine bleach solution for 10 minutes and rinsed 3 times with distilled water before testing for percent viability. Unfed seeds served as a control and were tested at the same time. From 1 to 100 seeds were tested depending on the number of seeds recovered. When possible seeds recovered daily from each subsample were divided into 5 groups to estimate variance of percent viability. We placed up to 20 seeds on moistened blotter paper in petri plates. Petri plates were placed in an uncovered box in a greenhouse with day and night temperatures of 21°C and 13°C, respectively. Distilled water was added as needed. Germinated seeds (radicles $\geq$ 5 mm) were counted every other day and removed. A 2 week germination period was followed by 1 month in cold moist storage (4°C) and a second 2 week germination test in the greenhouse. After the second germination test, seeds that did not germinate were tested for viability using a 0.1% unbuffered tetrazolium solution (Grabe 1970). Percent viability included seeds that germinated and seeds that tested positive with tetrazolium.

### Statistical Analyses

In Trial 1, repeated measures analysis of variance was used to determine the effect of animal species (deer or sheep) and day after dosing on the number of seeds recovered in manure (SAS 1988). Each animal was considered an experimental unit ($n = 3$ and $n = 4$ for deer and sheep respectively). The number of recovered seeds was the dependent variable in the repeated measures analysis of variance. Number of recovered spotted knapweed seeds was calculated by multiplying the number of recovered seeds from each animal each day by 2 (50% of the manure was washed to recover seed). Percent viability and estimated number of viable seeds were not analyzed because as the trial proceeded 1-3 sheep did not pass seed, and therefore percent viability could not be tested, and because the estimated number of viable seeds was a derived variable.

After determining sample variances of seed recovered, the ratio of sheep and deer variances exceeded the critical value of the Fmax test, thus these data were transformed [log 10 (# seed recovered + 1)] (Sokal and Rohlf 1981). Nontransformed means and standard errors are presented in tables. Numbers of seeds recovered each day were compared with the number recovered on day 2 because it was the first day that seeds were recovered from all of the animals. Probability levels are presented in the results (Gill 1981).

In Trial 2, repeated measures analysis of variance was used to determine the effect of day after dosing on the number of seeds recovered in manure (SAS 1988). The number of recovered seed from the 2 washed subsamples of manure were multiplied by the ratio of the total weight of manure relative to the sum of the weights of the 2 washed subsamples of manure. Similar to Trial 1, each ram was an experimental unit, and the number of recovered seeds was the dependent variable in the repeated measures analysis of variance.

## Results

### Seed Passage

We recovered 11% of the 5,000 knapweed seeds from 3 mule deer and 4% from the 4 sheep by the end of Trial 1. By the fifth day after pulse dosing, 84% and 89% of the recovered seeds had passed through the deer and sheep, respectively (Table 1, 2). We did not recover any seeds from 2 of the deer on day 1. The number of seeds recovered from both species declined over the 10 day period after dosing ($P < 0.03$), however the deer were still pass-

Table 1. Number of spotted knapweed seeds recovered, percent viability, and estimated number of viable seeds recovered from manure of 3 mule deer 10 days after dosing in Trial 1. Percent viability of control seeds = 98% ± 1.22 (SE). Percent viability included germinated seeds and seeds that tested positive with tetrazolium. Estimated number of viable seeds recovered was derived by multiplying the number of seeds recovered by percent viability. Values following means represent ± 1 SE.

| Day after ingestion | Seeds recovered | Viability | Estimated viable seeds |
|---|---|---|---|
| | (No.) | (%) | (No.) |
| 1 | 161 ± 161 | 11.5[1] | 18.5 |
| 2 | 134 ± 84 | 2.3 ± 2.3 | 3.1 |
| 3 | 89 ± 75 | 4.5 ± 2.9 | 4.0 |
| 4 | 38 ± 36 | 5.5 ± 5.5 | 2.1 |
| 5 | 27 ± 15 | 17.0 ± 0.8 | 4.6 |
| 6 | 11 ± 3 | 4.2 ± 4.2 | 0.5 |
| 7 | 6 ± 3 | 12.2 ± 6.2 | 0.7 |
| 8 | 14 ± 12 | 2.3 ± 2.3 | 0.3 |
| 9 | 19 ± 15 | 4.8 ± 4.8 | 0.9 |
| 10 | 35 ± 17 | 24.5 ± 12.8 | 8.5 |

[1]SEM was not calculated because seeds were recovered from only 1 animal.

Table 2. Number of spotted knapweed seeds recovered, percent viability, and estimated number of viable seeds recovered from manure of 4 sheep 10 days after dosing in Trial 1. Percent viability of control seeds = 98% ± 1.22 (SE). Percent viability included germinated seeds and seeds that tested positive with tetrazolium. Estimated number of viable seeds recovered was derived by multiplying the number of seeds recovered by percent viability. Values following means represent ± 1 SE.

| Day after ingestion | Seeds recovered | Viability | Estimated viable seeds |
|---|---|---|---|
| | (No.) | (%) | (No.) |
| 1 | 52 ± 20 | 14 ± 12 | 7.0 |
| 2 | 67 ± 36 | 0 | 0 |
| 3 | 29 ± 20 | 26 ± 15 | 7.4 |
| 4 | 16 ± 8 | 0.9 ± 0.9 | 0.1 |
| 5 | 13 ± 11 | 6 ± 6 | 0.7 |
| 6 | 7 ± 7 | 0 | 0 |
| 7 | 6 ± 5 | 2 ± 2 | 0.9 |
| 8 | 6 ± 4 | 0 | 0 |
| 9 | 2 ± 2 | 0 | 0 |
| 10 | 2 ± 1 | 0 | 0 |

ing numerous viable seed when the trial ended on day 10. Numbers of seeds recovered on day 4-10 were lower than the number of seeds recovered on day 2 ($P < 0.10$ for all comparisons).

We recovered 17% of the 5,000 spotted knapweed seeds in Trial 2. By the fifth day after dosing, we had recovered 99.5% of the seeds that passed (Table 3). Recovery of seeds decreased over time after dosing ($P < 0.001$).

### Percent Viability

In Trial 1, percent viability of seeds recovered from mule deer (2–25%) and sheep (0–26%) manure was much lower than of the control seeds (98%). We recovered viable seeds from deer manure each day for the 10 day period after dosing. Viable seeds were not recovered from sheep after day 7. In Trial 2, seeds recovered from the manure dried at 50°C did not germinate and did not test positive with tetrazolium. Embryos recovered from seed in manure dried at this temperature were brown, and had a rubber-like texture when they were placed in tetrazolium. Embryos of control seeds were white with a firm texture.

In Trial 2, percent viability of seeds recovered from sheep manure dried at 35°C (0–22%) was lower compared with seeds which were not fed to sheep (88%). Although some seeds were still being recovered on day 10, seeds recovered after day 2 were not viable. Cotyledons from 4 seeds recovered 1 day after dosing developed, but their radicles did not, and thus they were classified as not viable. With tetrazolium, some cotyledons stained red whereas the associated radicle did not stain red, indicating that the radicle was dead.

### Emergence

Few seedlings emerged from the manure placed on moist potting soil in Trial 1. From the manure of 1 deer, 5 and 10 spotted knapweed seedlings emerged from uncrushed and crushed manure, respectively. From another deer, 5 knapweed seedlings emerged from crushed manure, while only 1 seedling emerged from uncrushed manure. No seedlings emerged from sheep manure. With unfed seed, 92.7% (±1.83 S.E.) of the seeds established from soil.

No spotted knapweed plants emerged from any of the manure samples during the 1 month test period in Trial 2. With unfed seed, 42% (±3.90 S.E.) of the seeds established from soil.

## Discussion

In both trials, over 84% of the excreted knapweed seeds were recovered within 5 days of dosing. With jointed goatgrass (*Aegilops cylindrica* Host), the number of joints recovered from the rumen decreases approximately 80% 48 hours after being fed to cattle (Lyon et al. 1992). The recovery of leafy spurge (*Euphorbia esula* L.) seeds in manure of sheep and goats also decreases over time (Lacey et al. 1992). Nonetheless, we were still recovering viable spotted knapweed seed in the deer manure when we ended Trial 1 after 10 days. Janzen (1981) found seeds of the guanacaste tree (*Enterolobium cyclocarpum* (Jacq.) Griseb.) in horse manure 70 days after the seeds were ingested.

Morphophysiological differences between sheep and deer may result in different residence times of seeds within the rumen. Hofmann (1989) characterized sheep as animals that consume grass and roughage, that graze for relatively long periods, and that ruminate for long periods during which forage is repeatedly chewed. Long ruminating periods may enhance seed destruction. Hofmann (1989) described mule deer as intermediate feeders, animals that mix grass and roughage with more concentrated feed represented by forbs and shrubs. By consuming less roughage, mule deer should ruminate less and thus pass more seed, which they did. However, they were continuing to pass seed 10 days after dosing, indicating that some of the seed may have been temporarily caught in folds within the reticulo-rumen, and are then released at sporadic intervals. Despite this long residence time, percent viability of seeds that were excreted in the latter days of the trial was no lower than percent viability of seeds that had passed through the gastrointestinal tract during the first three days.

Table 3. Number of spotted knapweed seeds recovered, percent viability, and estimated number of viable seeds recovered from washed subsamples of manure from 4 rams 10 days after dosing in Trial 2. Percent viability of control seeds = 88% ± 6.2 (SE). Percent viability included germinated seeds and seeds that tested positive with tetrazolium. Estimated number of viable seeds recovered was derived by multiplying the number of seeds recovered by percent viability. Values following means represent ± 1 SE.

| Day after ingestion | Seeds recovered | Viability | Estimated viable seeds |
|---|---|---|---|
| | (No.) | (%) | (No.) |
| 1 | 430 ± 46 | 22 ± 2 | 93 |
| 2 | 282 ± 27 | 0.3 ± 0.3 | 0.9 |
| 3 | 91 ± 19 | 0 | 0 |
| 4 | 26 ± 5 | 0 | 0 |
| 5 | 9 ± 3 | 0 | 0 |
| 6 | 1 ± 1 | 0 | 0 |
| 7 | 0 | 0 | 0 |
| 8 | 1 ± 1 | 0 | 0 |
| 9 | 1 ± 1 | 0 | 0 |
| 10 | 1 ± 1 | 0 | 0 |

### Percent Viability

Initially, we thought that the viability of recovered seed from Trial 1 had been reduced by drying the manure samples at 50°C. Thus, in the second trial we compared oven drying at 50°C with drying at 35°C. Drying manure at 50°C in Trial 2 killed embryos of spotted knapweed seed. Embryos of these seeds were darker than embryos of unfed, unheated seed. However, viability of seed recovered from manure dried at 50°C in Trial 1 was similar to the viability of seed recovered from manure dried at 35°C in Trial 2. Apparently, drying at 50°C in Trial 1 had minimal effect on viability whereas it had a significant effect in Trial 2. These different responses could be attributed to water content of the manure, the length of time that the manure was stored before complete drying thereby allowing imbibition, or a combination of these factors.

Davis (1990) showed that seeds of spotted knapweed are fully imbibed after 13 hours and germinate within 18 hours. While dry seeds withstand heating to 50°C, imbibition and initiation of germination may be interrupted at high temperatures (Bradbeer 1988). The dark color of the embryos of recovered seeds in Trial 2 may have been due to the enzymes or proteins that were destroyed when the manure was heated at 50°C.

Viable seeds were recovered in deer manure 10 days after dosing, but few were recovered from sheep manure after 3 days. Workers collecting the manure observed that most of the deer feces were pellets whereas the sheep feces were patties. This indicates that deer feces were drier than sheep feces, therefore less moisture was available for knapweed seed imbibition. Oven drying may not kill unimbibed, or incompletely imbibed seeds.

Spotted knapweed seeds were not viable after 7 days inside the gastrointestinal system of sheep in Trial 1, whereas they were not viable after only 2 days in Trial 2. Blackshaw and Rode (1991) found that weed seeds are able to survive for a short period of time in the rumen but viability drops off rapidly. The period of exposure in the rumen varies for different weed species. They suggested that there may be a lag before rumen fluids degrade the embryo; however, this would not explain the viability of seed recovered from deer throughout the 10 day trial.

### Emergence

In Trial 1, the manure was dried and stored for several months before it was placed on potting soil to test for emergence, which may have induced dormancy in the seed (Bradbeer 1988). More seedlings established from mule deer manure compared with sheep manure, which agrees with the greater number of seeds that passed through deer.

The lack of seedling emergence from manure placed on potting soil in Trial 2 may have been partly due to the plywood floors in the pens since urine was mixed with fecal material, which does not normally occur in the field. Excessive urine in the manure may have affected the emergence of spotted knapweed seedlings. Overall, emergence from these trials may not represent field conditions. By misting the flats daily in a greenhouse that only varied 8°C, we did not replicate moisture or temperature conditions that can fluctuate widely in the field, which can enhance germination (Bradbeer 1988).

## Conclusions

Viable spotted knapweed seeds passed through the digestive systems of sheep and deer. Sheep manure contained viable spotted knapweed seeds up to 7 days after dosing in Trial 1. In the second trial, viable spotted knapweed seeds were found for only 2 days after dosing. From mule deer, we continued to recover viable seeds from their manure 10 days after dosing. Viability of seeds was reduced, but not eliminated, by passing through sheep and mule deer. Although few spotted knapweed seeds emerged from manure in the greenhouse, we believe that sheep and especially mule deer are likely to transport viable seeds of spotted knapweed and thus disseminate weed seeds. Managers cannot control the movements of deer, but can control the movements of sheep. Based on our 2 trials, we recommend that sheep be confined for at least 7 days after grazing a spotted knapweed infested area to allow viable seed to pass.

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# Measurements of water use by prairie grasses with heat balance sap flow gauges

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## Abstract

**Direct and continuous measurements of water use by range grasses are needed by both range scientists and land managers. This study tested a heat balance sap flow gauge on individual culms of the tallgrass prairie species big bluestem (*Andropogon gerardii* Vitman) and indiangrass [*Sorghastrum nutans* (L.) Nash]. Gauge performance was evaluated on potted plants in the laboratory, greenhouse, and field by comparing sap flow to gravimetric measurements of transpiration. In the laboratory, gauge-measured water loss was consistently within ±10% of gravimetric measurements for both species at flow rates ≤ 4 g hour$^{-1}$. The first-order time constant of the gauge was calculated to be <20 seconds. In the greenhouse, sap flow estimates were consistently below gravimetric water loss and negative flows were often computed because of suspected errors in the radial heat flux component. Laboratory data showed that despite the gauge being surrounded with insulation, errors in the heat balance could occur because of external air temperature changes. In the field, environmental alterations in the stem energy balance affected the accuracy of gauges placed outside a plant canopy, but accurate measurements did occur when the plants were placed within a plant canopy. Heat transfer analysis indicated that foam insulation should be 20 to 25 mm thick to minimize the effect of the environment on gauge performance.**

**Key Words: big bluestem, indiangrass, energy balance, heat flux**

The central role of plant- and soil-water relations in rangeland ecosystems has long been recognized by both scientists and land managers (Brown 1977). Forage plant breeders often evaluate plant water use in response to drought as a criterion in species selection programs (Johnson and Asay 1993), and removal of woody species often is prescribed by land managers to enhance soil water availability for grass species (Griffin and McCarl 1989). However, commonly used methods of measuring or estimating range-plant water use, such as porometers (Ansley et al. 1991), lysimeters (Parton et al. 1981, Wight and Hanson 1990), or evapotranspiration models (Massman 1992, Stannard 1993) do not provide information on transpiration from whole plants. Only with the recent development of sap flow gauge technology has water use by a rangeland shrub been measured directly and continuously under field conditions (Dugas and Mayeux 1991, Dugas et al. 1992).

In general, the use of sap flow gauges has been almost entirely restricted to large dicots (Fichtner and Schulze 1990, Ham and Heilman 1991, Steinberg et al. 1991, Groot and King 1992). Far fewer studies have been reported using sap flow gauges on grass species, and these have been limited to larger agronomic species like corn (*Zea mays* L.) (Gavloski et al. 1992). Only Sakuratani (1979, 1990) has reported sap flow measurements on a small cereal, rice (*Oryza sativa* L.), but the gauge used was not removable and had to be built directly on the plant stem. No studies document the use of sap flow gauges on rangeland grass species. A removable sap flow gauge has been designed that can accommodate the small diameter and often irregular shaped stems of native grasses (Senock and Ham 1993). The objective of this study was to test and validate this new gauge design for use on prairie grasses and assess the utility or value of this gauge for use on rangelands.

## Materials and Methods

Sap flow gauges used in the study had the same basic components described by Baker and van Bavel (1987), which included a thin-film electrical resistance heater, 2 thermojunctions (copper-constantan) each located above and below the heater, a 10-junction thermopile, and cork-neoprene gasket material to which the components are attached (Fig. 1a). Details on the design of the major components for a gauge configuration adapted for small plant stems can be found in Senock and Ham (1993). The gauge surrounds a small portion of plant stem (Fig. 1b), is covered with foam insulation and is held in place with plastic clips (Fig. 1c). The gauges are connected to a datalogger to record the analog voltage outputs.

Use of the gauges to measure sap flow is based on the steady state energy balance of a heated portion of plant stem defined as

$$Q = Q_r + Q_v + Q_f + S \quad (1)$$

where each component is a heat flux (watts, W) calculated from appropriate equations describing heat flow within the system. Indepth discussions regarding gauge theory and the mathematical equations involved are provided by Sakuratani (1979, 1981). For clarity in the discussion of the results from this study, the equations for each heat flux will be briefly presented.

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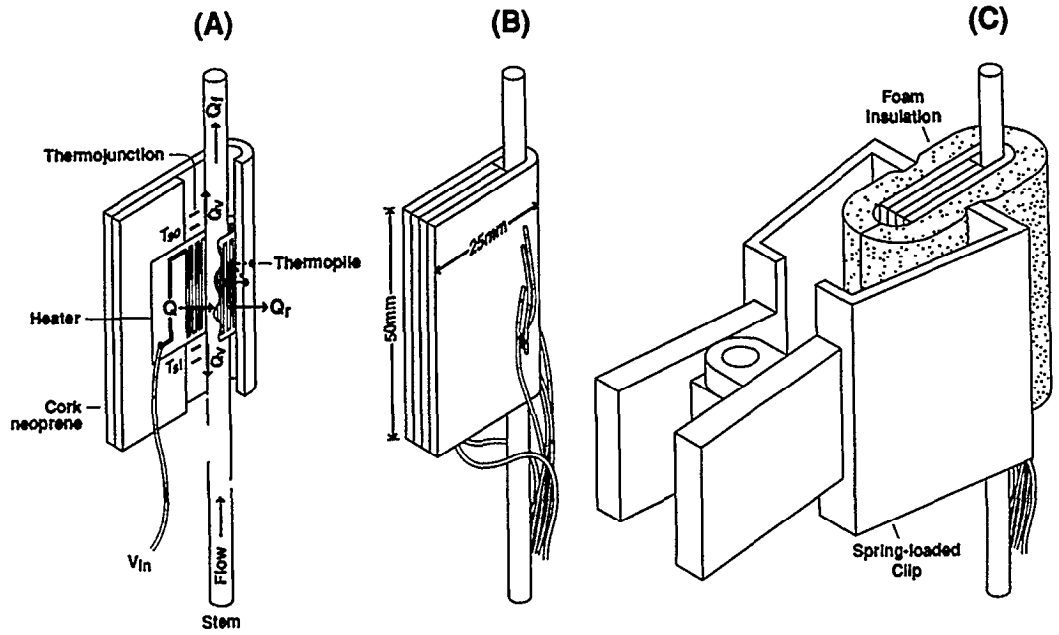


**Fig. 1. Schematic diagram of the sap flow gauge used in the study. Multiple views depict: (A) gauge components and associated heat fluxes, $Q$ = power input, $Q_f$ = convective heat flux, $Q_r$ = radial heat flux, $Q_v$ = axial heat flux, and $T_{so}$-$T_{si}$ = system temperature; (B) the U-shaped configuration when in place on the plant stem; (C) gauge appearance on the plant stem when covered with foam insulation and secured with a spring-loaded plastic clip.**

The total power, $Q$, is applied to the stem segment by the thin-film heater (Fig. 1a) and is calculated from the input voltage ($V$) and the resistance ($R$) of the heater ($Q = V^2/R$). For grasses with small stem diameters, $V$ ranges from 1.0-2.0 volts, $R$ ranges from 45-50 ohms, and $Q$ ranges from 0.02-0.08 Watts. The radial heat flux, $Q_r$, is the product of the radial temperature gradient ($E$) as measured with the thermopile (Fig. 1a) and the thermal conductivity ($K_g$) of the gauge ($Q_r = K_g \cdot E$). Values of $K_g$ typically range from 0.3-0.7 Watts/V and can be estimated from data during periods of minimal flow such as during the predawn hours (Steinberg et al. 1989, Senock and Ham 1993). The axial heat flux, $Q_v$, is determined from the stem thermal conductivity ($K_{st}$), the cross-sectional area of the stem ($A$), and the temperature gradient up and down ($\Delta T/\Delta X$) the stem surface ($Q_v = K_{st} \cdot A \cdot (\Delta T/\Delta X)$). Typical values of $K_{st}$ are in the range 0.40-0.60 Watts $m^{-1}$ $K^{-1}$ which Sakuratani (1984) calculated from the sum total of the products of conductivity for cellulose, water, and air and their fractional volumes in the plant stem. The variable $A$ represents the stem cross-sectional area ($m^2$) that can conduct heat, which would include epidermal, cortex, and vascular tissues. For many range grasses, the lower portion of culm that is surrounded by the gauge will be either hollow or semisolid (Gould and Shaw 1983). In determining the appropriate $A$ for the equation, the central hollow area can simply be subtracted from the total stem area. The degree of error in estimated sap flow introduced by an error in $A$ is minimal, because $Q_v$ is a minor portion (<10%) of the total energy balance (Sakuratani 1981). The $\Delta T$ is the difference in stem surface temperature ($K$) among the 4 thermojunctions located above and below the heater, and $\Delta X$ is the distance (3-5 mm) between 2 thermojunctions within a pair (Fig. 1a). The thermojunctions can be wired in either a differential or absolute mode if the datalogger used can produce an actual temperature (°C) from the analog signal inputs. The differential scheme reduces the required number of datalogger input channels (Steinberg et al. 1989). The term $S$ in equation 1 represents the rate change in heat storage within the stem. However, empirical data have shown that including this term has minimal effect on diurnal sap flow calculations (Dugas 1990) because it is typically ≤3% of the stem energy balance (Senock and Ham 1993), and thus it can usually be ignored when measuring sap flow for plants with small stems.

For calculating sap flow, equation 1 is rearranged as

$$F = \frac{Q - Q_r - Q_v}{C(T_{so} - T_{xi})} = \frac{Q_f}{C(T_{so} - T_{si})} \quad (2)$$

where $F$ is the sap flow rate (kg $s^{-1}$), $Q_f$ is the residual heat flux, $C$ is the heat capacity of the sap (4187 J $kg^{-1}$ $K^{-1}$), and $T_{so}$-$T_{si}$ represents the difference in temperature of the sap flowing into and out of the heated stem segment as estimated from the stem surface temperatures measured with the paired thermojunctions (Fig. 1a).

## Test Procedures

Plant species used in the study were big bluestem (*Andropogon gerardii* Vitman) and indiangrass [*Sorghastrum nutans* (L.) Nash] grown in the greenhouse from seed obtained from the USDA/SCS Manhattan Plant Materials Research Center in Kansas. Plants were grown in 0.25 liter plastic pots filled with a 50% by volume mixture of fritted clay and a commercial potting soil. Because the plants had several culms, all but 1 plant culm was removed, and the gauges were attached at the base of the culm, immediately above the soil surface and beneath all leaves and leaf sheaths. Stem diameters were ≤5 mm, and stem radial geometries were elliptical. Gauge heater width was 10 mm and lengths were 10 or 15 mm (Heater Designs, Bloomington, Calif.) depending on stem size. During testing, gauges were surrounded with foam insulation (7 to 12 mm thickness), held in place with plastic clips, and shielded from radiation with aluminum foil.

Performance tests were conducted in the laboratory from July to August, 1991, under 2 high pressure sodium lamps (Model LU400, Energy Technics, York, Penn.) with maximum irradiance at the top of the plant near 225 Watts $m^{-2}$ (pyranometer Model 8-48, Eppley Laboratory, Newport, R.I.). The lights were timed independently to produce different light intensity regimes and obtain various levels of transpiration. Tests were conducted from August to October, 1991, in a whitewashed greenhouse with evaporative cooling. Thermocouples were wired in the absolute mode to give actual measurements of stem surface temperatures with gauge signals sampled every 15 seconds and stored as 30-minute averages with a data logger (Model 21X, Campbell Scientific Ltd., Logan Ut.). Measured sap flow rates were compared with concurrent gravimetric estimates of water loss as measured by an electronic balance (0.01 g resolution) every 30 minutes.

To better examine the effects of external environmental conditions on gauge performance, an artificial flow system similar to the design of Sakuratani (1979) was built in the laboratory. Briefly, the main components were arranged in the order of a constant-pressure water delivery system, a 15 cm section of a senesced, hollow indiangrass flowering culm (5 mm diameter), and a 5 mm diameter glass extension tube at the distal end of the culm. Water flowed through the culm and into a covered catchment beaker placed on an electronic balance. The flow rate was monitored every 30 seconds with gravimetric measurements of the system outflow. The system was arranged horizontally, and a sap flow gauge with 7 mm thick insulation was attached and operated as in all performance tests. The surface temperature of the gauge insulation was raised with a heat gun and lowered with Freon to mimic sudden changes in air temperature. Gauge surface temperature was measured with a thermocouple placed on the insulation surface beneath the Al foil shield.

Field tests were conducted at Kansas State University's Ashland Research Farm during June and July, 1992. On each test day, 2 potted plants of each species were placed within a full canopy of mature oats (*Avena sativa* L.) and 2 in an adjacent open area. Thermocouples were wired in the differential mode. Daily estimates of total sap flow were compared with beginning- and end-of-day gravimetric weights. Global irradiance and air temperature within and outside the canopy also were measured. Gauge signals and environmental factors were sampled every 15 seconds with a data logger/multiplexer arrangement (Models 21X/AM416, Campbell Scientific Ltd., Logan, Ut.) and stored as 20 minute averages. Gauge insulation thickness was 12 mm. Prior to all tests, pots were well watered and allowed to drain before being sealed in plastic bags to minimize soil evaporation. Pots also were covered with aluminum foil to minimize radiation effects on soil temperature.

## Results and Discussion

### Laboratory Tests

Repeated tests on both species showed the gauges were consistently accurate within ±10% of the gravimetric measurements. For the specific examples presented in Figure 2, cumulative water loss measured with the gauge was within +7% for big bluestem and -3% for indiangrass. This degree of accuracy is equivalent to that reported for several herbaceous and woody dicots, despite maximum flow rates ≤4 g $hour^{-1}$. Such low maximum flow rates are one-tenth of commonly reported values (>50 g $hour^{-1}$) for larger crop species (Sakuratani 1987, Dugas 1990, Ham and Heilman 1990). Sakuratani (1979, 1990) also reported estimates within ±10% for rice plants when flows were >5 g $hour^{-1}$ but accuracy apparently decreased at lower flow rates because of poor gauge sensor response time and stem anatomy (Sakuratani 1990). The high degree of accuracy in this study can be attributed to the correct partitioning of the heat energy flux components and the dynamic response of the gauge to sudden changes in sap flow.

When partitioning the heat flux components, $Q_r$ and $Q_v$ are obtained from direct sensor measurements, whereas $Q_f$ is calculated as a residual (eq. 2). Because sap flow is directly proportional to $Q_f$, any heat flux not properly attributed to $Q_r$ or $Q_v$ will result in an inaccurate estimate of $Q_f$ and thus sap flow. With $Q_v$ typically <10% of $Q$ (Sakuratani 1981, Ham and Heilman 1990), the measurement of $Q_r$ then becomes the major source of potential error in estimating sap flow at low flow rates (Senock and Ham 1993). During high flows, convective heat transport in the sap stream causes $Q_f$ to be the dominant flux component, whereas during periods of low flow, $Q_r$ is the dominant flux component. In general, a wide fluctuation typically occurs in $Q_f$ as flows increase (>20 g $hour^{-1}$) and the fractional proportion of $Q_r$ (<0.20 of $Q$) becomes small (Steinberg et al. 1989, Dugas 1990, Ham and Heilman 1990, van Bavel 1991, Senock and Ham 1993). In contrast, for the grasses in this study, only small variations occurred in all the heat flux components, and the fractional proportion of $Q_r$ remained above 0.70 regardless of flow rate (Fig. 2b). For most range grasses, sap flows will probably be <20 g $hour^{-1}$, $Q_f$ will be a minor portion of the total heat flux and $Q_r$ will always dominate the heat loss components. The measurement of $Q_r$ will thus be critical to accurately estimating sap flow of range grasses. As previously stated, however, $Q_r$ is directly proportional to the radial temperature gradient and the thermal conductivity ($K_g$) of the gauge, with the later typically measured during a period of minimal sap flow. For each laboratory test, the value of $K_g$ used in calculating $Q_r$ was determined during the low flow period just prior to turning on the lights. Given the accuracy between the measured gravimetric and computed sap flow rates in the laboratory tests (Fig. 2), both $K_g$ and the radial temperature gradient were probably measured accurately, which resulted in an accurate accounting of the heat flux components.

In addition to partitioning correctly the heat flux components, the other important variable in calculating sap flow is $T_{so}$-$T_{si}$. This parameter is measured from the temperature sensors on the stem surface. The stem surface temperature is then assumed to be representative of the sap temperature in the radial cross-sectional (Sakuratani 1981). For the assumption to be true, thermal equilibrium has to be achieved between the exterior stem surface and the sap. According to the simulation study of Baker and Nieber (1989), this assumption is violated in the case of monocots because of the scattered arrangement of the vascular tissue within the stem. However, thermal equilibrium is not only dependent on stem anatomy but also on sap velocity and stem size. At high sap velocities thermal equilibrium may not be reached because of the rapid convective heat loss in the moving sap stream (Baker and Nieber 1989). At high flow rates, enlarging gauge heater width as stem diameter increases may be a solution to reducing stem temperature gradients and improving thermal equilibrium (Ham and Heilman, 1990). Using an estimate of the hydroactive xylem conducting area in a stem of 5 mm diameter (5 $mm^2$) and the maxi-

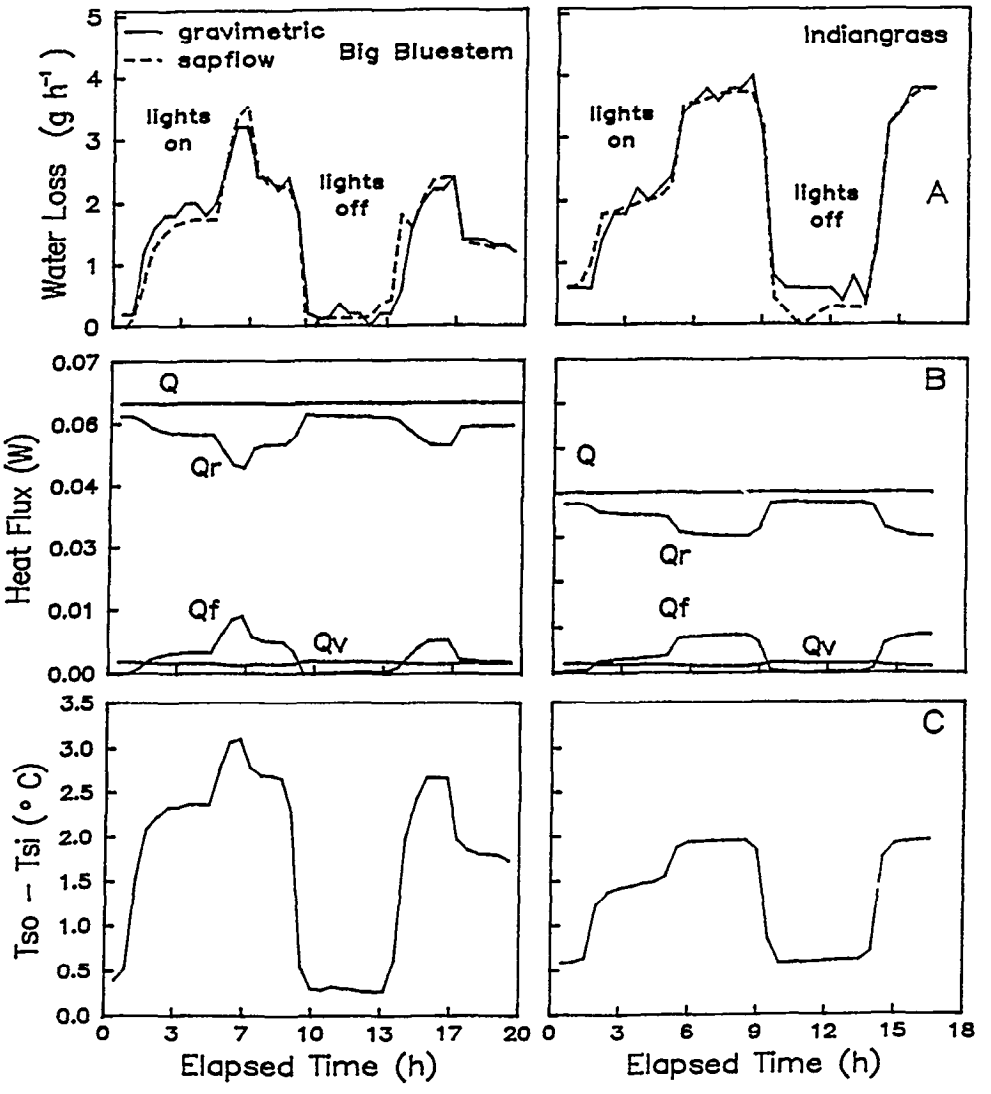


**Fig. 2. Representative laboratory examples of the performance of a sap flow gauge on individual culms of big bluestem and indiangrass: (A) gauge computed sap flow compared to gravimetric measurements of plant water loss; (B) heat balance components, $Q$ = power input, $Q_f$ = convective heat flux, $Q_r$ = radial heat flux, $Q_v$ = axial heat flux, and (C) $T_{so}$-$T_{si}$.**

mum flows of 4 g hour$^{-1}$ recorded in the laboratory tests the computed sap velocities would be $\leq$ 0.2 mm sec$^{-1}$. This is much less than the 0.55 mm sec$^{-1}$ computed for corn plants with flow rates near 100 g hour$^{-1}$ when sap flow was underestimated because of non-equilibrium temperatures (Cohen et al. 1993). Furthermore, as recommended by Sakuratani (1981), the ratio of the gauge heater width (10 mm) to stem diameter ($\leq$ 5 mm) was 2:1. Thus, it is unlikely that large interior cross-sectional temperature gradients could exist, and the assumption that radial temperature can be estimated from measurements at the surface is probably valid for the small stems that would typify most range grasses. The accuracy of the sap flow estimates in the laboratory tests for both species indicate that $T_{so}$-$T_{si}$ was probably estimated correctly by the sensors on the stem surface.

The nearly identical response of $T_{so}$-$T_{si}$ to abrupt changes in sap flow (Fig. 2c) was in contrast to the typical relationship expected when using thermal tracer techniques for measuring the flow of fluids in contained volumes (such as pipe or stems). Theory dictates that as flow increases from zero, $T_{so}$-$T_{si}$ initially increases very rapidly to a maximum and then begins to decrease as flow rates continue increasing. This response pattern is due to a distortion of the isothermal field in the direction of flow (Baker and Nieber 1989). For both species, $T_{so}$-$T_{si}$ increased as flow increased (Fig. 3), indicating that flows were in a range such that $T_{so}$-$T_{si}$ had not been maximized and the change in $T_{so}$-$T_{si}$ as flow rate changed ($\partial T_{so}$-$T_{si}/\partial F$) was greater than 0. The large value of $\partial T_{so}$-$T_{si}/\partial F$ at low flows is one of the key reasons why accurate measurements of sap flow are possible in small stems even when fluctuations in the heat balance components are minimal.

A large $\partial T_{so}$-$T_{si}/\partial F$ can be achieved with an optimum power input ($Q$) to the gauge. For the species in this study this was determined with a series of evaluations at different levels of $Q$ and plotting $T_{so}$-$T_{si}$ vs sap flow (Fig. 3). Although there were no differences in accuracy ($\leq$10%) among the individual evaluations for each species, the largest $\partial T_{so}$-$T_{si}/\partial F$ values were obtained with $Q$ in the range of 0.04 to 0.06 watts. A similar testing procedure identified the optimum $Q$ for soybean seedlings (Senock and Ham 1993). Even though the overall accuracy of sap flow gauges

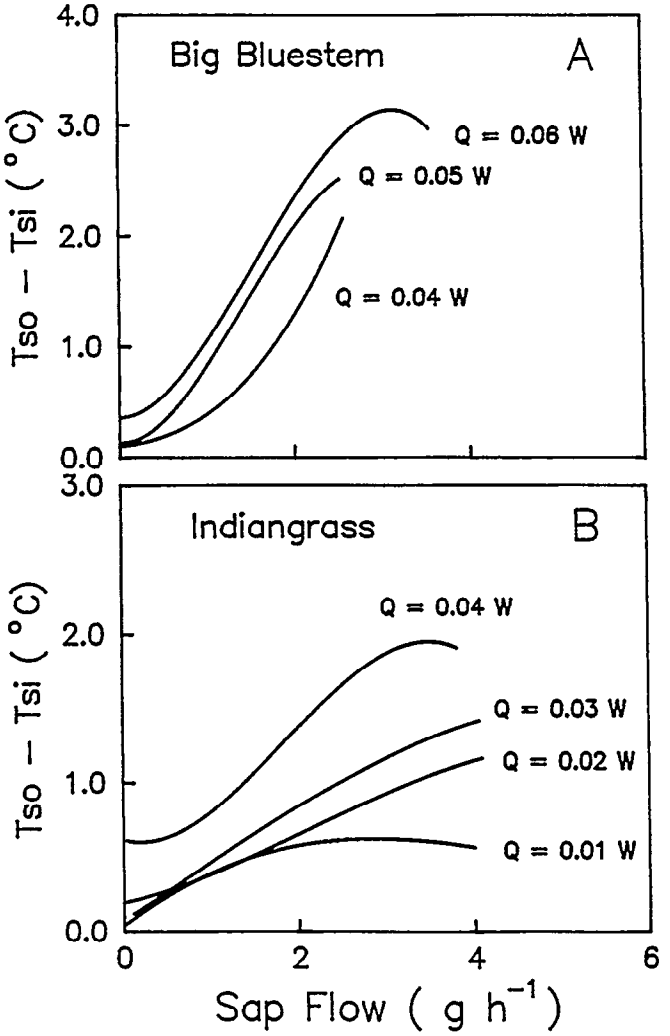


**Fig. 3. $T_{so}$-$T_{si}$ in relation to sap flow rate at different input power ($Q$) levels for big bluestem (A) and indiangrass (B). For all tests, gauge estimates were within 10% of gravimetric measurements.**

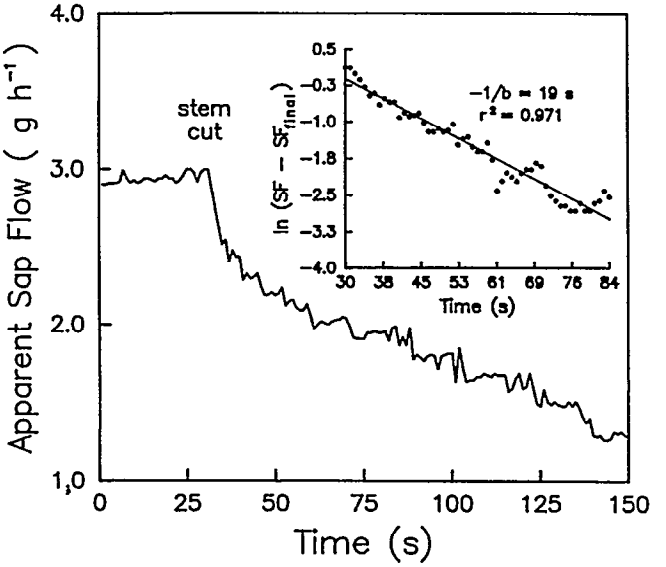


**Fig. 4. Change in apparent sap flow rate following stem excision, recorded every 1 s. The inset shows the system time constant derived from the difference between initial (SF) and final ($SF_{final}$) sap flow rate with the later value being 63% of the initial rate.**

at high flow rates is not a function of $Q$ (Ham and Heilman 1990), at the low flow rates probably typical of most range grasses, proper selection of $Q$ may avoid any physiological or structural damage to the plant stem while achieving optimum gauge response to sudden changes in sap flow.

The capability of the gauge to respond to sudden changes in sap flow can be quantified with a first-order time constant determined using a step change in flow rate (accomplished by severing the plant stem directly above the gauge) and monitoring the time rate change in computed sap flow. Time constants of 5 to 20 minutes have been reported for herbaceous and tree species with large stems at high flow rates (Baker and van Bavel 1987, Steinberg at al. 1989). Figure 4 shows that when the flow rate was near 3 g hour$^{1}$, the gauge time constant for indiangrass was only 19 seconds. This value is similar to that found for a soybean seedling (15 seconds) and can be attributed to the small mass of the heated stem segment (Senock and Ham 1993). Furthermore, for a given gauge configuration and plant, the time constant of a sap flow gauge will decrease as flow increases (Kucera et al. 1977). The laboratory tests in this study were conducted with light intensities only approximately 25% of full sunlight, thus suggesting that a similar or faster response time can be expected under higher light intensities when sap flow rates are higher.

## Greenhouse Tests

Environmental conditions in the greenhouse not only fluctuated in response to normal diurnal variations in solar radiation but there were also rapid changes in air temperature caused by the evaporative cooling system used to regulate interior temperatures (Fig. 5a). Gauge performance tests under these conditions always resulted in computed sap flow being consistently below gravimetric water loss and negative flows were often computed (Fig. 5b). This situation was never observed in any of the laboratory tests. The computed negative flows were not entirely the result of a negative $T_{so}$-$T_{si}$ (Fig. 5c). Additionally, using the thermocouples on the stem surface to measure $S$ (eq. 1) did not significantly change the heat balance or the flow estimates. The negative flows were largely a result of increases in $Q_r$ above $Q$ thus forcing a negative residual $Q_f$ (Fig. 5c). The explanation for $Q_r$ being greater than the total power input into the stem segment has to be presented in terms of the thermodynamics of a heat balance sap flow gauge and the approximate way the component heat fluxes are measured.

The radial heat flow, $Q_r$, is the product of the thermopile output (E) and the thermal conductivity of the gauge, $K_g$. Regardless of the method used to select $K_g$, once chosen it becomes constant for the measurement period under consideration. Fluctuations in $Q_r$ then become strictly a function of E which is the temperature differential ($DT$) between the interior (hot junctions) and exterior (cold junctions) of the cork-neoprene chassis (Fig. 1a). The greater the $DT$ the higher $E$, whereas a lower $DT$ means a lower $E$. Under normal conditions, when sap flow has ceased or is minimal, $DT$ is greatest because convective heat loss is minimal and the higher $E$ results in the highest $Q_r$ values. When sap flow is occurring within the plant, heat is removed from the stem segment by convection in the sap stream, which decreases $DT$ and produces a corresponding decrease in $E$, and thus $Q_r$. Because the

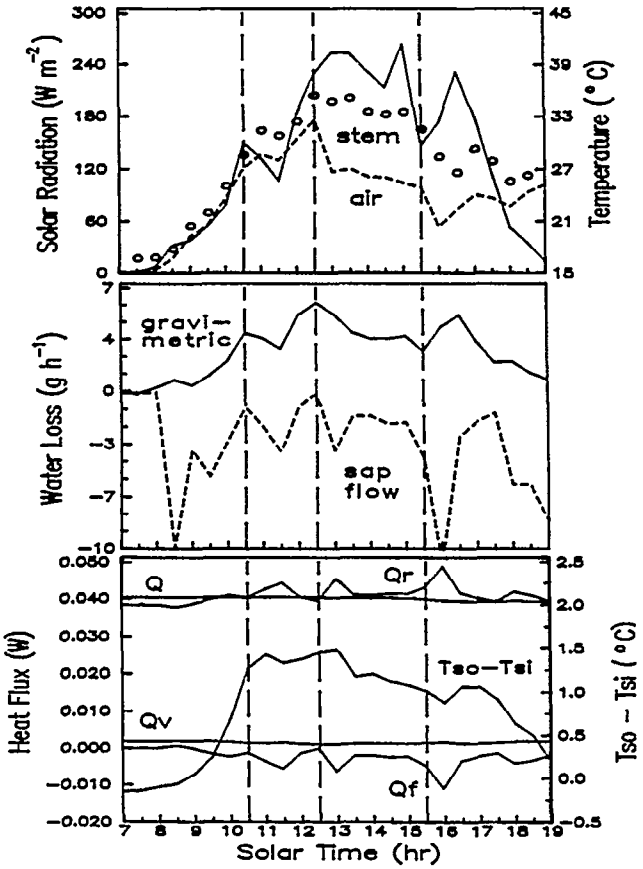


Fig. 5. Representative greenhouse example of the performance of a sap flow gauge on an individual culm of indiangrass: (A) ambient environmental conditions of global solar irradiance and air temperature, and plant stem surface temperature; (B) gauge computed sap flow compared to gravimetric measurements of plant water loss; (C) heat balance components, $Q$ = power input, $Q_f$ = convective heat flux, $Q_r$ = radial heat flux, $Q_v$ = axial heat flux, and $T_{so}$-$T_{si}$. Dotted vertical lines indicate specific times discussed in the text.

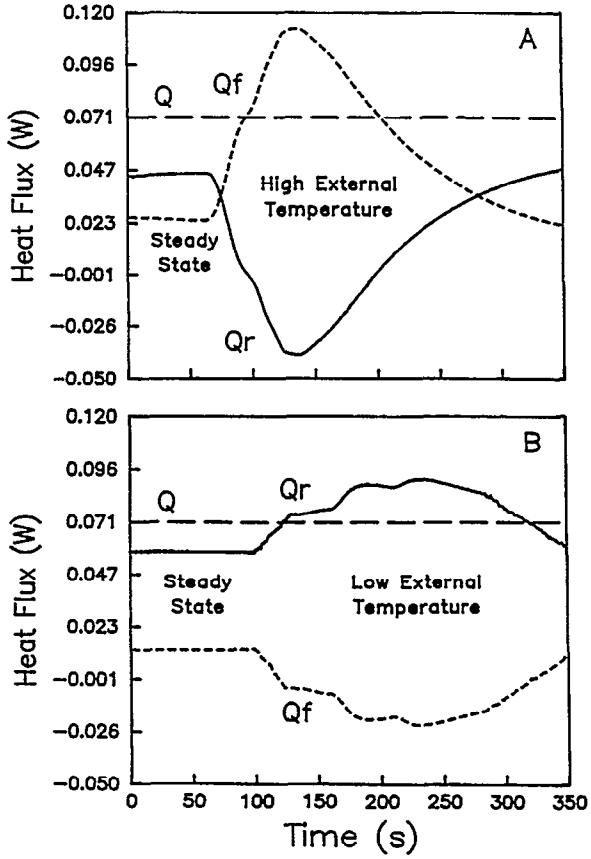


Fig. 6. Effects of sudden changes in steady-state gauge heat balance due to (A) increasing or (B) decreasing gauge insulation surface temperature. Data were collected in the laboratory with a sap flow gauge connected to an artificial flow system with constant water flow (4 or 7 g h$^{-1}$); $Q$ = power input, $Q_f$ = convective heat flux, and $Q_r$ = radial heat flux.

energy balance approach is used in calculating sap flow under the assumptions of steady-state conditions and heat energy input to the plant stem is predominately from the gauge heater, $Q_r$ should never be greater than $Q$ if $S$ is indeed zero. The fact that this did occur in the greenhouse when gravimetric measurements established that sap flow was occurring indicates that perhaps $Q_r$ was not being measured accurately by the thermopile. Accurate measurements of $Q_r$ by a thermopile in a single radial plane may be inadequate if spatial variability of thermal gradients exist within the gauge. However, with the assumption that $Q_r$ was accurately measured by the thermopile, the remaining explanation for $Q_r$ being greater than $Q$ was that the other important assumption of steady-state conditions within the heated stem segment was no longer valid.

The energy dynamics at the specific times indicated in Figure 5 can be used to illustrate how $Q_r$ was being influenced by changes in the external environment. Between 1030 hour and 1230 hour, the rapid 2 to 3° C decrease in air temperature increased the stem-air temperature gradient that resulted in a positive outward heat transfer away from the stem. At 1230 and 1530 hours, the cooling system in the greenhouse again switched on to rapidly decrease air temperature by 6° C while stem temperature remained steady. In all instances $Q_r$ increased with the result being a computed negative flow because of a negative $Q_f$. However, $Q_r$ also began to decrease once the air temperature became constant (1300 to 1530 hours) or increased (1600 to 1730 hours). The variations in $Q_r$ were thus all possibly due to changes in radial heat flux through the gauge insulation caused by sensible heat transfer at the stem-gauge and gauge-air interface. In a series of evaluations with no power input to the gauge, a strong correlation between $Q_r$ and the air-stem temperature gradient ($r$>0.81) also suggested that sensible heat transfer at the gauge-air interface promoted outward radial heat flow. The overall results of the greenhouse tests indicate that $Q_r$ in big bluestem and indiangrass with low flows (<10 g hour$^{-1}$) is highly sensitive to the external environment.

### Radial Heat Flux Analysis

Although results from the greenhouse tests suggested that sensible heat transfer at the gauge-air interface could effect $Q_r$, an independent evaluation of the effect could not be attempted because of the simultaneous changes in sap flow that also occurred in response to fluctuating solar radiation and air temperatures. To circumvent this problem, an artificial flow system was constructed in the laboratory to evaluate gauge responses to the environment while holding $F$ constant. Results showed that changes in external temperature could affect the stem energy bal-

changes in external temperature could affect the stem energy balance despite the gauge being surrounded with insulation and covered with aluminum foil (Fig. 6). When the insulation surface and foil on the exterior of the gauge was heated from 25 to 73° C, the steady-state $Q_r$ of +0.047 Watt was changed to a -0.040 Watts and the computed flow rate overestimated the known flow rate by 200% (Fig. 6a). Because $T_{so}$-$T_{si}$ changed by less than 0.5° C during the test and $S$ was minimal, the overestimate was due entirely to the change in $Q_r$ and subsequent error in the residual $Q_f$. Figure 6b shows the results for a test when the gauge surface temperature was cooled from 25 to 13° C and the steady-state $Q_r$ of +0.059 Watts was increased to +0.093 W. The variation in $T_{so}$-$T_{si}$ during the test was again minimal, as was $S$, and the subsequently computed negative flow rate (-6 g hour$^{-1}$) was due to the negative $Q_f$ residual. Although the data presented in Figure 6 represent extreme examples of changes in temperature, it was apparent from the tests that the rubber foam commonly used to cover sap flow gauges could not completely insulate the gauge or the plant stem from rapidly changing external air temperatures. Additional tests with smaller variations in gauge surface temperature produced the same relative changes in the heat flux components and errors in the computed flow rates.

Changes in air temperature produce a heat energy transfer (q) that can be quantified for the cylindrical system (Incropera and DeWitt 1990) of a sap flow gauge using the equation

$$q = \frac{\Delta T}{R_{cond}} = \frac{T_{gs}\text{-}T_i}{\ln(r/r_i)/2\pi Lk} \quad (3)$$

where $\Delta T$ is the temperature gradient (°C) between the plant stem ($T_i$) and the gauge surface ($T_{gs}$), and $R_{cond}$ is the thermal resistance (m•C/W) to conductive heat flow calculated using $r$, the distance to the insulation surface (9.5 mm), $r_i$ is the radius of the enclosed stem (2.5 mm), L is the heater width (10 mm) and k, the insulation (AP Armaflex Pipe Insulation, Armstrong World Industries, Lancaster, Penn.) thermal conductivity (= 0.039 W/m•C). The assumptions involved with using the equation are steady-state, one-dimensional heat transfer, and negligible convective or radiative heat exchange between the insulation surface and surroundings. Equation 3 shows that $q$ is directly proportional to $\Delta T$ but inversely proportional to $R_{cond}$ which, for a given insulation with constant $k$, is largely dependent on $r$, the insulation thickness. Increases in $r$ will thus decrease $q$ and lessen the impact of changing external temperatures on the stem energy balance. If $q$ were to represent the allowable maximum flux that altered $Q_r$ such that the final error in computed sap flow, $F$, was ≤10%, then $r$ could be evaluated as a function of $\Delta T$. Using the laboratory data ($F$ = 5 g hour$^{-1}$, $Q_r$ = 0.05 Watts), $r$ would have to

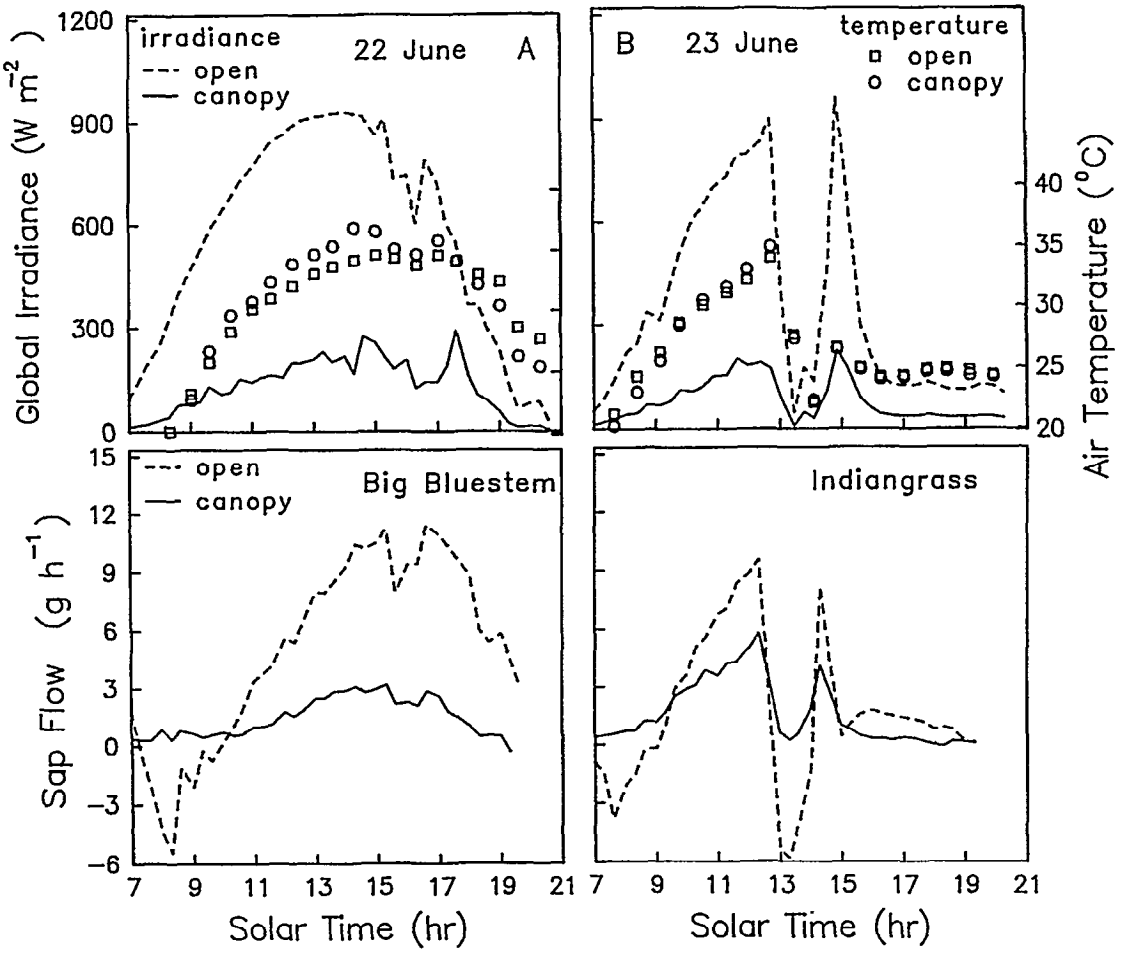


**Fig. 7. Representative field examples of global irradiance, air temperature, and sap flow of potted plants of big bluestem (A) and indiangrass (B) placed in the open or within a plant canopy. Sap flow data are from single gauges.**

be sufficient to limit $q$ to 5% of $Q_r$ or ±0.003 Watts. Sample calculations with equation 3 showed that at $\Delta T = 3^{o}$ C, more than 30 mm of insulation would have to be used to minimize $q$ below 0.003 Watts. However, there is only a small change in the limit of $\Delta T$ to be gained above 21 mm of insulation. In addition, because the use of a rapid change in $\Delta T$ to calculate $q$ (as compared to a gradual temperature change) produces a conservative estimate of $r$, the optimum insulation thickness would probably range from 20 to 25 mm when using sap flow gauges on range grasses under conditions of small temperature fluctuations. Equation 3 also shows that to hold $q$ constant, $r$ must be increased exponentially in response to linear increases in $\Delta T$ and sample calculations show that no reasonable amount of insulation could be used to maintain $Q_r$ at 0.05±0.003 Watts if $\Delta T > 3^{o}$ C. Although the maximum allowable error in $Q_r$ changes as a function of $F$, this simplified approach suggests that large abrupt changes in external temperatures may produce errors in the computed sap flow rates.

## Field Tests

Similar to the laboratory tests, gauge-estimated daily water loss for both species was consistently within ± 10% of gravimetrically measured water loss when the potted plants were placed within the plant canopy (Table 1). However, when both species were placed in the open, the gauges often severely over- or underestimated daily water loss. Examination of the diurnal patterns showed that the early morning estimates of sap flow of plants in the open were often negative (Fig. 7a,b). This suggests that when gauges on plants in the open accurately estimated daily values on June 23 and July 17 (Table 1), results may have been due to compensating periods of errors in computed sap flow. Sap flow for the plants within the shaded canopy, albeit lower, followed the diurnal course of irradiance with no apparent anomalies.

Because $T_{so}$-$T_{si}$ was always positive and generally above 0.5 $^{o}$C, the failure of the gauges to operate properly on plants in the open was due to the same alterations in the heat energy balance as occurred in the greenhouse tests. During the morning hours, $Q_r$ alone was greater than $Q$ (data not shown), thus resulting in a negative $Q_f$ as the residual heat flux (eq. 2) and consequently, a negative flow rate (Fig. 7a,b). This may have occurred because of a temperature gradient within the 12-mm thick gauge insulation caused by early morning dew that often coated the gauges on plants in the open but not those gauges on plants within the canopy. The latent heat flux caused by dew evaporation would have had a cooling effect on the surrounding insulation and thus altered $Q_r$. Data from a day when rapid midday changes in irradiance and air temperature occurred also showed large negative flow rates from gauges on plants in the open but not from those gauges on plants within the canopy (Fig. 7b). In contrast, large midday overestimates of sap flow for gauges on plants in the open were often suspected because of a very low or negative $Q_r$ that was possibly due to rapid heating of the gauge surface by solar radiation. Shading of the gauge from solar radiation with some sort of shield may have protected the gauge from the effects of rapid heating, but the only solution to changes in air temperature is to provide additional insulation. The distortions in the heat flux components for the gauges on plants in the open confirmed that rapid changes in the external environment will significantly affect the accuracy of sap flow measurements for range grasses, and that gauge insulation thickness will have to be maximized to protect against rapid heating or cooling of the gauge under field conditions.

**Table 1. Daily water use of potted plants placed in the open or within a plant canopy determined by gravimetric measurement and cumulative sap flow estimates. Sap flow data are measurements from single gauges.**

| Date | Treatment | Species | Gravimetric | Sap flow | Difference |
|---|---|---|---|---|---|
| | | | ----(g day)---- | | (%) |
| 6-22 | open | bluestem | 80.6 | 62.7 | -22.2 |
| | open | indiangrass | 48.2 | 35.6 | -26.1 |
| | canopy | bluestem | 19.7 | 20.5 | +4.1 |
| | canopy | indiangrass | 45.9 | 47.5 | +3.5 |
| 6-23 | open | bluestem | 36.7 | 35.6 | -3.0 |
| | open | indiangrass | 47.7 | 62.3 | +30.6 |
| | canopy | bluestem | 23.8 | 21.9 | -8.1 |
| | canopy | indiangrass | 24.3 | 26.7 | +10.0 |
| 7-13 | open | bluestem | 46.4 | 96.5 | +108.0 |
| | open | indiangrass | 59.7 | 74.2 | +24.3 |
| | canopy | bluestem | 36.1 | 34.7 | -3.9 |
| | canopy | indiangrass | 25.3 | 27.0 | +6.7 |
| 7-17 | open | bluestem | 93.3 | 64.4 | -31.8 |
| | open | indiangrass | 53.6 | 49.2 | -8.2 |
| | canopy | bluestem | 29.9 | 32.5 | +8.7 |
| | canopy | indiangrass | 31.4 | 28.7 | +8.6 |

## Implications for Rangeland Research

The dynamics of the gauge response and the consistent accuracy in the laboratory indicates the potential of heat balance sap flow gauges for directly measuring water use of range grasses. The greenhouse tests and some field tests, however, illustrated that limitations may also exist to using sap flow gauges to measure the low flow rates of grasses if the external environment is fluctuating rapidly. Accurate water use estimates obtained from the gauges placed within the protection of the oat canopy indicated that reliable measurements of sap flow for range grasses can be obtained in certain field situations.

The sap flow gauges used in this study have been successfully employed and validated under field conditions on several tallgrass prairie species (Ham et al., unpublished data). Although the tallgrass prairie may provide unusually high vegetative canopy cover in comparison to other rangeland ecosystems, the minimal amount of cover necessary to provide adequate gauge protection has yet to be determined. If the gauges are placed on the grass tiller directly above the soil surface and surrounding plant canopy is available to provide some protection from direct exposure to solar irradiance and other environmental factors, then accurate measures of range grass water use can be expected. It is also plausible that the interior of widely spaced bunchgrass species may provide enough protection to allow sap flow gauges to be successfully used in the field. Protection of heat balance sap flow gauges from extreme ambient conditions provided by a vegetative canopy appears to be important for any plant species (Gutierrez et al. 1994).

Regardless of the field situation or the species investigated, a critical evaluation of the effect of ambient conditions on gauge performance should be done to insure reliable plant water use estimates (Shackel et al. 1992). Examination of the heat flux components would allow the researcher to make an objective decision as to the validity of the gauge performance. The objectivity would come from understanding the stem energy balance

approach and fully considering the sap flow equation. Periods of computed negative flows because of a negative $Q_f$ or $T_{so}$-$T_{si}$ should alert the researcher to problems in the data (Shackel et al. 1992, Gutierrez et al. 1994). Experience gained from preliminary laboratory or greenhouse validation tests on the species of interest may also provide a reference point for deciding if the computed flows in a field setting were reasonable or should be suspect (Cohen et al. 1993). Similarly, comparison of computed sap flows with water loss estimates obtained from other field based methods (lysimeters, Bowen ratio-energy balance) may confirm or contradict the flow measurements (Gerdes et al. 1994). Like all other plant physiological measurement techniques a thorough examination of all relevant factors is necessary for any meaningful information to be extracted from data collected with modern instrumentation (Bloom 1991).

In comparison to many other methods, sap flow gauges can provide direct and non-invasive measurements of plant water use. Perhaps most important, the technique provides continuous data on the flow of water within the plant stem. Although 20-30 minute average values were used in this study, the rapid time constant would allow for even shorter time periods of average sap flow to be calculated. Because grasses have limited internal plant water capacitance (Nobel and Jordan 1983), water use by range grasses as measured with sap flow gauges is nearly equivalent to transpiration and could be related directly to various environmental factors (net radiation, air saturation deficit, temperature, and wind speed) that influence plant water use. Sap flow can be summed easily over time for determining the total amount of water used by individual species in different treatments (Steinberg et al. 1991, Gavloski et al. 1992). In breeding and selection programs, cumulative sap flow could provide an quantitative measure of water use over the life of a grass plant that is not feasible with instantaneous measures of stomatal conductance or transpiration (Johnson and Asay 1993). Regardless of application, the previous reports of sap flow measurements on honey mesquite in the field (Dugas and Mayeux 1991, Dugas et al. 1992) and the results on range grasses presented here are establishing the use of heat balance sap flow gauges as a viable method of measuring range-plant water use.

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# Satellite-based herbaceous biomass estimates in the pastoral zone of Niger

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## Abstract

**Pastoralists in the Sahel of northern Africa are entirely dependent on their livestock, which graze on the annual vegetation produced during a relatively short summer rainfall season. The satellite-based normalized difference vegetation index, calibrated with ground-truth sampling of herbaceous biomass throughout the pastoral zone of Niger, was used to estimate standing biomass for the entire Nigerien pastoral zone. Data were obtained and analyzed during a 5-year period from 1986 through 1990. Techniques developed allow officials with the Government of Niger to estimate herbage available to support animal populations throughout the pastoral zone at the end of the growing season and plan grazing strategies for the impending dry season. End-of-season herbage standing crop varied from less than 200 kg ha$^{-1}$ to nearly 1,700 kg ha$^{-1}$ with locations and years. Strong biomass gradients were evident from mesic conditions in the southern pastoral zone to xeric conditions in the north.**

**Key Words: herbage standing crop, pastoralists, livestock grazing, geographic information systems**

The African Sahel is an ecological zone on the southern edge of Sahara Desert. The rainfall pattern represents a unimodal distribution of monsoon origin, with most of the rains occurring from July to September. Average rainfall is low (100 mm) in the northern Sahel adjacent to the Sahara Desert while in the southern Sahel, adjacent to the Sudanian ecological zone, average rainfall may total up to 600 mm (Le Houerou 1980). Droughts are common in the Sahel and affect the livelihoods of many pastoralists and agriculturalists (Glantz 1987).

In Niger, a landlocked Sahelian country, United States Agency for International Development has supported the development of a national range assessment program. This range assessment program uses satellite images to extrapolate herbaceous biomass estimated from ground truth sites to the entire Nigerien pastoral zone. Rapid detection and quantification of drought extent and magnitude within the pastoral zone facilitate adjustments in national and international policies directed toward drought relief. The range assessment program also facilitates comparison among years and may encourage policies which take into account regional historical herbaceous biomass production levels. Such annual assessment is an important component of drought strategy (Wallen and Gwynne 1978). The objective of this paper is to demonstrate the utility of herbaceous biomass data within a geographic information system to assist policy and management decisions.

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## Materials and Methods

### Biomass Estimates

The rangeland assessment system in Niger employed herbaceous biomass estimates from ground truth sites to calibrate the relationship between satellite-derived vegetation indices and herbaceous biomass (Wylie et al. 1992). The ground truth sites were selected to represent the major ecological communities mapped by Milligan (1982). In addition, ground truth sites also had to be accessible because they were sampled 2-4 times during the rainy season. The satellites used in this study were the National Oceanic Atmospheric Administration meteorological satellites, numbers 7, 9, and 11. Since the field of view of these satellites is 1.2 km$^2$, the ground truth sites initially were 10 by 10 km (1986-1987) as recommended by Wagenaar and De Ridder (1987). Biomass sampling site sizes were subsequently reduced to 5 by 5 km (1988) and 3 by 3 km (1989-1990). Ground truth site's size reductions were based on analysis using subsets of the biomass and satellite values from the larger ground truth stations used in 1986-1987 (Wylie 1991, Wylie et al.1992).

Herbaceous biomass estimates for the ground truth sites were obtained using a double sampling technique (Wilm et al. 1944, Bonham 1989). The number of estimated plot weights (0.5 m$^2$) per ground truth site varied with ground truth site's size across years, ranging from 180 quadrats per ground truth site in 1987 to 60 per ground truth site in 1989 and 1990. The percentage of quadrats clipped per ground truth site ranged from 10 to 14%. Double sampling regression analysis used the weighted least squares technique. The location of quadrats within the ground truth site was determined using hierarchical randomization, except for 1986 when a 26 km zig-zag transect was used to strati-

fy the ground truth sites into low, medium, and high biomass strata.

These polar orbiting satellites have the Advanced Very High Resolution Radiometer on board, which records radiance in the visible (primarily red and some green; channel 1), near infra-red (channel 2) and thermal infra-red wavelengths (channels 3-5). Because photosynthetically active pigments strongly absorb light in the red wavelengths and the mesophyll structure within leaves causes a high near infra-red reflectance, a number of vegetation indices utilizing the differences in red and near infra-red radiance have been created (Kauth and Thomas 1976, Jackson 1983). The normalized difference vegetation index (Townsend and Justice 1986) employed in this study is defined by the formula: normalized difference vegetation index = (infra-red - red)/(infra-red + red). Normalized difference vegetation index values associated with actively photosynthesizing vegetation range from 0.1 to 0.6.

The National Oceanic Atmospheric Administration normalized difference vegetation index coverages for 1986-1988 were obtained from the National Aeronautical Space Administration Goddard Space Flight Center. Scientists in the Laboratory for Terrestrial Physics did the initial analysis of the data. Only satellite data within ± 20 degrees of nadir were used. Thermal data (channel 4) were used to identify areas covered by clouds and these were replaced with zero values in the normalized difference vegetation index coverage (Holben 1986). National Oceanic Atmospheric Administration normalized difference vegetation index coverages for 1989 and 1990 were obtained from the receiving station at the Centre Regional de Formation et d' Application Agrometeorologie et Hydrologie Operationnelle office in Niamey, Niger. Cloud masking and selection of near nadir coverages were not performed on the 1989 and 1990 data. National Oceanic Atmospheric Administration normalized difference vegetation index coverages are available on a daily basis, but near nadir data were obtained on approximately 50% of the days (Harrington and Wylie 1989).

Maximum value composites are obtained by overlaying several normalized difference vegetation index coverages for successive dates in a raster geographic information system and retaining only the highest normalized difference vegetation index value for each pixel. Maximum normalized difference vegetation index values tend to be near nadir, have little or no cloud cover, and have minimal atmospheric contamination (Holben 1986, Harrington and Wylie 1989). The number of days associated with the normalized difference vegetation index coverages used to create the maximum value composite periods for 1986-1988 varied from 2 to 11 days as a function of available imagery and cloud contamination. For the 1989-1990 data obtained from the Centre Regional de Formation et d' Application Agrometeorologie et Hydrologie Operationnelle, maximum value composite periods were 10 days each.

The seasonally summarized normalized difference vegetation index statistic used in this study was the average integrated normalized difference vegetation index. Average integrated normalized difference vegetation index is a time-weighted daily normalized difference vegetation index average (Tucker et al. 1980). Each maximum value composite normalized difference vegetation index value is time-weighted by the number of days it represents such that the entire growing season, or integration periods, is accounted for. Depending on the data available each year, 9 or 10 maximum value composites were used to determine the average integrated normalized difference vegetation index.

Ground truth site herbaceous biomass estimates and average integrated normalized difference vegetation index values were used to develop equations for estimating herbaceous biomass for all pixels. Regressing average integrated normalized difference vegetation index for each ground truth site on September herbaceous biomass produced the linear model relating biomass in September (the end of the growing season) with the seasonally summarized satellite observations. Weighted least squares linear regressions were employed (Wylie 1991). Inverse predictions, which provide estimates of independent variables given dependent variable values (Neter et al. 1983), were used to convert satellite average integrated normalized difference vegetation index to herbaceous biomass.

### Determining the Extent of the Pastoral Zone Using a Geographic Information System

Raster geographic information system functions were used to convert average integrated normalized difference vegetation index to biomass estimates for each year. Extrapolation of the average integrated normalized difference vegetation index and September biomass relationship to cover the entire pastoral zone was appropriate because ground truth sites were located throughout the region. However, extrapolation to the agricultural zone and the Sahara desert would be inappropriate because of the lack of ground truth sites in those regions. In addition, desert anomalies of normalized difference vegetation index associated with the Sahara (Holben 1986) and the incidence of cropland and higher percent coverages of trees in the agricultural zones make extrapolation of the pastoral average integrated normalized difference vegetation index to September biomass in these areas questionable. Delineation of the pastoral zone was thus necessary.

The southern limit of the pastoral zone was interpreted visually from Landsat thematic mapper images from 1986. This boundary is quite distinct because of the change in tone and texture associated with millet fields to the south of the southern boundary of the pastoral zone. The location of the boundary was transferred to a map of the whole country, digitized, and stored as a vector file. The northern limit was defined as areas having grazable forage at any year throughout the study period. Grazing trails conducted in Niger indicated that residual herbage levels after grazing of 250-350 kg $ha^{-1}$ were appropriate for heifers (Wylie et al. 1983). Grazable forage was thus defined as herbaceous biomass production greater than 350 kg $ha^{-1}$.

Satellite-derived estimates were used as inputs for a geographic information systems model which delineated the northern limit of the pastoral zone. Geographic information system masking techniques were used to restrict subsequent analysis and extrapolations to areas having greater than 350 kg $ha^{-1}$ biomass for any of the 5 years during the study. This, together with the vector southern boundary of the pastoral zone, resulted in a pastoral zone mask (0 = not in the pastoral zone and 1 = within the pastoral zone).

### Carrying Capacity Estimates

Geographic information system functions, polygon cutting, and statistics generation, were used to produce annual estimates of herbaceous biomass levels and hectarages for each pastoral zone department (or state) for areas within the pastoral zone (as defined above). Average herbaceous biomass for each department was used to calculate livestock carrying capacities. Carrying capacity estimates were based on a residual herbage level after

grazing of 250 kg $ha^{-1}$. Pase (1985) found dry matter disappearance of herbaceous biomass without grazing to be about 4% a month in Niger. Dry matter disappearance for the 9 month dry season was accounted for before total available dry season forage was calculated. A daily dry matter disappearance rate of 7.5 kg $ha^{-1}$ was attributed to one tropical livestock unit day, a 250 kg live weight equivalent. Total available dry season forage for each department among years was a function of the respective average herbaceous biomass and its associated surface area. However, expression of the carrying capacity in ha per tropical livestock unit was based on the size of the pastoral zone in each department.

Carrying capacity calculations assumed livestock grazing not to be limited by availability of drinking water. However, rangelands do exist where grazing is restricted by water availability, resulting in an overestimation of carrying capacities. The extent of such rangelands was unknown but was assumed to be negligible as Knight (1982) found water availability was not a major constraint for herd management in the pastoral zone of Niger.

### Classifying Nigerian Rangeland

To effectively evaluate drought and to assist in national natural resource management decisions and policy identification, mapping of long-term range productivity classes would be useful. A multi-pass clustering algorithm, "interactive self-organizing data technique" (Earth Resources Data Acquisitions System 1990), was employed to divide the pastoral zone into 3 clusters based on recent biomass values. Classes identified using data from central Niger, where biomass estimates from 1986-1990 were available, were extrapolated to eastern and western Niger where estimates were only available for 1989-1990 using a maximum likelihood supervised classification.

## Results

Regression statistics for average integrated normalized difference vegetation index regressed on September biomass are shown in Table 1. Weighted least squares analyses proved to be acceptable with the weighing factor being $1/(\text{September biomass})^2$ (Wylie 1991, Wylie et al. 1991). The 1986 and 1987 ground truth site herbaceous biomass and average integrated normalized difference vegetation index data were pooled because ground truth site size was similar. The extra sum of squares principle indicated no significant difference in the slopes of different years or y intercepts from the 1986-1987 pooled regression. The 1989 regression had a low $r^2$ value and a relatively low standard error. This probably is in part due to the restricted range of September biomass associated with the ground truth sites in 1986 and the $r^2$ statistic's sensitivity to the range of the independent variable.

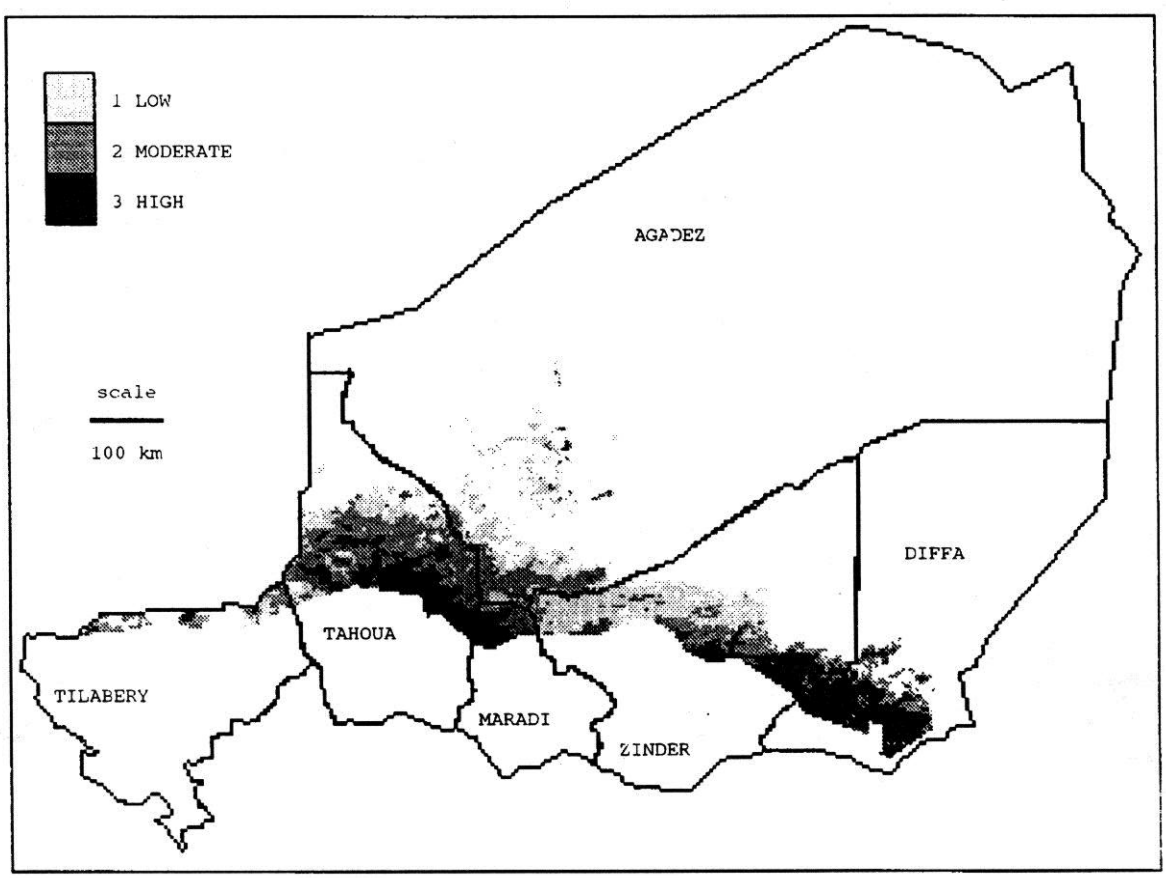


**Fig. 1. Biomass classes within the pastoral zone of Niger based on 1986-1990 herbaceous biomass.**

Table 1. Statistics used to develop regression analysis showing relationship between normalized difference vegetation index and biomass, 1986-1990.

| Year | No. ground truth sites | Ground truth site size | $r^2$ | NDVI S.E.[1] |
|---|---|---|---|---|
| | | ($km^2$) | | |
| 1986-87 | 44 | 100 | 0.74 | 0.00003 |
| 1988 | 29 | 30 | 0.80 | 0.00004 |
| 1989 | 29 | 9 | 0.25 | 0.00003 |
| 1990 | 29 | 9 | 0.67 | 0.00009 |

[1]Weighted least squares standard error of normalized difference vegetation index.

Satellite coverages obtained for 1986-1988 were for central Niger and excluded the eastern and western portions of the country. Because 1986 and 1988 were favorable years, the eastern extent of the coverage is evident as a vertical line in the pastoral zone with the pastoral zone being much more restricted in the extreme east and west where data were only available for 1989-1990 (Fig. 1). Livestock production is not restricted to this pastoral zone delineation. This delineation, however, is a best estimate based on available data and includes areas where the bulk of dry season native forage is produced. The pastoral zone contains 134,663 $km^{-2}$ of which the departments Tahoua, Zinder, and Tchirozerine contain the largest surface areas (Table 2).

Average pastoral herbaceous biomass available to grazing is presented in Table 3 for the study period. Due to the limited satellite coverages for 1986-1988, herbaceous biomass estimates could not be made for the entire pastoral zone of the Tilabery, Zinder, and Diffa departments. Higher average grazable herbaceous biomass and larger areas having grazable forage were associated with the favorable years 1986 and 1988 while lower values were associated with the drought years 1987 and 1990. The year 1989 was considered an intermediate year. Though the portion of the pastoral zone within the Maradi department was relatively small, it had high herbaceous biomass levels.

These data were used to calculate department annual carrying capacities (Table 4). The number of hectares needed to support one tropical livestock unit through the dry season was relatively low in the favorable years of 1986 and 1988. Conversely the drought of 1987 and 1990 were evident in the large number of hectares needed to support one tropical livestock unit through the dry season. During drought years, long term dry season carrying capacities of over 100 ha per tropical livestock unit were observed in the Tilabery and Agadez departments. The estimated long-term carrying capacity of the southern, highly productive department of Maradi was only 6 ha per tropical livestock unit

Table 2. Size of each department in the pastoral zone of Niger.

| Department | Size | Percent of total |
|---|---|---|
| | ($km^2$) | (%) |
| Tilabery | 5,483 | 4 |
| Tahoua | 42,568 | 32 |
| Tchirozerine | 23,952 | 18 |
| Maradi | 5,617 | 4 |
| Zinder | 39,701 | 29 |
| Diffa | 17,341 | 13 |
| Pastoral zone | 134,663 | 100 |

Table 3. Mean biomass estimates for departments (states) and arrondissements (counties) in the pastoral zone of Niger.

| Department | Arrondissement | Year 1986 | 1987 | 1988 | 1989 | 1990 |
|---|---|---|---|---|---|---|
| | | | | (kg $ha^{-1}$) | | |
| Diffa | Diffa | | | | 936 | 880 |
| | Maine | | | | 914 | 710 |
| | Nguigmi | | | | 305 | 518 |
| Tilabery | Filingue | | | | 325 | 290 |
| | Quallan | | | | 592 | 274 |
| | Tilabery | | | | 655 | 177 |
| Zinder | Goure | | | | 344 | 391 |
| | Tanout | 589 | 369 | 919 | 203 | 155 |
| Agadex | Tchirozerin | 486 | 233 | 548 | 264 | 176 |
| Maradi | Dakoro | 1,406 | 909 | 1,686 | 644 | 588 |
| Tahoua | Tchin-Tabaraden | 695 | 283 | 830 | 673 | 383 |
| Diffa | Diffa | | | | 936 | 880 |
| | Maine | | | | 914 | 710 |
| | Nguigmi | | | | 305 | 518 |
| Tilabery | Filingue | | | | 325 | 290 |
| | Quallan | | | | 592 | 274 |
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| Tahoua | Tchin-Tabaraden | 695 | 283 | 830 | 673 | 383 |

(Table 5). The average long term carrying capacity for the entire pastoral zone was 23 ha per tropical livestock unit or nearly 600,000 tropical livestock units. Departments with the largest interannual average dry season carrying capacity were Tahoua, Diffa, Zinder, and Maradi.

Stocking rate estimates for 1988 for the arrondissements (counties) within the departments of the pastoral zone, obtained from an annual report of the Ministry of Agriculture and Livestock, Niamey, Niger, were totaled by department (state) and presented in Table 5. The semi-nomadic movements of pastoralists complicate comparisons between carrying capacities and stocking rates. The bulk of the pastoralists leave the pastoral zone with their herds once the croplands in the agricultural zone have been harvested. Indeed, pastoralist movements often cross national boundaries and may contribute to high rainy season and early dry season stocking rates, particularly in the Diffa, Zinder, and Tilabery departments. In addition, stocking rate estimates for entire arrondissements include livestock within the agricultural zone while carrying capacity calculations were restricted the pastoral zone. Better estimates of dry season stocking rates within the pas-

Table 4. Annual carrying capacity estimates for departments of the pastoral zone of Niger.

| Department | Years 1986 | 1987 | 1988 | 1989 | 1990 |
|---|---|---|---|---|---|
| | (ha tropical livestock unit[1]) | | | | |
| Tilabery | | | | 19 | 148 |
| Tahoua | 8 | 45 | 6 | 8 | 35 |
| Tchirozerine | 15 | 102 | 14 | 45 | 408 |
| Maradi | 3 | 5 | 2 | 9 | 12 |
| Zinder | | | | 32 | 38 |
| Diffa | | | | 10 | 12 |

Table 5. Estimated ling-term carrying capacity and 1988 stocking rate by department in the pastoral zone of Niger.

| Department | Long-term average carrying capacity | | Stocking rate |
|---|---|---|---|
| | (ha tropical livestock unit)[1] | ----(tropical livestock units)---- | |
| Tahoua | 21 | 207,087 | 370,802 |
| Diffa | 11 | 158,271 | 1,195,239 |
| Zinder | 35 | 113,855 | 526,019 |
| Maradi | 6 | 88,483 | 39,466 |
| Tchirozerine | 117 | 20,509 | 58,992 |
| Tilabery | 83 | 6,575 | 319,644 |
| Total | | 594,780 | 2,510,162 |

toral zone are needed. Of the 1988 tropical livestock units within the pastoral arrondissements, we estimated that 80% would be in the pastoral zone during the rainy season, the remaining 20% being milk produced animals and animals used in animals traction for sedentary agriculturalists. During the 2 month post rainy season period, October-November, 60% of the livestock in the pastoral zone were expected to return to the agricultural zone. During the 7 month period from December-June, only 20% of the livestock present during the rainy season were expected to remain in the pastoral zone, the other animals moving into the agricultural croplands after sorghum had been harvested in December and pastoralists were no longer liable for their animals damaging crops. Using this crude model, average 1988 dry season stocking rate for the pastoral zone was 580,126 tropical livestock units and was similar to the long term average dry season carrying capacity for the pastoral zone.

Three long-term range production classes were identified and mapped using the interactive self-organizing data analysis technique that took into account the spatial variation in herbaceous biomass from 1986-1990 (Fig. 1). Biomass class 1 seems to be poorly represented in the extreme eastern and western Niger where only 1989 and 1990 biomass estimates were available. However, given the continuity of biomass classes 2 and 3 across the satellite data limitation boundaries, the lack of biomass class 1 in eastern and western Niger may be attributed to the lack of herbaceous biomass estimates in the favorable years 1986 and 1988. Table 6 shows yearly mean biomass averages for each biomass class. Class 1, which made up 32% of the pastoral zone, represents rangelands having low biomass production potential Class 2 made up 37% of the pastoral zone and represents rangelands with intermediate herbaceous biomass production potentials. Class 3 made up 31% of the pastoral zone and represents rangelands with high herbaceous biomass production potentials. Evident in all 3 biomass classes are the higher herbaceous biomass means associated with the favorable years 1986 and 1988 as well as the lower herbaceous biomass means associated with the drought years 1987 and 1990.

Table 6. Herbaceous biomass yearly means within biomass classes and their respective standard deviations (sd) for the pastoral zone of Niger.

| | Year | | | | |
|---|---|---|---|---|---|
| | 1986 | 1987 | 1988 | 1989 | 1990 |
| Class 1 | | | | | |
| Mean (kg ha$^{-1}$) | 378 | 153 | 456 | 179 | 174 |
| sd | 183 | 130 | 232 | 174 | 124 |
| Class 2 | | | | | |
| Mean (kg ha$^{-1}$) | 670 | 294 | 835 | 494 | 304 |
| sd | 222 | 193 | 262 | 265 | 152 |
| Class 3 | | | | | |
| Mean (kg ha$^{-1}$) | 1,170 | 683 | 1,489 | 949 | 553 |
| sd | 403 | 316 | 374 | 384 | 209 |

## Conclusions

Carrying capacity estimates based on correlations with Advance Very High Resolution Radiometer satellite data with ground truth sites appear to be reasonably reliable, with the long term dry season pastoral zone carrying capacity estimated to be 23 ha per tropical livestock unit. The delineation of the pastoral zones appears representative and confines the use of the relationship between average integrated normalized difference vegetation index and herbaceous biomass to areas within the pastoral zone. Stocking rate estimations should be refined to better reflect the dynamics of the dry season pastoral zone stocking levels.

Identification of rangeland production potentials will assist in drought monitoring and management of natural resources. The grazing strategies of the pastoralists allow them to deal with annual droughts, but when droughts occur for 2 or more successive years the results are catastrophic (Sollod 1990). As the human population and the animals needed to support them expand, flexibility of moving to ungrazed areas decreases and the effects of extended drought become less manageable.

Knowledge of the extent and location of areas with high production potentials is important to policy-decision makers. Productive rangelands pose a fire danger in the early dry season. Productive rangelands also may be considered for possible hay or silage production and may have potential for dryland agriculture whereas an extension of dryland agriculture into marginal rangelands (biomass classes 1 and 2) should be discouraged. Productive areas could possibly serve as drought indicator areas. If vegetation phenology and growth are retarded in these regions, other drought monitoring and possible preliminary drought interventions might be considered.

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# Nitrogen and atrazine on shortgrass: Vegetation, cattle and economic responses

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## Abstract

**Application of nitrogen (N) fertilizer and atrazine [6-chloro-*N*-ethyl-*N'*-(1-methylethyl)-1,3,5-triazine-2,4-diamine] have each increased grazeable forage on shortgrass prairie, but their effects are unknown when applied in combination. Therefore, a 9-year study was conducted to determine effects of N and atrazine applications on 1) herbage production, 2) steer gains, and 3) profitability of grazing on shortgrass prairie in north-central Colorado. Treatments were 1) untreated control, 2) atrazine applied at 1.1 kg ha$^{-1}$ in the autumn of alternate years, 3) N applied at 22 kg ha$^{-1}$ each autumn, and 4) N + atrazine at the rates specified above. Pastures were stocked at 21–41 (control), 27–54 (atrazine), 24–82 (N), or 18–84 (N + atrazine) cattle-days ha$^{-1}$ during summer. Pastures were stocked with yearling steers 1979–1983 and yearling steers and spayed heifers 1984–1985, using put-and-take stocking. All treatments increased total October standing crop and blue grama (*Bouteloua gracilis* [H.B.K.] Lag. ex Griffiths) standing crop. Nitrogen increased cool-season grass and forb standing crops; atrazine nearly eliminated cool-season grasses but did not affect forbs. Under put-and-take stocking, atrazine and/or N appeared to increase stocking rate and gain/ha, but not average daily gain or average returns to land, labor, and management. Under optimum stocking rates and grazing strategies, N or atrazine but not both together might increase returns.**

**Key Words: blue grama, fertilization, grazing, herbicide, intensive early stocking, put-and-take grazing, weed control, 6-chloro-*N*-ethyl-*N'*-(1-methylethyl)-1,3,5-triazine-2,4-diamine**

Although nitrogen (N) fertilization and herbicide application often have increased forage production on rangelands, livestock producers have been reluctant to use them because of uncertainty about profitability. Nitrogen applied at 22 kg ha$^{-1}$ to shortgrass prairie nearly doubled beef production in a study on heavily grazed miniature pastures (Hyder et al. 1975). Each additional kilogram of liveweight gain obtained from applying N returned about $0.55 above fertilization costs. Despite the potential for increasing profits, N has increased drought mortality of blue grama (*Bouteloua gracilis* [H.B.K.] Lag. ex Griffiths), and has increased abundance of annual forbs and sixweeks grass (*Vulpia octoflora* Rydb.), an unpalatable annual grass. The effects of N plus a herbicide on production and profitability of shortgrass prairie are unknown.

Earlier researchers determined that application of atrazine [6-chloro-*N*-ethyl-*N'*-(1-methylethyl)-1,3,5-triazine-2,4-diamine] benefited vegetation on shortgrass range in 3 ways. Atrazine controlled annual plants (Houston 1977), increased crude protein content of grasses (Houston and van der Sluijs 1973), and reduced blue grama susceptibility to drought mortality (Hyder et al. 1976). Some members of the *s*-triazine family of compounds, to which atrazine belongs, have increased yield of some forage species (Ries 1976). Demonstration that atrazine could materially increase herbage production on rangelands could lead to study of similar compounds to increase herbage yields. Manufacturers have not yet applied to the Environmental Protection Agency (EPA) to relabel atrazine, a restricted-use pesticide for agriculture, for use on rangelands in the United States. Knowledge of the effects of applying *s*-triazine herbicides to rangeland, alone or with N, and over long periods, is needed.

This study was conducted to determine the effects of treating native shortgrass range with N and atrazine alone and in combination on herbage production, steer gains and net return to a stocker steer enterprise. As an unintended consequence, the study demonstrated the difficulty of interpreting data from grazing experiments using put-and-take stocking.

## Materials and Methods

### Study Site

The study was conducted from 1977-1985 (1977 and 1978 data were incomplete; only 1979-1985 data will be reported) on the Central Plains Experimental Range. The Range is at 40° 50' N,

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Authors gratefully acknowledge the support of CIBA-GEIGY, who supplied atrazine. Wycon Chemical Co. (now Coastal Chem Inc.), Cheyenne, Wyo.; Simplot Soilbuilders, Pocatello, Ida.; American Fertilizer & Chemical Co., Henderson, Colo.; and CPER/LTER Shortgrass Steppe Program (NSF Grant BSR 8612105) supplied nitrogen fertilizer. D. N. Hyder and W. R. Houston, retired Range Scientists, USDA-ARS, helped plan the study, and Gary V. Richardson, Statistician, USDA-ARS, Northern Plains Area, Ft. Collins, Colo. advised on statistical analysis.

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104° 43' W, about 40 km northeast of Fort Collins, Colo. near the western edge of the shortgrass plains. Precipitation during the growing season was below the 54-year average during 1985; average during 1980; and above average during all other years (Table 1). Soils were primarily Ascalon fine sandy loam (mixed, mesic Aridic Argiustoll) and Vona sandy loam (mixed, mesic Ustollic Haplargids). Both soils have a pH of about 6.6 in the surface 5-cm layer and 7.8 at 50 cm.

**Table 1. Precipitation at the Central Plains Experimental Range.**

| Growing season | 1 April–30 Sep | Preceding 1 Oct–30 Sep |
|---|---|---|
| | Precipitation, mm | |
| 1979 | 397 | 472 |
| 1980 | 263 | 410 |
| 1981 | 334 | 380 |
| 1982 | 423 | 510 |
| 1983 | 345 | 424 |
| 1984 | 362 | 449 |
| 1985 | 225 | 320 |
| 1937-1985 mean | 261 | 320 |

Blue grama was the dominant forage species on all soils. Vona soils initially supported about 2,500 fourwing saltbush (*Atriplex canescens* [Pursh] Nutt.) plants ha$^{-1}$ and a small amount of cool-season grasses, mostly western wheatgrass (*Pascopyrum smithii* [Rydb.] A. Love), and needleandthread (*Stipa comata* Trin. & Rupr.). Ascalon soils generally supported few cool-season grasses. Annual grasses were rare during the study. Common forbs included scarlet globemallow (*Sphaeralcea coccinea* [Pursh.] Rydb.), miner's candles (*Cryptantha* spp.), stickseeds (*Lappula* spp.), prairie spiderwort (*Tradescantia occidentalis* [Britt.] Smyth), and prairie pepperweed (*Lepidium densiflorum* Schrad.) Plains pricklypear (*Opuntia polyacantha* Haw.) was also common.

### Treatments

Treatments were 1] control, 2] atrazine at 1.1 kg ha$^{-1}$ a.i., 3] nitrogen (N) fertilizer at 22 kg ha$^{-1}$ of N, and 4] N + atrazine, both at the above rates. On the N and N + atrazine treatments, ammonium nitrate was broadcast between 16 October and 20 November each year except 1977. The application scheduled for 1977 was postponed until after rain in May 1978, because applying N could have intensified drought mortality of blue grama (Hyder et al. 1975). Atrazine was applied to dormant vegetation in October or November of 1976, 1978, 1979, 1981, and 1983 in 7.6 l ha$^{-1}$ of water.

The control and atrazine treatments were assigned to 64.8-ha pastures, and the N and N + atrazine treatments to 32.4-ha pastures. Each treatment was applied to 2 pastures; the pastures were arranged in 2 randomized blocks, an east and west block. East block pastures had been lightly grazed during the summers of 1957–1973. West block pastures had been moderately grazed during the winters of the same years, except for the control pasture which had been moderately grazed during summers. All pastures were moderately grazed during the summers of 1974–1976. No chemical or mechanical treatments had been applied 1938–1975.

### Vegetation Measurements

Current standing crop of herbage was estimated on grazed and exclosed areas of each pasture in October of 1979-1985. Estimates were to a precision of < 10% of the mean of total herbage, using the micro-unit forage inventory method (Shoop and McIlvain 1963). Two quadrats were estimated inside and 2 outside of each of 80 exclosures/pasture, with every fifth quadrat clipped, dried, and weighed as well as estimated to develop equations for correcting estimated values. Standing crop is expressed as oven-dry weight. Standing crop outside exclosures was similarly estimated each time cattle were weighed.

### Livestock and Grazing Management

In 1979 through 1983, pastures were stocked about 1 June each year with 12- to 15-month-old Hereford steers. In 1984 and 1985, only about half the animals in each pasture were steers; the other half were spayed heifers, weighing an average of 174 kg in 1984 and 223 kg in 1985. Average steer weights ranged from 210 to 243 kg. Put-and-take cattle were added or removed to adjust stocking needs (Fig. 1), as determined from herbage estimates each time the steers were weighed.

All steers were implanted with Ralgro[1] before grazing began. Grazing continued into October each year; the goal was to reduce the herbage remaining to about 400 kg ha$^{-1}$, an amount slightly above the level recommended by Bement (1969). Grazing seasons lasted an average of 132 days.

Average daily gain and gain ha$^{-1}$ were calculated from total gains of all cattle on each pasture during the grazing season. At the beginning and end of the grazing season, weights of each animal were the average of 2 weights taken at 5-day intervals. Weights during the season are single-day weights.

### Economic Analysis

Returns to land, labor and management were calculated using recent prices for cattle, fertilizer, atrazine, application, and miscellaneous costs. Cattle prices were taken from the weekly market reports in Bridges (1992, 1993) and fitted to a response surface (Table 2) in which price was the dependent variable and date and cattle weight were the independent variables. The equation of the response surface was used to calculate the value of each animal, according to its weight and the date, when it was put on pasture and again when it was removed. The sum of these changes in value represented the gross return to the pasture. Sands and Robb (1993) calculated "other expenses (interest, marketing, health care, etc.) of $55...for a 550-pound (250-kg) feeder steer ...over a 5-month grazing season," equivalent to $0.36/day. Hart et al. (1988) calculated similar costs from data of Jose et al. (1985). These expenses and the costs of nitrogen, atrazine, and their application were subtracted from gross returns to provide net returns to land, labor, and management.

Fertilizer, herbicide, and application costs were supplied by Jirdon Agrichem, Torrington, Wyo. Ammonium nitrate cost $0.208 kg$^{-1}$ ($189 ton$^{-1}$) plus $7.50 ha$^{-1}$ ($3.00 A$^{-1}$) to apply. Atrazine cost $9.61 kg$^{-1}$ a.i. ($15.00 gal$^{-1}$, 43% a.i.) plus $8.75 ha$^{-1}$ ($3.50 A$^{-1}$) to apply. Annual atrazine cost was only $9.66 ha$^{-1}$ because it was applied approximately every 2 years.

[1]Mention of a trademark or proprietary product does not constitute a guarantee or warranty of the product by the U.S. Department of Agriculture, and does not imply its approval to the exclusion of other products that may also be suitable.

### Statistical Analysis

The study was conducted as a randomized complete block with 2 replications and repeated measurements over years, which were treated as split-plots. Data were subjected to analysis of variance; when significant differences among means were indicated, means were separated by Duncan's multiple range test (Hruschka 1973) at $P < 0.05$.

In 1979 through 1982, when initial stocking rates on all pastures were increased as the season progressed, a strong relationship was apparent between average daily gain and grazing pressure. This relationship was defined by standard regression methods.

## Results and Discussion

### Herbage Production and Botanical Composition

Nitrogen or atrazine increased October standing crop of blue grama by about half; N + atrazine increased blue grama 77% (Table 3). Years were a significant source of variation in total forage production (Table 4), but the treatment × year interaction was non-significant. Nitrogen alone doubled standing crop of cool-season grasses and nearly tripled standing crop of forbs, while atrazine alone or with N had no effect on forbs and nearly eliminated cool-season grasses. Atrazine and N + atrazine did not significantly reduce forbs below the control level in the current study because the crop of forbs was very small on all 3 treatments. Although atrazine alone did not reduce the forb standing crop below that on the control, reduction of forbs by atrazine was obvious in areas along fences between treatments. Atrazine reduced annual but not perennial forbs in a 3-year study at CPER (Houston 1977).

Standing crop left at the end of the grazing season ranged from a mean of 327 kg ha$^{-1}$ with N + atrazine to 383 kg ha$^{-1}$ with nitrogen alone. Residual forage was somewhat less than the 400 kg ha$^{-1}$ objective of this study, but slightly more than the 335 kg ha$^{-1}$ (300 lb A$^{-1}$) recommended by Bement (1969). Utilization (standing crop minus residual divided by standing crop) ranged from 34% on the control to 60% on N + atrazine. Utilization on the latter was higher than the common "take half, leave half" recommendation, but did not appear to reduce average daily gain.

The increase in total herbage standing crop by N over the control was caused by a large increase in the standing crop of blue grama and small increases in standing crops of cool-season grasses and forbs (Table 3). Application of N at 22 kg ha$^{-1}$ in an earlier CPER study increased abundance of western wheatgrass, a cool-season grass, 66% over the control and increased abundance of some forbs when weather conditions favored their growth (Hyder et al. 1975). The increase in herbage production from N fertilization in the current study is consistent with other studies on ranges where blue grama is the dominant grass. Nitrogen at rates up to 45 kg ha$^{-1}$ increased herbage production as much as 71% (Hyder and Bement 1964, Rauzi et al. 1968, Dwyer and Schickendanz 1971, Donart et al. 1978). Increased blue grama production from N + atrazine over N alone appears to be partially related to a combination of the increased drought mortality of blue grama caused by N and the drought-reducing effect of atrazine (Hyder et al. 1975, Hyder et al. 1976).

Increases in total herbage standing crop by atrazine and N + atrazine over the control were caused entirely by increases in blue grama and occurred in spite of reductions in cool-season grasses (Table 3). Application of atrazine in another CPER study (Houston 1977) also reduced abundance of cool-season grasses. On typical shortgrass range, most cool-season grasses could be

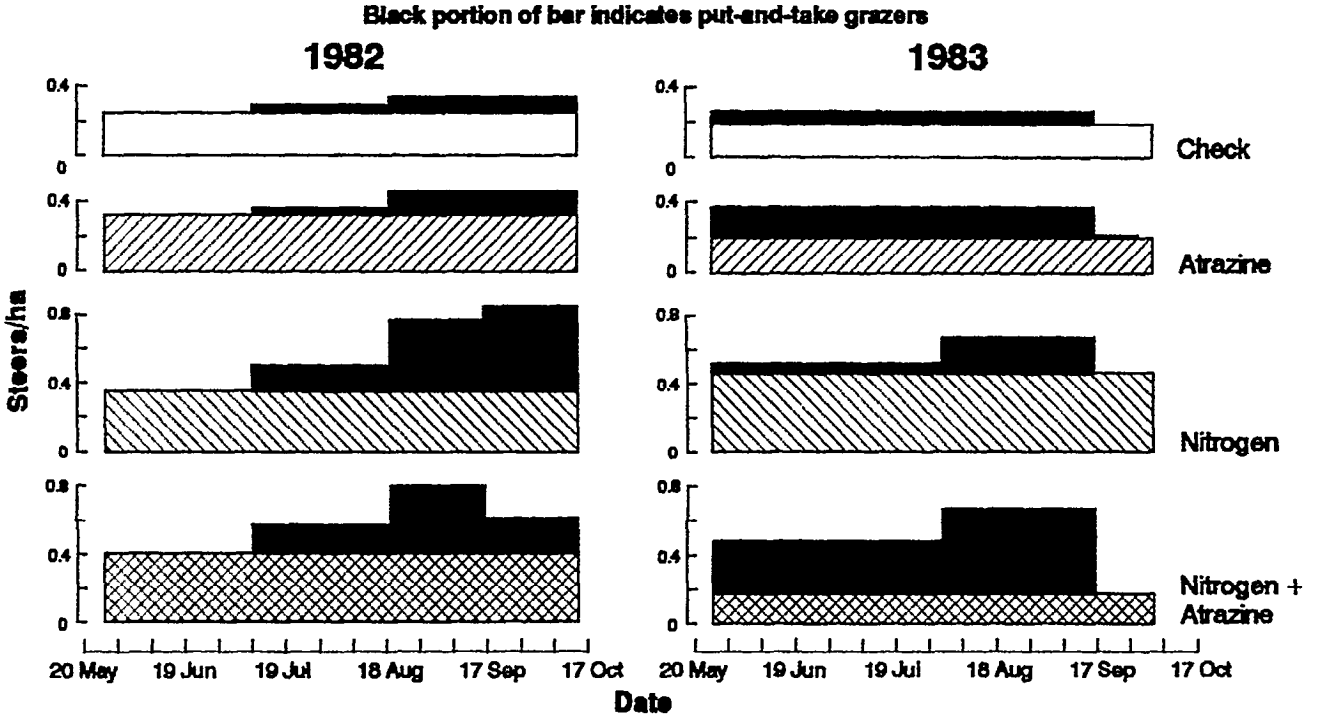


Fig. 1. Seasonal stocking patterns, 1982 and 1983.

Table 2. Steer weights, dates, and steer prices; data from Bridges (1992, 1993). Price = $131.94 + (2093/date) + (16402/weight).

| | Steer weight, kg | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| | 230 | 252 | 274 | 296 | 318 | 340 | 362 | 384 | 406 |
| | Calculated steer price, $ per 100 kg | | | | | | | | |
| May 25 | 217.68 | 211.46 | 206.23 | — | — | — | — | — | — |
| June 5 | 216.67 | 210.44 | 205.21 | 200.77 | — | — | - | — | — |
| June 15 | 215.86 | 209.63 | 204.41 | 199.96 | — | — | — | — | — |
| June 25 | 215.14 | 208.92 | 203.69 | 199.24 | 195.41 | — | — | — | — |
| July 5 | — | 208.28 | 203.05 | 198.60 | 194.77 | — | — | — | — |
| July 15 | — | 207.70 | 202.48 | 198.03 | 194.19 | 190.86 | — | — | — |
| July 25 | — | — | 201.96 | 197.51 | 193.68 | 190.34 | — | — | — |
| August 5 | — | — | 201.55 | 196.99 | 193.16 | 189.82 | 186.89 | — | — |
| August 15 | — | — | — | 196.57 | 192.74 | 189.40 | 186.47 | — | — |
| August 25 | — | — | — | 196.18 | 192.35 | 189.01 | 186.08 | 183.48 | — |
| September 5 | — | — | — | — | 191.96 | 188.62 | 185.69 | 183.09 | — |
| September 15 | — | — | — | — | 191.63 | 188.29 | 185.36 | 182.76 | 180.45 |
| September 25 | — | — | — | — | — | 187.99 | 185.06 | 182.46 | 180.15 |
| October 5 | — | — | — | — | — | 187.71 | 184.78 | 182.18 | 179.87 |
| October 15 | — | — | — | — | — | — | 184.51 | 181.92 | 179.60 |

retained by avoiding application of atrazine to sites where they grow, such as sandy or run-on sites. Plots in an earlier CPER study treated with simazine, another *s*-triazine herbicide, were preferentially grazed by cattle over nontreated plots (Hyder and Bement 1964). Eliminating atrazine application to areas with appreciable amounts of cool-season grasses might be a desirable practice to reduce grazing pressure on these grasses.

Reducing the standing crop of annual plants and cool-season grasses by applying atrazine probably did little to increase standing crop of blue grama. The proportion of annuals and cool-season grasses before atrazine application was too small to provide significant competition. Forb standing crop did not differ in any year between control and atrazine treatments, and the difference in standing crop of cool-season grasses, although significant, was small (29 kg $ha^{-1}$). Various *s*-triazine treatments increased total herbage production up to 60% in plot studies at CPER (Hyder and Bement 1964, Tapia 1973, Houston and van der Sluijs 1973) and increased total herbage elsewhere (Ries 1976, Waller and Schmidt 1983, Currie et al. 1987). These reports did not contain data upon which to judge whether increases in total herbage were caused by herbicidal reduction of competition or by some other response to an *s*-triazine. Some *s*-triazine treatments have not increased total herbage production, especially where application rates were relatively high or when annual plants or *s*-triazine-susceptible grasses were abundant (Allinson 1972, Houston and van der Sluijs 1973, McConnell and Waller 1986).

Table 3. October standing crop, excluding plains pricklypear and shrubs, 1979–1985.

| Species or group | Control | Atrazine | Nitrogen | Nitrogen + atrazine |
|---|---|---|---|---|
| | kg/ha | | | |
| Blue grama | 450 c[1] | 710 b0 | 680 b | 800 a |
| Cool-season grasses | 40 b | 10 c | 80 a | 10 c |
| Other grasses | 80 a | 50 a | 60 a | 70 a |
| Total grasses | 570 c | 760 b | 820 ab | 880 a |
| Forbs | 40 b | 30 b | 130 a | 40 b |

[1]Standing crop figures within a species or species group, followed by the same letter, are not significantly different ($P \leq 0.05$).

## Cattle Gains

Average daily gains (ADG) of cattle did not differ significantly among treatments in any year or over all years (Table 4). Gains may have been reduced in 1984 and 1985 because cattle were about half steers and half spayed heifers. Shoop et al. (1984) reported that spayed heifers pastured with zeranol-implanted steers gained 0.78 kg $day^{-1}$ while the steers gained 0.88 kg $day^{-1}$. In 1984, among cattle which remained on the pastures for the entire grazing season, heifers gained 0.81 kg $day^{-1}$ vs 0.92 kg $day^{-1}$ for steers. It was not possible to make a season-long comparison in 1985 because all the steers were removed from all the pastures from 18 June to 7 August and only heifers grazed the pastures during that time.

Nitrogen fertilization of other ranges with a major blue grama component also has increased gain per head, carrying capacity, and total beef production over no fertilization (Dwyer and Schickendanz 1971, Retzlaff et al. 1974, Donart et al. 1978). In an earlier CPER experiment in which 1.4-ha pastures were grazed heavily for various 1-month periods each summer, N applied at 22 kg $ha^{-1}$ increased steer days of grazing 17 days $ha^{-1}$ and daily gain by 0.15 kg $head^{-1}$ (Hyder et al. 1975). The increase in days of grazing on moderately grazed range in the current study was greater than that reported by Hyder et al. (1975), but daily gain did not increase.

Average daily gains of cattle in the current study (Table 3) were much higher than gains reported by Klipple and Costello (1960) in a study of 3 grazing intensities, but they grazed heifers for 175 to 184 days whereas we grazed mostly steers, treated with Ralgro, for 132 days in the present study. All these factors increased gains in the present study over those reported by Klipple and Costello (1960). Gains probably were much reduced in the last month or so of the Klipple and Costello (1960) study. Klipple (1964) found that ADG of a mixture of steers and heifers, beginning on the tenth of each month, were 0.92, 0.89, 0.84, 0.73, 0.60, and 0.12 kg in May, June, July, August, September, and October, respectively.

Under set-stocking, maximum heifer gains of 0.66 kg $day^{-1}$ were reached at about 23 heifer-days $ha^{-1}$ (Bement 1969) on unfertilized range producing about 600 kg $ha^{-1}$ $yr^{-1}$ at the CPER (unpublished data). As in the Klipple and Costello (1960) study,

Table 4. Vegetation, management, steer gain, and returns to land, labor and management, 1979-1985.

| Year & management | Treatment | October standing crop | Stocking rate | Gain ADG | Return to land, labor ha$^{-1}$ management |
|---|---|---|---|---|---|
| | | kg ha$^{-1}$ | Cattle days ha$^{-1}$ | kg | $ ha$^{-1}$ |
| 1979 | Check | 540 | 21.1 a[2] | 1.00 | 21.6 a | 21.68 a |
| | Atrazine | 698 | 26.7 a | 0.99 | 26.3 a | 14.62 b |
| | Nitrogen | 986 | 25.6 a | 1.04 | 26.4 a | 3.76 c |
| | N + atrazine | 864 | 28.9 a | 1.01 | 28.9 a | -3.82 c |
| | Mean | 772 C | | 1.01 A | | |
| 1980 | Check | 549 | 29.2 b | 0.78 | 22.8 b | 18.20 a |
| | Atrazine | 576 | 40.2 ab | 0.78 | 31.4 ab | 15.52 a |
| | Nitrogen | 783 | 43.8 a | 0.87 | 37.9 a | 11.70 a |
| | N + atrazine | 588 | 47.8 a | 0.69 | 33.0 a | -6.71 b |
| | Mean | 624 C | | 0.78 D | | |
| 1981 | Check | 712 | 37.3 b | 0.68 | 25.7 b | 18.16 a |
| | Atrazine | 1042 | 50.5 ab | 0.76 | 38.2 ab | 19.87 a |
| | Nitrogen | 993 | 55.8 a | 0.80 | 44.7 a | 15.22 ab |
| | N + atrazine | 1053 | 56.1 a | 0.81 | 45.6 a | 11.45 b |
| | Mean | 950 AB | | 0.76 D | | |
| 1982 | Check | 704 | 41.3 c | 0.72 | 29.7 c | 22.16 a |
| | Atrazine | 993 | 54.0 b | 0.76 | 40.7 b | 21.98 a |
| | Nitrogen | 1150 | 82.0 a | 0.74 | 60.9 a | 26.17 a |
| | N + atrazine | 1339 | 83.6 a | 0.71 | 58.6 a | 12.39 b |
| | Mean | 1047 A | | 0.73 D | | |
| 1983 | Check | 589 | 35.0 b | 0.96 | 33.4 b | 30.08 b |
| | Atrazine | 755 | 48.7 b | 0.96 | 46.6 b | 31.25 b |
| | Nitrogen | 1010 | 70.1 a | 0.94 | 66.5 a | 38.81 a |
| | N + atrazine | 857 | 69.4 a | 0.97 | 67.4 a | 30.73 b |
| | Mean | 803 BC | | 0.96 B | | |
| 1984 | Check | 526 | 29.4 c | 0.98 | 28.8 c | 25.91 a |
| | Atrazine | 612 | 43.6 b | 0.93 | 40.8 b | 25.22 a |
| | Nitrogen | 950 | 64.6 a | 0.85 | 55.4 a | 26.67 a |
| | N + atrazine | 891 | 54.0 ab | 0.98 | 52.8 ab | 18.29 b |
| | Mean | 745 C | | 0.93 B | | |
| 1985 | Check | 689 | 24.4 ab | 0.83 | 20.4 ab | 17.04 a |
| | Atrazine | 874 | 34.7 a | 0.88 | 31.2 a | 15.20 a |
| | Nitrogen | 743 | 23.5 ab | 0.89 | 21.2 ab | -2.43 b |
| | N + atrazine | 809 | 18.4 b | 0.94 | 17.2 b | -15.20 c |
| | Mean | 779 C | | 0.88 C | | |
| Mean | Check | 616 X | | 0.85 Z | | 21.88 Z |
| | Atrazine | 793 Y | | 0.87 Z | | 20.52 Z |
| | Nitrogen | 945 Z | | 0.88 Z | | 21.70 Z |
| | N + atrazine | 915 YZ | | 0.87 Z | | 6.73 Y |

[1] Ammonium nitrate costs $0.208 kg$^{-1}$ ($189 T$^{-1}$) + $7.50 ha$^{-1}$ ($3.00/A$^{-1}$) to apply, for a total cost of $20.96 ha$^{-1}$ yr$^{-1}$. Atrazine costs $9.61 kg$^{-1}$ a.i. ($15.00 gal$^{-1}$, 43% a.i.) + $8.75 ha$^{-1}$ ($3.50 A$^{-1}$) to apply; total cost is only $9.66 ha$^{-1}$ yr$^{-1}$ because atrazine is applied every 2 years. Prices from Jirdon Agrichem, Torrington, Wyo.

[2] Figures in the same column and year, followed by the same lower-case letter, and year means and treatment means, followed by the same upper-case letter (A-D and X-Z, respectively) are not significantly different ($P < 0.05$).

heifers gain more slowly than steers and the grazing season was longer, 183 days (1 May to 31 October), than in the present study.

Ashby et al. (1993) reported gains of steers for 7 years under heavy stocking only and grazing seasons of 138 to 147 days. Average daily gain these 7 years was predicted by ADG = 0.665 - 0.00185 GP, when grazing pressure (GP) was expressed as steer-days Mg$^{-1}$ of peak standing crop; $r^2 = 0.25$. In the present study, ADG on the control pastures averaged 0.83 kg at a grazing pressure of 50.6 cattle-d Mg$^{-1}$ of forage; calculated ADG at the same grazing pressure, using the equation of Ashby et al. (1993), was 0.57 kg.

From 1979 through 1982, initial stocking rate was low and then was increased later in the grazing season; the stocking pattern in 1982 is illustrated in Figure 1. In these years, ADG decreased sharply and linearly as total stocking rate for the season increased (Fig. 2). Under this management, the highest stocking rates and grazing pressures occurred at the end of each grazing season when, as noted above, gains are much reduced. In 1983 and 1984, initial stocking rate was high but then was reduced later in the season; the stocking pattern in 1983 is also illustrated in Figure 1. In these years, ADG was not affected by grazing pressure. The latter management is similar to intensive early stocking, which supports higher stocking rates and higher gains than set-stocking (McCollum et al. 1990, Owensby et al. 1988 and Smith and Owensby 1978).

## Economic Analysis

Under put-and-take management and recent prices, estimated returns to land, labor and management were 6%, 1%, and 69% less on the atrazine, N and N + atrazine pastures, respectively, than on the control pastures (Table 4). However, gains and returns were influenced by stocking rate decisions, by the time of year when cattle were added or subtracted from the pastures, and by differences among years, as well as by the impact of treatments on forage production.

Initially, we intended to base our economic analysis on gains ha$^{-1}$ calculated by multiplying the average daily gain of the tester cattle (those that remained on the pastures season-long) by the number of cattle-days ha$^{-1}$. Mott and Lucas (1952) point out that this is not a valid method because forage consumption rates and gains vary widely throughout the season. The gains of put-and-take animals, for whatever part of the season they are on the pasture, are seldom the same as the gains of tester animals for the entire season. For example, in 1982 large numbers of put-and-take animals were on the pastures only during the latter part of the season when gains were reduced, while in 1984 large numbers of put-and-take animals were on the pastures only during the first part of the season when gains were near maximum. In 1982, gain on the N + atrazine pastures was estimated at 70.5 kg ha$^{-1}$ when tester gains were multiplied by cattle-days ha$^{-1}$, but actual gain was only 58.6 kg ha$^{-1}$. In 1984 on the same pastures, gain was estimated at 48.6 kg ha$^{-1}$ when tester gains were multiplied by cattle-days ha$^{-1}$, but actual gain was 52.8 kg ha$^{-1}$. Put-and-take animals contributed as little as 10% (control 1979) to as much as 68% (N + atrazine 1983) of the total cattle-days on pasture.

Although no other treatment produced higher average returns to land, labor, and management than did the check, returns from the N-fertilized pastures were 29% higher in 1983 than returns from the check pastures. These increased returns were attained by a combination of a favorable growing season which produced a large increase in forage when N was applied, and a high stocking rate, particularly early in the grazing season, which efficiently converted forage into cattle gains. Nitrogen increased forage production in other years, but low stocking rate and/or increased stocking rate late in the grazing season did not allow maximum gains and returns.

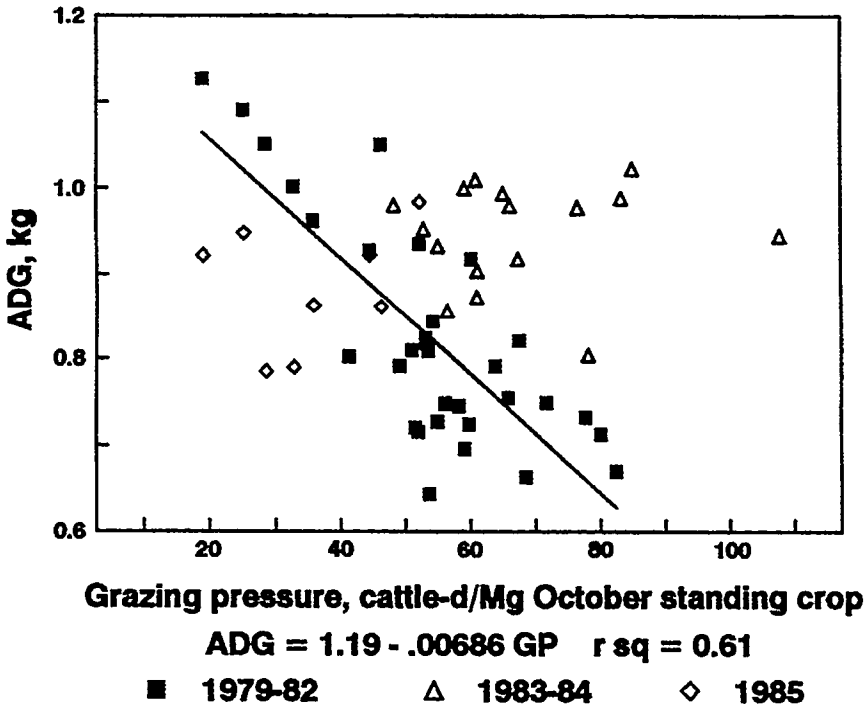


Figure 2. Average daily gain (ADG) vs. grazing pressure (GP) of cattle grazing shortgrass prairie. Response of ADG to GP did not differ significantly among control pastures and pastures receiving N, atrazine, or N + atrazine.

## Conclusions

The most meaningful comparisons of profitability should be made at optimum grazing pressures and stocking strategies. Optimum grazing pressures would have been achieved under heavy stocking early in the season and lighter stocking later. In 1983 and 1984, when pastures were stocked in this way, grazing pressures on all treatments were below the critical grazing pressure, and the data were insufficient for the development of the necessary grazing pressure × gain equations (Hart et al. 1988). Optimum grazing pressures and returns would be somewhat higher than those employed in this study, and it is possible that application of nitrogen or atrazine might be profitable at optimum grazing pressures.

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# Indiangrass and caucasian bluestem responses to different nitrogen sources and rates in the Ozarks

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## Abstract

**Alternatives to cool-season grasses are needed for summer forage production on droughty, infertile soils in the Ozarks. The objective of this research was to compare nitrogen (N) sources and application rates for improving forage production, crude protein concentration, and apparent fertilizer N recovery by 'Rumsey' indiangrass [*Sorghastrum nutans* (L.) Nash] and caucasian bluestem [*Bothriochloa caucasia* (Trin.) C.E. Hubbard]. Pure stands of each species were treated with urea, $NH_4NO_3$, or $(NH_4)_2SO_4$ at 0, 56, 112, and 168 kg N ha$^{-1}$ from 1985-1987. In 1988 the $(NH4)_2SO_4$ treatment was discontinued and in 1990 the N rates were increased to 0, 78, 157, and 235 kg N ha$^{-1}$. Forage yields, crude protein concentrations or both were greater with $NH_4NO_3$ compared to urea in 3 out of 6 years for indiangrass and 4 out of 6 years for caucasian bluestem. Indiangrass forage yields increased with increasing N rates up to 168 kg N ha$^{-1}$. Caucasian bluestem forage yields peaked at 101 kg N ha$^{-1}$ in 1985, 132 kg N ha$^{-1}$ in 1986, 122 kg N ha$^{-1}$ in 1987, 129 kg N ha$^{-1}$ in 1989, and 161 kg N ha$^{-1}$ in 1990. Crude protein concentrations of both species increased linearly with N rates in most years. At the lowest N rate (56 kg N ha$^{-1}$) caucasian bluestem was more efficient than indiangrass in apparent fertilizer N recovery, but at greater N rates the 2 species were similar in fertilizer N recovery. Forage yield and crude protein concentration of both species responded similarly to $(NH_4)_2SO_4$ and $NH_4NO_3$.**

Key Words: *Sorghastrum nutans* (L.) Nash, *Bothriochloa caucasia* (Trin.) C.E. Hubbard, urea, ammonium-nitrate, ammonium-sulfate, fertilizer N recovery.

Tall fescue (*Festuca arundinacea* Schreb.) and other cool-season grasses are the predominant pasture species in the Ozarks. However, Ozark soils are generally shallow, rocky, and low in available nitrogen (N), phosphorus (P), water holding capacity, and pH. Low soil fertility and water holding capacity, combined with high summer temperatures and periodic drought severely reduce cool-season grass forage production during the summer months.

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Native warm-season grasses grow well in acid soils (Jung et al. 1988, Staley et al. 1991), are more efficient in the use of water (Stout et al. 1986), N (Brown 1978, Brown 1985, Staley et al. 1991), P (Wuenscher and Gerloff 1971, Morris et al. 1982), and maintain growth at higher temperatures (Black 1971) than cool-season grasses. Griffin et al. (1980) compared the quality of big bluestem (*Andropogon gerardii* Vitman) and switchgrass (*Panicum virgatum* L.) to tall fescue and concluded that warm-season grass dry matter intake and dry matter digestibility were equal to or superior to summer or fall harvested tall fescue.

Nitrogen fertilizer can increase forage production and quality in warm-season grasses (Perry and Baltensperger 1979, Hall et al. 1982). However, not all N sources are equally efficient in increasing forage production and quality. Economic and environmental concerns require that the most efficient source and rate of N be evaluated before recommendations are made to livestock producers. Urea is more concentrated, less hazardous to store and transport, and generally cheaper than ammonium nitrate ($NH_4NO_3$), but is considered to be an inferior source of N for use on pastures (Wilkinson and Langdale 1974). The presence of plant residues may increase ammonia ($NH_3$) volatilization losses (Hargrove 1988), reducing recovery of N applied as urea. However, Westerman et al. (1983) concluded that urea was an efficient source of N for bermudagrass (*Cynodon dactylon* L.) growing on moderately acid soils in Oklahoma. The low pH of Ozark soils and the practice of burning warm-season grass residues in the spring prior to urea application could reduce $NH_3$ volatilization losses (Jackson and Burton 1962), making urea an efficient source of N for warm-season grasses under these conditions.

Surface application of soluble sulfate salts may decrease exchangeable aluminum ($Al^{3+}$) through the formation of Al-hydroxyl-sulfate minerals or precipitation of $Al^{3+}$ as $Al(OH)_3$ following the exchange of $SO_4^{2-}$ for the OH ligand on hydrous oxide surfaces (Mathews and Joost 1989). Sulfate ($SO_4^{2-}$) salts could improve subsoil fertility and root penetration by reducing exchangeable $Al^{3+}$ toxicity (Mathews and Joost 1989). This suggests that the use of ammonium sulfate [$(NH_4)_2SO_4$] may be an efficient source of N for warm-season grasses on acid soils with high Al content.

Indiangrass [*Sorghastrum nutans* (L.) Nash] and caucasian bluestem [*Bothriochloa caucasia* (Trin.) C.E. Hubbard] grow later into the fall than other warm-season grasses (Waller et al.

1985, Soil Conservation Service 1993) and could be used in the Ozark region to provide high quality forage during the summer months. However, there is no information on appropriate N sources and rates to use in management of these species in the Ozarks. The objective of this research was to identify the best N source and appropriate application rates for improving yield and protein content of indiangrass and caucasian bluestem grown for forage production in the Ozarks.

## Materials and Methods

The research was conducted from 1985–1990 using established pure stands of 'Rumsey' indiangrass and caucasian bluestem at the University of Missouri Southwest Center, Mt. Vernon, Mo. The Hoberg silt loam (fine-loamy, siliceous, mesic Mollic Fragiudalf) soil at the study site is gently sloping (2–5%) with a fragipan at a depth of 40–90 cm. The fragipan limits root growth, produces a perched water table from December through March, but reduces soil water availability during periods without rain in the summer. The available water holding capacity in the top 40 cm is low, ranging from 4.1–6.4 cm. Soil pH of the top 15 cm was 5.57 with an organic matter content of 34 mg $kg^{-1}$. Precipitation was measured at the site with a rain gauge (Table 1).

**Table 1. Growing season precipitation at the University of Missouri Southwest Center during April through September 1985–1991 and the 28-year average.**

| | Year | | | | | | 28-year |
|---|---|---|---|---|---|---|---|
| Month | 1985 | 1986 | 1987 | 1988 | 1989 | 1990 | average |
| | (cm) | | | | | | |
| April | 7.4 | 10.8 | 3.2 | 8.2 | 0.8 | 7.3 | 10.3 |
| May | 11.5 | 5.2 | 9.8 | 5.3 | 12.3 | 36.5 | 11.5 |
| June | 19.7 | 12.6 | 7.1 | 12.6 | 12.0 | 12.0 | 13.0 |
| July | 4.2 | 2.9 | 9.3 | 10.7 | 19.6 | 5.8 | 7.2 |
| August | 23.0 | 10.9 | 14.3 | 18.2 | 9.5 | 7.8 | 10.7 |
| September | 8.1 | 27.0 | 6.0 | 14.6 | 9.9 | 13.3 | 11.8 |
| Total | 73.9 | 69.4 | 49.8 | 62.1 | 64.1 | 82.7 | 64.5 |

Each stand was divided into 3 blocks of 12 plots (3 × 6 m) and each block was treated with a factorial combination of urea, $NH_4NO_3$, or $(NH_4)_2SO_4$ at 4 rates equivalent to 0, 56, 112, and 168 kg N $ha^{-1}$. After 1987 the $(NH_4)_2SO_4$ treatment was discontinued and comparisons were limited to urea and $NH_4NO_3$ at the same rates. In 1990, the N rates were increased to 0, 78, 157, and 235 kg N $ha^{-1}$. The stands were burned in April each year and the N treatments applied 4 weeks later in mid to late May. All plots received spring applications of 22 kg P $ha^{-1}$ and 112 kg K $ha^{-1}$ in 1986 and 1987, and 33 kg P $ha^{-1}$ and 112 kg K $ha^{-1}$ in 1988–1990, to replace P and K removed in the forage harvests.

Forage was harvested from a 1 × 2 m strip in the center of each plot at a 5 cm cutting height using a flail type harvester. Fresh forage weights were measured in the field and a subsample collected from each plot, dried at 65°C for 48 hours in a forced-air oven, and weighed to determine percentage dry matter. The dried subsamples were ground in a Wiley mill to pass a 1-mm screen and analyzed for Kjeldahl-N (Bremner and Mulvaney 1982) and crude protein concentrations were estimated (N × 6.25). Apparent fertilizer N recovery was calculated using the formula of Caswell and Godwin (1984). Indiangrass was harvested on 19 July 1985, 26 June 1986, 25 June 1987, 16 August 1988, 4 August 1989, and 7 July 1990. In 1985–1987, caucasian bluestem was harvested on the same dates as indiangrass. In 1988–1990, an initial caucasian bluestem harvest was taken on 5 July 1988, 6 July 1989, and 9 July 1990 and regrowth was harvested on 16 August 1988, 20 September 1989, and 30 August 1990.

### Statistical Analysis

Data were analyzed separately for each species and harvest using analysis of variance, and fertilizer sources were compared using preplanned orthogonal contrasts. Contrasts compared forage responses to urea versus the average of $NH_4NO_3$ and $(NH_4)_2SO_4$, and $NH_4NO_3$ versus $(NH_4)_2SO_4$. Plant responses to the different N rates were analyzed using orthogonal polynomials for significant linear and quadratic responses (Steel and Torrie 1980). Year effects were treated as repeated measures in time and analyzed using a split-plot design described by Steel and Torrie (1980). Analysis over years was performed for the years 1985 through 1987 and 1988–1989. Data from 1990 were analyzed separately because different N rates were used. Treatment differences were considered significant at the 0.05 probability level.

## Results

### Indiangrass

*Forage Yields*

Indiangrass forage yields varied significantly with years, reflecting yearly differences in growing season precipitation (Table 1) and harvest dates. Year by N source and year by N rate interactions were not significant in 1985–1987 or 1988–1989. Indiangrass forage yields did not differ with N source in 1985–1987, and the N source by rate interaction was not significant for these 3 years. Within years, indiangrass forage yields increased linearly with N rate in 1985, but increased curvilinearly with N rate in 1986 and 1987 (Fig. 1). May and June precipitation was below normal in both 1986 and 1987 (Table 1), which may have limited forage production at the higher N rates, producing the curvilinear yield response.

Indiangrass forage yields in 1988 (Fig. 1) and 1989 (Fig. 2) were the greatest for the 6 year period of study. In 1988 and 1989, indiangrass was harvested in August and growing season precipitation prior to harvest was near the long term average (Table 1). Good growing season precipitation and a delay in the forage harvest combined to produce high forage yields. In 1988, indiangrass forage yields did not differ between $NH_4NO_3$ and urea, and yields increased curvilinearly with N rate. In 1989 and 1990, indiangrass forage yields increased linearly with increasing rate of urea, but increased curvilinearly with increasing rate of $NH_4NO_3$ (Fig. 2). At intermediate N rates, indiangrass produced 1,300–1,550 kg $ha^{-1}$ more forage when treated with $NH_4NO_3$ compared to urea, but produced similar yields at the highest rate of both N sources.

*Crude Protein Concentrations*

Indiangrass crude protein concentrations increased linearly with N rate in 1985 and 1986, but increased curvilinearly with N rate in 1987. In addition, the magnitude of the linear increase in

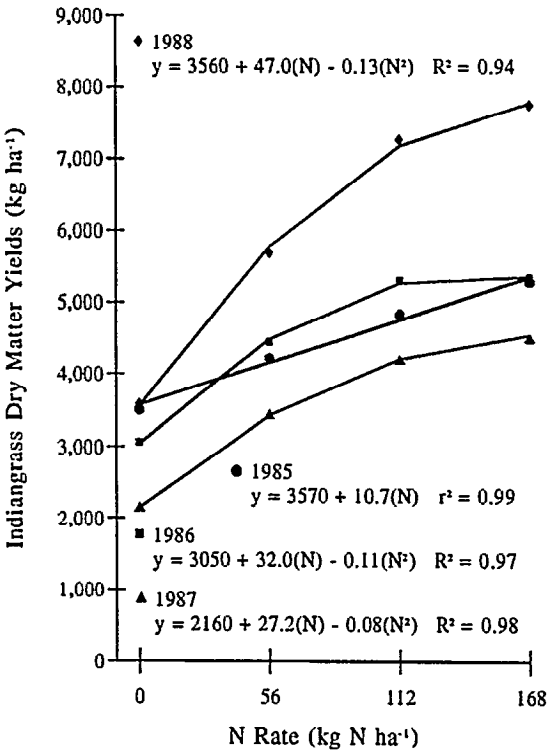


**Fig. 1. Indiangrass forage dry matter yields averaged over N sources (urea, $NH_4NO_3$, and $(NH_4)_2SO_4$) at 4 application rates from 1985-1988.**

crude protein concentrations with N rate was greater in 1986 than in 1985, causing an N rate by year interaction (Fig. 3). In 1985, $NH_4NO_3$ and $(NH_4)_2SO_4$ produced an additional 0.98–1.59% (absolute) crude protein compared to urea at all N rates (Fig. 3). In 1986 and 1987, indiangrass crude protein concentrations did not differ significantly between the 3 N sources (Fig. 3). In 1988 and 1990, indiangrass crude protein concentrations increased linearly with N rate, but the increase was greater for $NH_4NO_3$ than urea, causing a significant N source by rate interaction (Fig. 4). At low N rates (56 kg N $ha^{-1}$ in 1988 and 78 kg $ha^{-1}$ in 1990), indiangrass crude protein concentrations were similar for $NH_4NO_3$ and urea. However, at rates greater than 112 kg N $ha^{-1}$, crude protein concentrations were 0.38–1.50% greater with $NH_4NO_3$ than urea.

In 1989, indiangrass crude protein concentrations were low at all N rates, with no difference between $NH_4NO_3$ and urea (Fig. 4). In 1989, abundant May, June, and July precipitation (Table 1) produced the greatest indiangrass forage yields for the 6 year period. The abundant growth may have diluted tissue N levels and high precipitation amounts may have leached fertilizer N from the soil, reducing N uptake.

*Apparent Fertilizer N Recovery*

Apparent fertilizer N recovery by indiangrass varied significantly with years (Table 2). However, the year by N source and year by N rate interactions were not significant for apparent fertilizer N recovery. In 1985, 4–18% more fertilizer N was recovered by indiangrass fertilized with $NH_4NO_3$ and $(NH_4)_2SO_4$ compared to urea. Apparent fertilizer N recovery by indiangrass was not significantly different between the 2 $NH_4^+$ sources. In 1986, apparent fertilizer N recovery by indiangrass was not significantly different between the N sources or rates. In 1987, apparent fertilizer N recovery decreased linearly with increasing N rate, but N recovery did not differ with N source. In 1988–1990, indiangrass recovered 4.3–23.9% more fertilizer N from $NH_4NO_3$ than from urea. In addition, in 1990 apparent fertilizer N recovery decreased

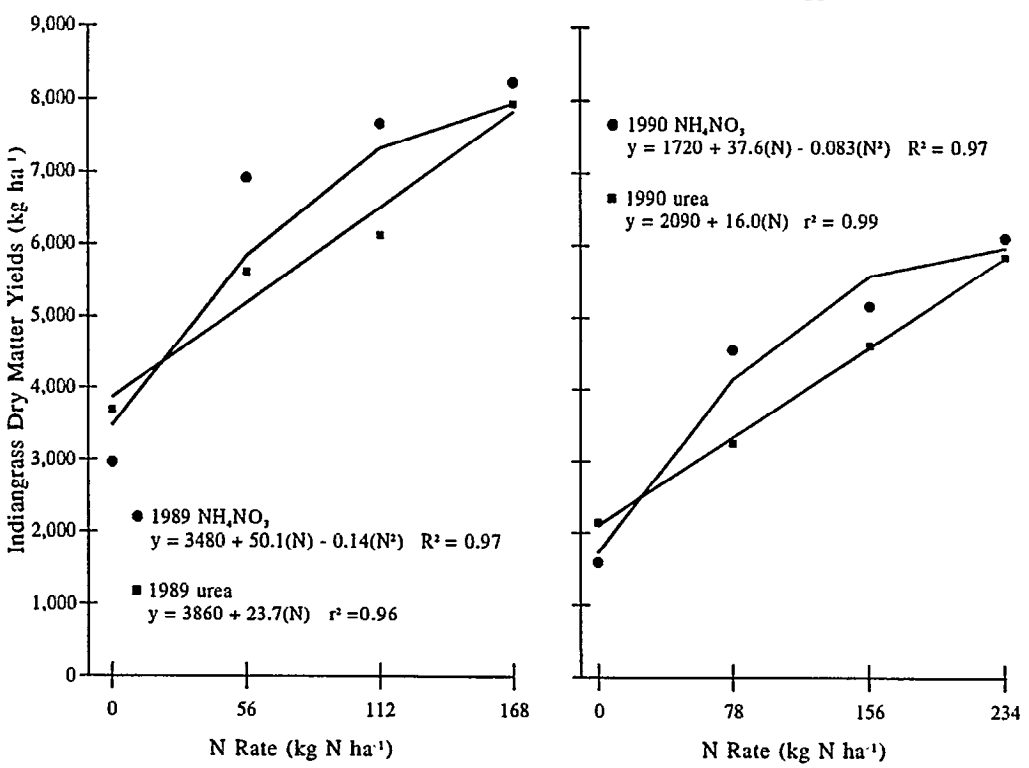


**Fig. 2. Indiangrass forage dry matter yields treated with urea or $NH_4NO_3$ at 4 application rates in 1989 and 1990.**

Table 2. Nitrogen uptake in unfertilized control plots and apparent fertilizer N recovery by indiangrass during 1985-1990 when N was applied as urea (U), $NH_4NO_3$ (AN), or $(NH_4)_2SO_4$ (AS).

| N rate | Year | | | | | | 6-year average |
|---|---|---|---|---|---|---|---|
| | 1985 | 1986 | 1987 | 1988 | 1989 | 1990[1] | |
| N uptake in unfertilized control plots | | | | | | | |
| | (kg ha$^{-1}$) | | | | | | |
| | 31 | 30 | 20 | 29 | 20 | 17 | 25 |
| Apparent fertilizer N recovery | | | | | | | |
| | (%) | | | | | | |
| Urea | | | | | | | |
| 56 | 19 | 42 | 43 | 24 | 29 | 30 | 31 |
| 112 | 19 | 49 | 45 | 42 | 29 | 28 | 35 |
| 168 | 24 | 42 | 39 | 32 | 31 | 33 | 33 |
| Ammonium nitrate | | | | | | | |
| 56 | 37 | 51 | 48 | 48 | 39 | 53 | 46 |
| 112 | 35 | 51 | 41 | 50 | 40 | 41 | 43 |
| 168 | 27 | 38 | 36 | 41 | 35 | 37 | 36 |
| Ammonium sulfate | | | | | | | |
| 56 | 38 | 47 | | | | 50 | 45 |
| 112 | 36 | 51 | | | | 43 | 43 |
| 168 | 9 | 40 | | | | 34 | 34 |
| Analysis of variance | | | | | | | |
| | (P>F) | | | | | | |
| N source | 0.01 | NS | NS | 0.05 | 0.05 | 0.01 | |
| AN + AS vs U | 0.01 | NS | NS | — | — | — | |
| AN vs AS | NS | NS | NS | — | — | — | |
| N rate | NS | NS | 0.05 | NS | NS | NS | |
| N linear | NS | NS | 0.05 | NS | NS | NS | |
| N quadratic | NS | NS | NS | NS | NS | NS | |
| N source NS × rate | NS | NS | NS | NS | 0.05 | | |

[1]N rates in 1990 were 78, 157, and 235 kg N ha$^{-1}$.

with increasing rate of $NH_4NO_3$, but changed little with increasing rate of urea (Table 2), resulting in a significant N source by rate interaction. Other than the linear decrease in apparent fertilizer N recovery with increasing N rate in 1987 and the N source by rate interaction in 1990, N rate had little effect on apparent fertilizer N recovery.

Fertilizer N recovery by indiangrass in our study was lower than the values of 52–66% reported by McMurphy et al. (1975) in Oklahoma. However, apparent fertilizer N recovery was 2-fold greater than values calculated from data by Jung et al. (1990) for indiangrass treated with 75 kg N ha$^{-1}$ in Pennsylvania. Nitrogen uptake by indiangrass on control plots in our study averaged 24.5 kg ha$^{-1}$ and varied considerably with years (Table 2), but was lower than the 40 kg N ha$^{-1}$ reported by Jung et al. (1990) for indiangrass harvested at head emergence in Pennsylvania. Soils at our site and the Pennsylvania site were similar, but the longer growing season in southern Missouri compared to Pennsylvania may in part explain the differences in apparent fertilizer N recovery.

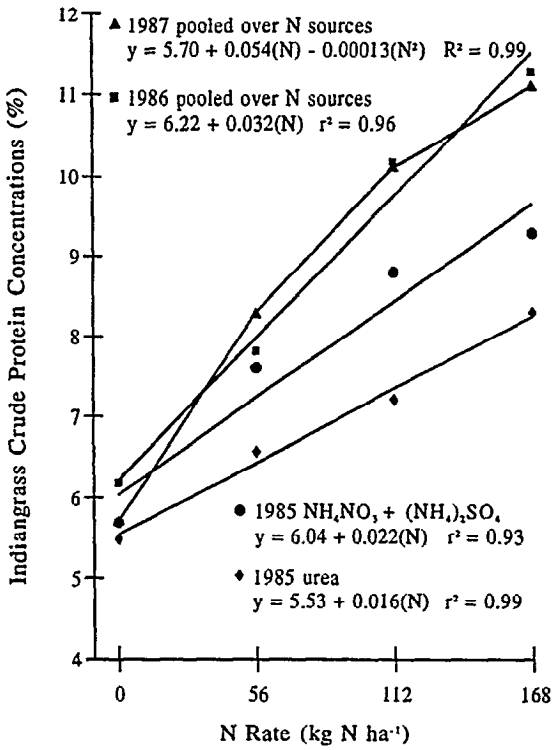


Fig. 3. Crude protein concentrations of indiangrass treated with urea, $NH_4NO_3$ or $(NH_4)_2SO_4$ at 4 application rates in 1985, and averaged over N sources in 1986 and 1987.

## Caucasian Bluestem

### *Forage Yields*

Caucasian bluestem yields varied significantly with years in 1985–1987 and 1988–89, reflecting differences in growing season precipitation (Table 1) and harvest dates. In addition, in 1988–1989 the year by N rate interaction was significant for both the first and regrowth harvest forage yields. The year by N source interaction was not significant in 1985–1987 or for either harvest in 1988-1989.

In 1985, caucasian bluestem forage yields were significantly greater with $NH_4NO_3$ and $(NH_4)_2SO_4$ than urea at all N rates (Table 3). Caucasian bluestem forage yields increased linearly with increasing rates of $(NH_4)_2SO_4$, but increased curvilinearly with increasing rates of $NH_4NO_3$ and urea, with a 1,000 kg ha$^{-1}$ yield decrease at the highest N rate. Campbell et al. (1977) reported decreased dry matter accumulation by spring wheat (*Triticum aestivum* L.) with rates of N exceeding 61.5 kg N ha$^{-1}$. They concluded that greater rates of N stimulated excessive growth early in the spring which increased transpiration and more rapid use of soil moisture. As a result, plants suffered greater levels of moisture stress during extended periods between rains, depressing dry matter production.

In 1985, caucasian bluestem forage yields peaked at 5,450 kg ha$^{-1}$ at 101 kg N ha$^{-1}$ with $NH_4NO_3$ and 4,720 kg ha$^{-1}$ at the same N rate with urea. In 1986 and 1987, caucasian bluestem forage yields increased curvilinearly with N rate, with no difference between the N sources both years (Table 3). A maximum yield of 5,590 kg forage ha$^{-1}$ was reached at 132 kg N ha$^{-1}$ in 1986 and a yield peak of 5,690 kg forage ha$^{-1}$ was attained at 122 kg N ha$^{-1}$ in

Table 3. Forage dry matter yields and crude protein concentrations of caucasian bluestem treated with $NH_4NO_3$ (AN), $(NH_4)_2SO_4$ (AS) or urea (U) at 4 rates.

| N rate | 1985 | | | 1986 | | | 1987 | | |
|---|---|---|---|---|---|---|---|---|---|
| | $NH_4NO_3$ | $(NH_4)_2SO_4$ | urea | $NH_4NO_3$ | $(NH_4)_2SO_4$ | urea | $NH_4NO_3$ | $(NH_4)_2SO_4$ | urea |
| Dry matter yields | | | | | | | | | |
| | | | | (kg ha$^{-1}$) | | | | | |
| 0 | 2440 | 2510 | 2420 | 3110 | 2880 | 2490 | 3450 | 3540 | 3550 |
| 56 | 5000 | 4450 | 4200 | 5170 | 4890 | 4660 | 5880 | 5570 | 5530 |
| 112 | 5280 | 4830 | 4730 | 5760 | 4940 | 5270 | 5790 | 5870 | 5470 |
| 168 | 4250 | 5940 | 3690 | 5610 | 5530 | 5240 | 5810 | 6230 | 5410 |
| Analysis of variance | | | | | | | | | |
| | | | | (P>F) | | | | | |
| N source | | 0.05 | | | NS | | | NS | |
| AN + AS vs U | | 0.05 | | | NS | | | NS | |
| AN vs AS | | NS | | | NS | | | NS | |
| N rate | | 0.01 | | | 0.01 | | | 0.01 | |
| N linear | | 0.01 | | | 0.01 | | | 0.01 | |
| N quadratic | | 0.01 | | | 0.01 | | | 0.01 | |
| N source × rate | | 0.05 | | | NS | | | NS | |
| Crude protein concentrations | | | | | | | | | |
| | | | | (%) | | | | | |
| 0 | 5.5 | 5.7 | 5.9 | 5.7 | 5.7 | 6.0 | 5.3 | 5.2 | 5.0 |
| 56 | 6.3 | 6.0 | 5.3 | 8.0 | 8.0 | 7.1 | 7.3 | 7.8 | 7.1 |
| 112 | 7.6 | 8.4 | 7.1 | 9.9 | 10.3 | 9.0 | 9.0 | 8.8 | 8.1 |
| 168 | 8.8 | 8.3 | 8.8 | 12.8 | 11.8 | 10.3 | 8.5 | 10.0 | 9.1 |
| Analysis of variance | | | | | | | | | |
| | | | | (P>F) | | | | | |
| N source | | | | | NS | 0.01 | NS | | |
| AN + AS vs U | | NS | | | 0.01 | | | NS | |
| AN vs AS | | NS | | | NS | | | NS | |
| N rate | | 0.01 | | | 0.01 | | | 0.01 | |
| N linear | | 0.01 | | | 0.01 | | | 0.01 | |
| N quadratic | | NS | | | NS | | | 0.01 | |
| N source × rate | | NS | | | 0.01 | | | NS | |

1987.

In 1988, caucasian bluestem forage yields from the first harvest increased linearly with N rate, and did not differ significantly between $NH_4NO_3$ and urea. However, with the regrowth forage harvest caucasian bluestem forage yields increased curvilinearly with N rate, and the magnitude of the increase was greater for $NH_4NO_3$ than urea at intermediate N rates, causing an N source by rate interaction (Table 4). Caucasian bluestem forage yields from the regrowth harvest were 2,450 to 2,600 kg ha$^{-1}$ greater than forage yields from the first harvest. In 1988, April precipitation was 2.1 cm below normal, and May precipitation was less than half of normal (Table 1), reducing first harvest yields. In contrast, July precipitation was 3.5 cm and August precipitation 7.5 cm above normal (Table 1), stimulating high regrowth forage yields (Table 4).

In 1989, May and June precipitation was near normal, and caucasian bluestem forage yields were the greatest of the 6 year period. First harvest forage yields increased curvilinearly with N rate, but did not differ significantly between $NH_4NO_3$ and urea. A maximum forage yield of 7,550 kg ha$^{-1}$ was attained with 129 kg N ha$^{-1}$. In 1989, July precipitation was 12.4 cm above normal, delaying the regrowth harvest until 20 September, and resulting in the greatest caucasian bluestem regrowth yields for the 3 year period. Regrowth forage yields increased linearly with N rate, with no difference between $NH_4NO_3$ and urea.

In 1990, first harvest and regrowth forage yields were low, with no significant difference between $NH_4NO_3$ and urea (Table 4). First harvest yields increased curvilinearly with N rate, in which forage yields peaked at 3,000 kg ha$^{-1}$ with 161 kg N ha$^{-1}$. Cool spring temperatures and excessive precipitation in 1990 may have reduced first harvest forage yields. The site received 36.5 cm precipitation (25 cm above normal) in May 1990 (Table 1). Inhibition of percolation by the fragipan caused saturated soil conditions which persisted for an extended period of time. Caucasian bluestem does not tolerate saturated soils (Soil Conservation Service 1993).

Caucasian bluestem regrowth yields were also low in 1990. This may reflect slow recovery from the saturated soil conditions in the spring, or below normal July and August precipitation (Table 1). Regrowth forage yields increased linearly with N rate, with no difference between $NH_4NO_3$ and urea.

### *Crude Protein Concentrations*

In 1985–1987, caucasian bluestem crude protein concentrations increased linearly with N rate in 1985 and 1986, but increased curvilinearly with N rate in 1987. In addition, the magnitude of the linear increase in caucasian bluestem crude protein concentrations was greater in 1986 than in 1985, causing a significant year

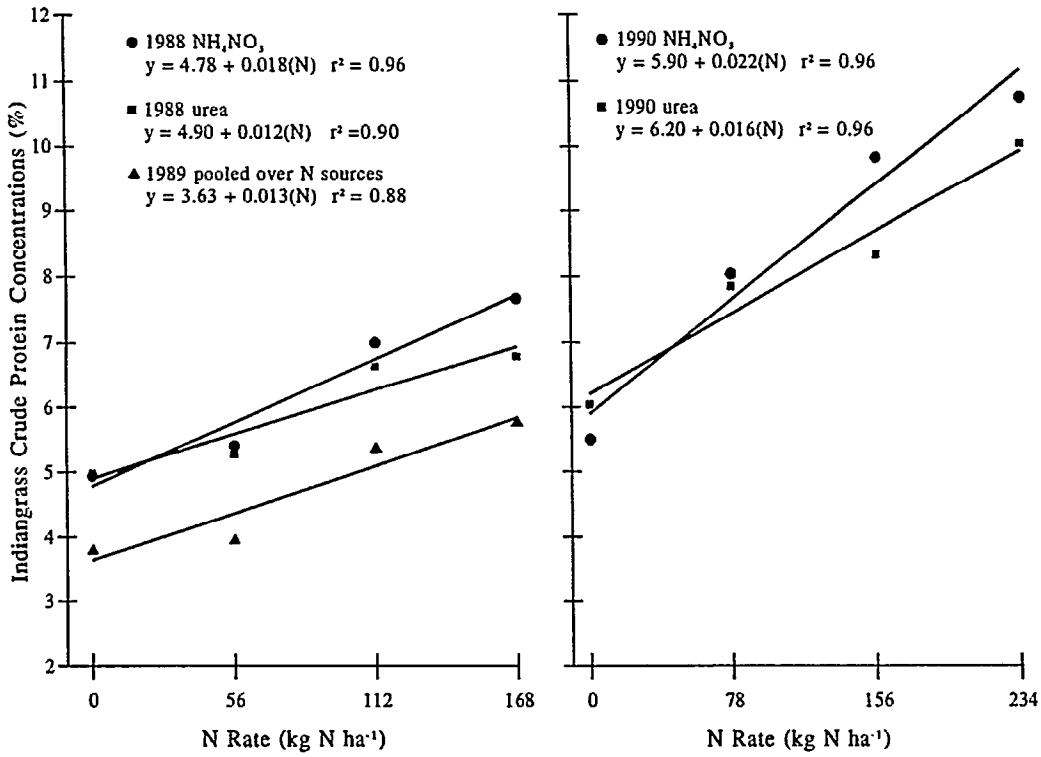


**Fig. 4. Indiangrass crude protein concentrations treated with urea or $NH_4NO_3$ at 4 application rates in 1988-1990.**

by N rate interaction. The year by N source interaction was not significant.

In 1985, caucasian bluestem crude protein concentrations did not differ significantly between the 3 N sources (Table 3). In 1986, caucasian bluestem crude protein concentrations increased linearly with N rate, and the magnitude of the increase was greater with $NH_4NO_3$ and $(NH_4)_2SO_4$ than urea, causing an N source by rate interaction (Table 3). There was no difference between the 2 $NH_4^+$ sources. In 1987, caucasian bluestem crude protein concentrations increased curvilinearly with N rate, and did not differ significantly between the 3 N sources (Table 3).

In 1988, caucasian bluestem crude protein concentrations from the first harvest increased linearly with N rate, and were greater with $NH_4NO_3$ than urea. However, with the regrowth harvest in 1988, caucasian bluestem crude protein concentrations increased curvilinearly with N rate, and the increase was greater with $NH_4NO_3$ than urea, causing an N source by rate interaction (Table 4). This suggests that with the regrowth harvest in 1988, $NH_4NO_3$ provided a greater residual N response than urea.

Caucasian bluestem crude protein concentrations for the first and regrowth harvests in 1989 were the lowest of the 6 year period. Crude protein concentrations did not differ significantly between $NH_4NO_3$ and urea for either harvest. Caucasian bluestem crude protein concentrations increased linearly with increasing N rate for the first harvest, but increased curvilinearly with the regrowth harvest (Table 4). The abundant precipitation in 1989 stimulated the greatest caucasian bluestem forage yields for the 6 year period, which may have diluted crude protein concentrations and leached fertilizer N from the soil.

In 1990, caucasian bluestem crude protein concentrations from the first harvest increased linearly with N rate, and were significantly greater for $NH_4NO_3$ than urea (Table 4). Caucasian bluestem crude protein concentrations for the 1990 regrowth harvest increased linearly with N rate, and the magnitude of the increase was greater for $NH_4NO_3$ than urea, causing an N source by rate interaction.

### Apparent Fertilizer N Recovery

Nitrogen uptake by caucasian bluestem in untreated control plots varied from a high of 29 kg N $ha^{-1}$ in 1987 to a low of 11 kg N $ha^{-1}$ in 1990 (Table 5). These values were lower than an average value of 34.5 kg N $ha^{-1}$ reported for unfertilized caucasian bluestem growing on droughty soils in Pennsylvania (Jung et al. 1990), but greater than an average value of 7 kg $ha^{-1}$ reported for old world bluestem (*Bothriochloa ischaemum* L.) in western Oklahoma (Berg 1990). However, in western Oklahoma, old world bluestem forage yields averaged only 800 kg $ha^{-1}$ without N fertilization (Berg 1990) compared to 2,730 kg $ha^{-1}$ for caucasian bluestem in this study.

Apparent fertilizer N recovery by caucasian bluestem during 1985 through 1987 was significantly greater with $NH_4NO_3$ and $(NH_4)_2SO_4$ than urea, but did not differ significantly between the 2 $NH_4^+$ sources (Table 5). In 1985, apparent fertilizer N recovery declined linearly with increasing rate of $(NH_4)_2SO_4$, but showed no consistent change with increasing rates of $NH_4NO_3$ and urea, causing an N source by rate interaction (Table 5). In 1986 and 1987, apparent fertilizer N recovery declined linearly with increasing N rate, with no significant difference between the 3 N sources.

In 1988, apparent fertilizer N recovery by caucasian bluestem did not differ significantly between N sources or rates (Table 5). In 1989, apparent fertilizer N recovery by caucasian bluestem

Table 4. Forage dry matter yields and crude protein concentrations of caucasian bluestem treated with $NH_4NO_3$ (AN) or urea (U) at 4 rates.

| | 1988 | | | | 1989 | | | | 1990[1] | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | first | | regrowth | | first | | regrowth | | first | | regrowth | |
| N rate | $NH_4NO_3$ | urea | $NH_4NO_3$ | urea | $NH_4NO_3$ | urea | $NH_4NO_3$ | urea | $NH_4NO_3$ | urea | $NH_4NO_3$ | urea |
| Dry matter yields | | | | | | | | | | | | |
| | (kg ha$^{-1}$) | | | | | | | | | | | |
| 0 | 490 | 690 | 2040 | 2370 | 1750 | 1870 | 1860 | 1620 | 400 | 460 | 730 | 880 |
| 56 | 1320 | 1400 | 4010 | 3540 | 5570 | 6740 | 2290 | 2740 | 2060 | 2470 | 1200 | 930 |
| 112 | 1560 | 1930 | 4510 | 3930 | 7100 | 6980 | 4220 | 4510 | 2780 | 3330 | 1460 | 1320 |
| 168 | 2510 | 2270 | 4790 | 5070 | 7020 | 7300 | 6000 | 5480 | 2270 | 2620 | 1660 | 1920 |
| Analysis of variance | | | | | | | | | | | | |
| | (P>F) | | | | | | | | | | | |
| N source | NS | | NS | | NS | | NS | | NS | | NS | |
| N rate | 0.01 | | 0.01 | | 0.01 | | 0.01 | | 0.01 | | 0.01 | |
| N linear | 0.01 | | 0.01 | | 0.01 | | 0.01 | | 0.01 | | 0.01 | |
| N quadratic | NS | | 0.05 | | 0.01 | | NS | | 0.01 | | NS | |
| N source × rate | NS | | 0.05 | | NS | | NS | | NS | | NS | |
| Crude protein concentrations | | | | | | | | | | | | |
| | (%) | | | | | | | | | | | |
| 0 | 9.0 | 8.1 | 4.4 | 4.6 | 4.5 | 4.3 | 3.7 | 3.7 | 7.7 | 6.3 | 4.3 | 4.5 |
| 56 | 12.1 | 10.8 | 5.1 | 4.6 | 4.4 | 4.7 | 3.4 | 3.5 | 7.6 | 6.1 | 5.2 | 4.6 |
| 112 | 14.8 | 11.4 | 5.6 | 5.8 | 6.0 | 6.8 | 3.5 | 3.6 | 9.9 | 8.2 | 7.2 | 5.3 |
| 168 | 14.0 | 13.7 | 7.9 | 6.4 | 6.8 | 6.8 | 4.5 | 4.2 | 10.7 | 9.2 | 8.3 | 6.3 |
| Analysis of variance | | | | | | | | | | | | |
| | P>F) | | | | | | | | | | | |
| N source | 0.05 | | 0.05 | | NS | | NS | | 0.01 | | 0.01 | |
| N rate | 0.01 | | 0.01 | | 0.01 | | 0.05 | | 0.01 | | 0.01 | |
| N linear | 0.01 | | 0.01 | | 0.01 | | 0.05 | | 0.01 | | 0.01 | |
| N quadratic | NS | | 0.01 | | NS | | 0.05 | | NS | | NS | |
| N source × rate | NS | | 0.05 | | NS | | NS | | NS | | 0.01 | |

[1]N rates in 1990 were 78, 157 and 235 kg N ha$^{-1}$.

decreased linearly with increasing rate of urea, but did not change significantly with increasing rates of $NH_4NO_3$, causing an N source by rate interaction (Table 5). Caucasian bluestem had greater apparent fertilizer N recovery when treated with urea compared to $NH_4NO_3$ only in 1989 (Table 5). This response was not observed with indiangrass. At the 56 and 112 kg N ha$^{-1}$ rates in this study, apparent fertilizer N recovery was generally greater than values calculated from data by Jung et al (1990) for caucasian bluestem treated with 75 kg N ha$^{-1}$ in Pennsylvania, and for old world bluestem treated with 35 and 70 kg N ha$^{-1}$ in western Oklahoma (Berg 1990).

At 56 kg N ha$^{-1}$, an average of 13% more fertilizer N was recovered by caucasian bluestem than by indiangrass. However, at greater N rates, apparent fertilizer N recovery was similar for the 2 warm-season grasses. Greater apparent fertilizer N recovery by caucasian bluestem was expected because caucasian bluestem was harvested twice in 1988 through 1990, while indiangrass was harvested once. Differences in apparent fertilizer N recovery among warm-season grass species have been reported. For instance, weeping lovegrass [*Eragrostis curvula* (Schrad.) Ness] recovered significantly more fertilizer N than 'Kaw' big bluestem, 'Caddo' switchgrass or indiangrass in Oklahoma (McMurphy et al. 1975).

## Discussion

All 3 N sources increased indiangrass and caucasian bluestem forage yields and crude protein concentrations on shallow, droughty soils of the Ozarks, but they were not equally effective. With indiangrass, urea was as effective as $NH_4NO_3$ in increasing both forage production and crude protein concentrations in 3 of 6 years (1986, 1987 and 1990). With caucasian bluestem, urea was as effective as $NH_4NO_3$ in increasing both forage production and protein concentrations only 2 of 6 years (1987 and 1989). Similar results were reported by Berg (1993) for old world bluestem in western Oklahoma. Forage yields were greater with $NH_4NO_3$ than urea 2 out of 4 years, but there was no difference between the 2 N sources the other 2 years. This suggests that despite the low soil pH and the practice of removing grass residues by burning in the spring, urea was less reliable as a N source than $NH_4NO_3$ at this site.

Because urea is more concentrated, less hazardous to store and transport, generally cheaper and more readily available than $NH_4NO_3$, it will continue to be widely used by producers. Therefore, other management techniques may be needed that will reduce N losses from urea and improve its effectiveness relative to $NH_4NO_3$ for increasing forage yields and crude protein concentrations.

Indiangrass and caucasian bluestem forage yield and crude pro-

**Table 5. Nitrogen uptake in unfertilized control plots and apparent fertilizer N recovery by caucasian bluestem during 1985-1990 when N was applied as urea (U), $NH_4NO_3$ (AN), or $(NH_4)_2SO_4$ (AS).**

| N rate | Year 1985 | 1986 | 1987 | 1988 | 1989 | 1990[1] | 6-year average |
|---|---|---|---|---|---|---|---|
| N uptake in unfertilized control plots | | | | | | | |
| | (kg ha$^{-1}$) | | | | | | |
| | 22 | 26 | 29 | 24 | 23 | 11 | 22 |
| Apparent Fertilizer N Recovery | | | | | | | |
| | (%) | | | | | | |
| Urea | | | | | | | |
| 56 | 22 | 48 | 60 | 47 | 77 | 26 | 47 |
| 112 | 28 | 44 | 38 | 43 | 70 | 28 | 42 |
| 168 | 18 | 36 | 29 | 46 | 56 | 20 | 34 |
| Ammonium nitrate | | | | | | | |
| 56 | 50 | 71 | 70 | 61 | 52 | 31 | 56 |
| 112 | 38 | 58 | 49 | 48 | 62 | 32 | 48 |
| 168 | 21 | 53 | 30 | 55 | 57 | 21 | 40 |
| Ammonium sulfate | | | | | | | |
| 56 | 37 | 65 | 72 | | | | 58 |
| 112 | 39 | 50 | 47 | | | | 45 |
| 168 | 34 | 47 | 42 | | | | 41 |
| Analysis of Variance | | | | | | | |
| | (P>F) | | | | | | |
| N source | 0.01 | 0.05 | 0.05 | NS | 0.05 | NS | |
| AN + AS vs U | 0.01 | 0.05 | 0.05 | — | — | — | |
| AN vs AS | NS | NS | NS | — | — | — | |
| N rate | 0.05 | 0.05 | 0.01 | NS | NS | NS | |
| N linear | 0.05 | 0.05 | 0.01 | NS | NS | NS | |
| N quadratic | NS | NS | NS | NS | NS | NS | |
| N source × rate | 0.05 | NS | NS | NS | 0.05 | NS | |

[1]N rates in 1990 were 78, 157 and 235 kg N ha$^{-1}$.

tein concentration responses to $(NH_4)_2SO_4$ and $NH_4NO_3$ were similar each year. There appears to have been no benefit from the $SO_4^{2+}$ salt in increasing indiangrass or caucasian bluestem forage yield, crude protein concentration, or fertilizer N recovery at this site. Warm-season grasses display good tolerance to low soil pH and high exchangeable Al levels (Jung et al. 1988), and did not appear to be limited by these soil properties.

Although this study was not designed to compare the 2 grasses, some interesting differences stand out. Caucasian bluestem forage yields varied considerably with year, and may have been more dependent upon precipitation amounts and distribution during the growing season. Berg (1990) reported significant year-to-year variation in old world bluestem forage yield responses to N fertilizer due to wide variation in growing season precipitation in western Oklahoma. In our study, caucasian bluestem produced greater forage yields than indiangrass in 1987 with a single forage harvest, and in 1989 with 2 forage harvests. But indiangrass produced greater forage yields than caucasian bluestem in 1988 and 1990, even though caucasian bluestem was harvested twice. Indiangrass tended to have greater crude protein concentrations than caucasian bluestem from 1985–1987 when the forage was harvested on the same day. However, in 1988–1990, when the first caucasian bluestem harvest was taken earlier in the growing season to allow for a regrowth harvest, caucasian bluestem had greater crude protein concentrations.

Indiangrass yields increased with increasing N rates up to 168 kg N ha$^{-1}$. In Iowa, Hall et al. (1982) reported that indiangrass generally responded positively to N through 75 kg N ha$^{-1}$, and often through 150 kg N ha$^{-1}$, and in Nebraska warm-season grasses responded to rates of up to 180 kg N ha$^{-1}$ (Rehm et al. 1976).

Caucasian bluestem yields peaked at 101 kg N ha$^{-1}$ in 1985, 132 kg N ha$^{-1}$ in 1986, 122 kg N ha$^{-1}$ in 1987, 129 kg N ha$^{-1}$ in 1989, and 161 kg N ha$^{-1}$ in 1990. In this study, caucasian bluestem forage yields peaked at greater N rates than the 66 kg N ha$^{-1}$ recommended for caucasian bluestem (Berg 1985) and the 70 kg N ha$^{-1}$ recommended for old world bluestem (Berg 1990) in northwestern Oklahoma. However, average growing season precipitation is over 20 cm greater in southwestern Missouri compared to northwestern Oklahoma, allowing greater responses to N.

Our results suggest that for a single forage harvest, indiangrass would be preferred due to its better yield stability. However, under multiple harvests and for late summer forage production, caucasian bluestem would be better. Both grasses grew well on infertile soils of the Ozarks.

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# Viewpoint: The rangeland condition concept and range science's search for identity: A systems viewpoint

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## Abstract

**This paper analyzes the rangeland condition concept, and discusses how the search for a general concept has been part of the larger search for the identity of range science. It distinguishes between the concept and the assessment of rangeland condition, and distinguishes between the concept and ecological theories used in condition assessment. It proposes a general condition concept of modular character in which different ecological theories and field data are interchangeable components applied locally on appropriate, specific areas. It discusses past distinctions between range management and range science, implores the development of *range management science*, and discusses efforts needed in research, education, and administration to pursue its development. It interprets past and current events related to range science, including the advent of *rangeland health*, and discusses their relationships to range science's unfulfilled development as a management science. The paper encourages systematic design of concepts needed to allow range science to fulfill its philosophical potential as a management science.**

**Key Words: rangeland health, range management, rangeland trend**

This paper is in part a techno-philosophical analysis of the rangeland condition concept. But the paper goes beyond rangeland condition to examine how the search for a rangeland condition concept has been part of the larger search for the identity of range science. It begins by distinguishing between the rangeland condition concept *per se* and the ecological theories used in condition *assessment*. It explores how inadequate conceptualization of rangeland condition and other range science concepts has produced a range science of weak identity. The paper implores systematic conceptual design. It supports the development of range science as a management science. It interprets past and current events related to range science, including the advent of *rangeland health*, and discusses their relationships to range science's unfulfilled potential as a management science. The paper discusses efforts needed in research, education and administration to pursue development of range management science. It is written as a *Viewpoint* paper, so philosophical and stylistic latitude are requested. The discussion begins with range condition, addresses a network of matters related to range management science, then returns to range condition, with the goal of edifying both the concept and the science.

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### The Rangeland Condition Concept—Objectives

Failure to conceptually isolate the *concept* of range condition from ecological theory has caused inevitable frustration, and has produced conceptual inadequacies summarized by Risser (1989), Smith (1989), and others. The rangeland condition concept should be conceptualized as a *tool* (Scarnecchia, 1991) to apply ecological theory in rangeland assessment. This conceptualization requires that the range condition concept itself not be an ecological theory, and more specifically, that the concept *per se* be *devoid and independent of any ecological theory, including theories involving succession, climax, stable states, and threshholds.* A general, adaptable range condition concept must be designed to *apply, but not consist of,* regionally applicable, partially validated, ever-evolving ecological theories.

Isolation of the concept can be accomplished by limiting the concept of range condition to an objective function. This objective function could take the form of an objective-based, decision-aiding model, i.e., an expert system, serviced by appropriate ecological theories utilizing ecological data. An application of such an approach is described by Bosch and Booysen (1992). Range condition becomes only a weighted function of a group of variables representing values considered important on rangelands. Range condition assessment takes on a modular character as ecological theories (submodels) become interchangeable components. Data sets become interchangeable modules as well. The range condition concept (model) can then have a fixed structure in which individual variables can be added, removed, emphasized or deemphasized through its weighting function and parameters. The concept *per se*, whether no more than a weighted function of a few variables, or a sophisticated expert system, *can have its own identity apart from evolving ecological theories.* It becomes purely integrative, a distinctly interpretive part of the management science of range science. The concept now has the advantage of heuristic design, so that it can accomodate ever-increasing ecological data and evolving or regional theories by modular sub-

stitution without loss of identity. If desired, the condition model can be easily modified to accomodate changing social values, but the character of the *concept* remains intact.

### Confounded Concepts—Some Symptons

As explained, the advantages of defining the range condition concept as an integrative concept independent of ecological theory are clear. But nearly all papers on range condition, both early and recent, grapple with limitations of ecological theory and data which are properly peripheral or even irrelevant to a well-designed range condition concept. Most papers have not distinguished between the range condition *concept* and range condition *assessment.* They have not distinguished between *ecological theories* and a *range science concept.* The rangeland condition concept has been *confounded.* Rangeland researchers, working with specialized objectives, have often integrated (and confounded) within concepts rather than integrating concepts within applications. Many concepts have developed unsystematically, with *ad hoc* integration passing for systematic, unconfounded design based on multiple objectives. The problem has been acute in the case of rangeland condition, but has characterized many other range science concepts.

The inadequacy of range science concepts is sufficiently pervasive that range science *per se* seems to be dying a slow death. As the range management discipline has recently experienced declining political fortunes in public lands issues, range science, to the extent it can be identified, has been scrutinized. Meanwhile, the name *range science* has been disappearing from department names at our academic institutions. In 1991 the Range Science Department at Texas A&M University was renamed the Department of Rangeland Ecology and Management. The Range Science Department at Utah State University has been renamed the Department of Rangeland Resources. In the latter case, management preferences of undergraduate students, and a desire to emphasize the land helped motivate the change, as did the perception that the name range science inadequately addressed the social dimensions of range management (See Fig. 1). But the Department Head (J.C. Malechek, personal comm.) confided that few could agree on what range science really *was.*

These name changes can offhandedly be explained as simple politics and economics, but the identity problem of range science is more profound than politics. The explanation is better transposed to assert that *the political and economic disenfranchisement of range science reflects the failure of range science to establish credibility as a distinct science worthy of political and economic support.*

If range science were simply a technical science directed at a low value resource, the loss of the science might be acceptable. But of the land management sciences, range science has been conceived as a broadly-based, integrative science, integrating more technical sciences such as forest science, hydrology, wildlife biology, sociology, ecology, and others (Fig 1.) Its technical, conceptual development has never approached its philosophical potential. Nonetheless, range scientists have often been recognized as good interdisciplinary scientists, and good natural resource administrators, due largely to their integrative philosophical backgrounds, rather than to any technical training in the analysis of complex systems. The shortage of technical expertise in systems analysis among researchers in forestry, animal sciences, wildlife biology, and even ecology has hindered development of these sciences, but the longer histories of these sciences, their economic constituencies, and institutional inertia have helped maintain their integrities.

### Other Symptons—Enter a Stranger

The marketing success and staying power of the Savory Grazing Method, later to become Holistic Resource Management (Savory 1988) are partly attributable to the unfulfilled technical development of range management science. Based on the philosophy of Jan Smuts and the grazing principles of Voisin, this information product, purportedly inspired by simple observation of the African bush (Savory 1988), has many analogues in the information marketplace. Most such promotions practice information arbitrage, exploiting knowledge-gap or communication niches between science and management. Some, such as schools or institutions of holistic medicine, have developed by presenting a systems philosophy in the face of a formidable, institutionally entrenched, technically developed science.

To Holistic Resource Management, range science has been a less formidable adversary. Allan Savory incrementally observed that range management involved complex, synergetic, "holistic" systems. With the management science (range science) yet primordial, it was necessary only for him to enunciate (reenunciate, see Fig 1.) the basic systems principles of range management, without undertaking any substantive and challenging holistic science. Real holistic management (beyond art) involving rangelands is not possible without an holistic range science, but it has mattered little. With some exceptions, Savory was well received. *He reminded us who we were.* With holistic rhetoric, he has disparaged the technical development of range management science. But that probably has not mattered much either, because range scientists and educators have never been anxious to develop their management science beyond philosophical generalities. To paraphrase G.K. Chesterton, range science "was not tried and found wanting, it was found difficult and not tried." Without a developed range science, range management has proven disoriented, easy prey for airy philosophical predators. Now *that* is a principle that can be inspired by simple observation of the African bush.

### Management, Art, Science and Management Science

Range science has never developed significantly as a management science. But much energy has been spent philosophizing about the distinction between range management and range science. Recently, Provenza (1992) characterized them as complementary but distinct endeavors, citing Stoddart, Smith, and Box (1975), who characterized *range management* as an attempt to optimize returns from rangelands in combinations desired by and suitable for society through the manipulation of range ecosystems. Provenza went on to say that as such, "*range management* is a planning process, in which alternative management options are exposed to the decision maker's values, and the option with the highest value is selected." The unmade distinction is whether the "optimization" and "planning" are informal, mental analyses (i.e. *art* ) or formal systems analyses (i.e., *science*). If *range science* is substituted for *range management* in the characterizations cited above, the results are good characterizations of range sci-

ence as a *management science*. The original descriptions cited lump *all* optimization and planning analyses into range management. This long-standing placement has been, and still is hindering the development of range science, because not only are multi-objective, multi-variable optimization, interaction and planning concepts, and analyses (beyond experiential art) a part of range science, they are the *core* of range science.

At least, they seem the only core, the only distinct identity, that range science can have. That identity involves range science concepts like range condition in the *core* area of Fig. 2. These concepts are the basic tools used to operate across Boundary A and then within the *mantle* of Fig 2. Quantitatively, these concepts can take the form of simple independent variables, to complex dependent variables, to complex functions of core variables, to analytical models and expert systems. The core includes rigorously defined and limited concepts such as animal-unit equivalents (Scarnecchia and Gaskins 1987), stocking variables and other interactive variables, palatability, preference, species substitution ratios, carrying capacity (Scarnecchia, 1990), harvest and production efficiencies, range condition, range trend, and the myriad other concepts and variables, including many not yet conceived (Scarnecchia 1994). Many such concepts of range management science should be designed to link ecosystem components for multi-objective management. The opportunity to develop the systematic core concepts is itself immense, and the challenge of developing analytical models, and appropriate field research applying them within the mantle of range science is still greater.

The mantle area graphically represents where range economists, range wildlife scientists, range ecologists, and the other combinations of Fig. 2 have conducted most of the research conventionally termed range science. The undeveloped core represents the management science—not simple components of rangelands, but basic core concepts like range condition which give range science its identity. Maybe the presence of this core, and the identity of range science as a management science were implicit in Fig. 1. The literature cited in the first paragraph of this section suggest that the idea, if implied, was not received.

**About Education**

Range science as a management science has been difficult to face. Most range scientists are not trained to deal with range science as a management science. Most scientists who consider themselves range scientists work on plant ecology, hydrology, animal science, fire ecology, wildlife biology, etc. on rangelands. Like many specialists in these other sciences, they often have little conceptual or technical education in systems analysis. What training exists is often intellectually discrete from their mainstream disciplinary knowledge, much as range modeling research

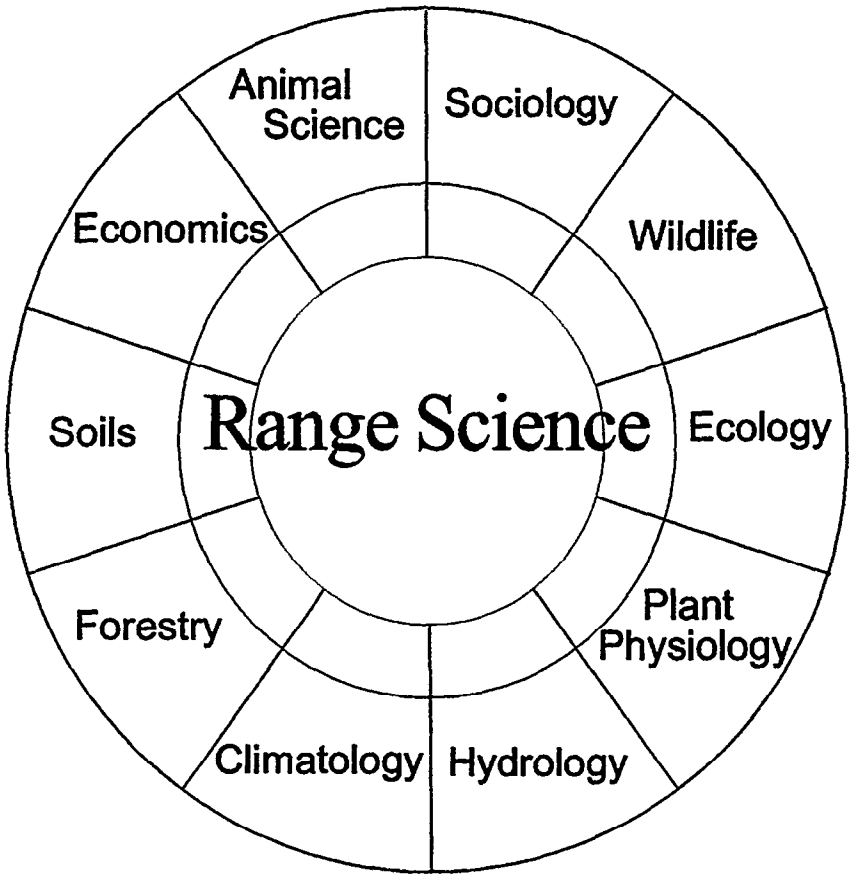


**Fig. 1. Range science and its supporting sciences as conceived twenty years ago, and as widely taught since then. Reproduced from Stoddart, Smith, and Box (1975).**

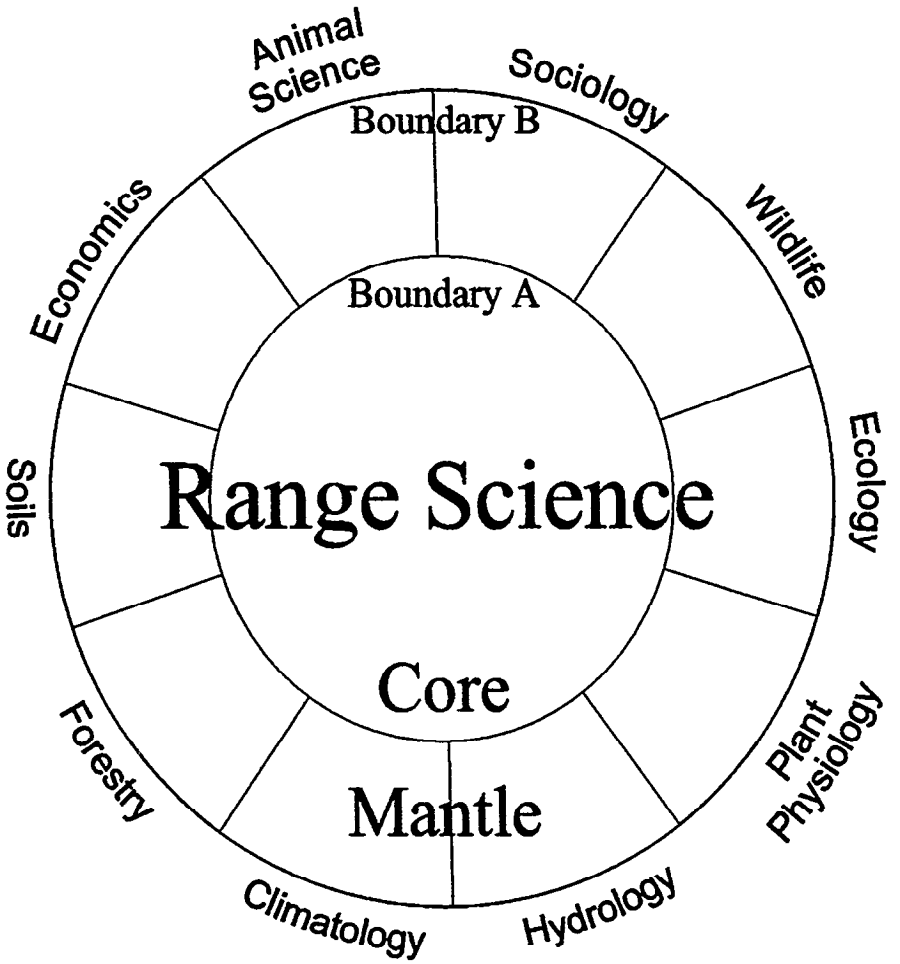


**Fig. 2. Adaptation of Fig. 1. showing conceptual core, mantle and boundaries of range science as a management science. The core of range science, consisting of systematically designed concepts and models relating them remains largely undeveloped.**

is tacitly isolated from range science proper.

Most university range science departments have better addressed the development of range management than range science. The encouragement to do so has come from several sources. Often our range science departments are in land grant universities, where a management mission has been emphasized. Some undergraduate students in these departments are refugees from quantitative sciences; many enter range management programs with the idea that the analytical demands on them will be fewer than in other fields. Some undergraduates have little interest in science and come only to study what they see as applied management. Often these students come from rural backgrounds where economic pragmatism and local culture foster a desire to learn management without learning science.

Most graduate education in range science provides little training in range science as a management science. Because Ph.D. level researchers and professors in range science frequently have little systems training, and because retraining possibilities are inhibited by institutional constraints (tenure, etc.), the unfulfilled potential and future of range science may be in the hands of the next generation of range scientists. Future-thinking programs with a long-term interest in range science need to begin educating their graduate students in the technical, analytical methods needed to analyze complex systems so that they can effectively apply basic physical, chemical, and biological sciences. This redirection will involve more than adding an isolated course or 2 in systems analysis to graduate programs. It will involve redirecting some program efforts toward the philosophical, conceptual, and technical design of range science, based on principles of multi-objective, multi-variable analysis of systems. But because this range science core has never developed, research will be needed.

### About Research, Funding and Publication

Future concepts within range science will need to be designed with a strong sense of general applicability. Concepts will need to be rigorously limited in content so that they can be used to describe unconfounded relationships among many variables. Some concepts, such as range condition, are best designed to be compatible with modular components while remaining conceptually intact themselves. Research institutions interested in range science will need to direct research efforts at these design-integration problems.

Such research will likely require less research funding than traditional field research, but it will require more creativity of researchers. Supporting field research should be gradually reoriented toward the more systematic structure of the evolving range

science. Internal and external funding sources will need to recognize the value of conceptual design research, and support it. It should be given at least equal weight with traditional range research, some of which has produced little of lasting value.

Publication of such research will require support of journals such as the *Journal of Range Management.* The *Journal* could reconsider becoming the *Journal of Range Science*, even though a recent opinion poll favored retention of the *Journal of Range Management.* The name *Journal of Range Management Science* is worth considering. It could consider adding 1 or 2 philosophically oriented systems analysts as associate editors. Currently, dataless papers on conceptual design are given second-class consideration with opinion papers on policy, etc. as *Viewpoint* papers, even though conceptual work is a bottleneck in range science development. Generally, the *Journal* could support the development of range management science by becoming more of a forum for technical discussion of range science concepts—not just topical ones like range condition, but other systematically designed range science concepts, approaches and models. And individual researchers who develop concepts in their modeling work will need to be more effective in explaining their ideas in simple language to allow their evaluation and possible adoption within the mainstream of range science.

## About Leadership

In 1961, Forrester wrote that "thus far, management science has still not penetrated the inner circle of top management ." Thirty-three years later, this statement still applies to range science. Building range science, the management science, will require leadership, preferably by individuals in influential positions. Too often individuals currently in range science administration have abandoned their roles as scientists and pursued political challenges rather than the challenge of developing range science.

Young entry-level scientists apparently have received the message; success in obtaining research funding and in political networking are better rewarded than technical efforts at developing range science. So young scientists, many lacking systems skills, take the obvious course.

Leadership will be needed from *somewhere* if range science is to fulfill the potential of its philosophy, and survive as an integrative land management science. Its survival is important as a central science among the more technical, factional resource sciences. Also, range management will likely not prosper *as a distinct discipline* without a conceptually adequate range science.

## Range Condition Again

Developing an effective range condition concept is basic in developing range science, the management science. The range condition *concept* is properly in the *core* (Fig. 2) of range science, while the process of range condition *assessment* involves the core, mantle, and supporting sciences, linking the concept with ecological theories and ecological data outside the mantle for area-specific assessment. This distinction allows the concept to have a clean, universal identity as a multi-objective function or model, without having it confounded with the theories it is designed to apply. Unlike many other core concepts (e.g., stocking variables), range condition is a kind of terminal concept in that it is not likely to be used in more complex models where subsequent mathematical confounding (Scarnecchia 1988) with other variables would be a problem.

We need to design a universal rangeland condition concept. This activity is *much* simpler than misdirected attempts to develop a universally applicable approach to rangeland condition assessment. Recently, the Task Group on Unity in Concepts and Terminology of the Society for Range Management (1991) "has tried to follow a course of developing an approach to 'Range condition' assessment which accommodates modern viewpoints of the nature of vegetation changes, but is not excessively dependent on the correctness of any of them." The quotation marks around *range condition* belong to the Task Group, and they suggest that the group had so nebulous an idea about what the range condition concept *per se* is that they were uncomfortable using the term without placing it in undirected quotation marks, *"you know."*

Foran et al. (1986) stated that "the philosophical concepts which form the basis of range condition assessment are now in a period of considerable ferment and change." As long as theoretical and community ecologists exist this observation will remain valid. Joyce (1992), drawing little distinction between *concept* and *assessment* of range condition, speculated that innovation will require emergence of a *single* transcendent ecological theory linked to an equally inspired field method. This scenario, the emergence of a unifying ecological theory and a multi-dimensional field method adequate to assess it, would be a miracle—actually a compound miracle. It will not happen any time soon. For this reason, we need a discrete range condition concept which can accomodate evolving general or area-specific theories. Then *range condition* will not need to be placed in vague quotation marks. We will have a concept which can be applied universally, and a dynamic, modular, assessment capability which can be applied locally.

Recently, the National Research Council (NRC) (1994) has promulgated the concept of *rangeland health* based on the "integrity" of the soil and the ecosystem processes on rangeland. This approach willingly abandons the conceptual weaknesses and socio-political baggage (e.g., "fair", "poor", etc.) of *rangeland condition,* embracing the profound but inscrutable ecological processes of ecosystem management. The historically unfettered term *rangeland health* is as comfortably familiar as it is conceptually imprecise. From sentence one, the NRC (1994) definition that "Rangeland health should be defined as the degree to which the integrity of the soil and the ecological processes of rangeland ecosystems are sustained" leaves unclear whether *rangeland health* is a state or rate concept (variable), i.e., it combines and confounds the old concepts of *rangeland condition* and *rangeland trend.* Clearly this committee effort is not the unconfounded conceptual design which this paper implores.

Range scientists have long understood that ecosystem processes, while difficult to assess, are the functional essence of rangelands. Most of the early methods of rangeland condition assessment explicitly or implicitly used plant community variables or simple soil variables as measurable indicators of the extent of these processes on rangelands. Evaluation of these elusive underlying ecosystem processes may be the objective of the unifying "ecological theory tied to a field method" envisioned by Joyce (1992). In any case, the concept of *rangeland health* is neither a

needed systematic step backwards in conceptual design, nor a practical step forward in rangeland assessment. It is a change in terminology without a change in conceptuality—a confounding step sideways out of the line of fire. The challenges in conceptualizing rangeland health are the same as those of rangeland condition and trend, and based on past experience, they are unlikely to be addressed effectively by large committees concerned mostly with designing palatable terminology for communicating rangeland policy.

If they can be adequately assessed, soil integrity and basic ecosystem processes can be accommodated like other ecological theories and data within the modular range condition concept proposed in this paper. But because of our limited understanding of ecosystem processes, and for ease of measurement, the role of indicator variables in assessing these processes will remain.

### Much to Do

The search for a range condition concept is part of the parallel, wider struggle to find an identity for range science. The core of range science is composed of a wealth of other concepts, which, if properly designed, can describe clear relationships in the core and mantle of Fig. 2. Much work and communication are needed to design effective, understandable core concepts. The concepts and their interactions should have minimal confounding, and be designed to describe and analyze complex relationships, and synergies in the core and mantle. These core concepts will give range science its identity, and enable it to fulfill its philosophical potential as an integrative management science. And as disciplinary boundaries gradually dissolve in the natural resource sciences, a conceptually developed management science will ensure the role range science and range scientists in future policy affecting rangelands.

To get a core of systematic concepts for range science will require focused efforts at concept design. As a bonus, well-designed concepts may have artistic qualities such as symmetries, interchangeability, unity, and simplicity. Then range science, like this paper, will have come full circle—from a management art, to an experimental science, to a management science, and back to art again.

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48:187-190 March 1995

# Assessing the power of the point-line transect to monitor changes in plant basal cover

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## Abstract

**To assess the power of point data (collected systematically at each meter along a permanently-situated, 100-m line transect) to detect actual changes in plant basal cover, we developed a computational approach whereby a simplified shortgrass steppe community was spatially simulated on a computer screen. Cover was then reduced using a random disturbance pattern. One transect could detect an actual decrease in cover from 12% to 8% with less than 20% probability, while 5 transects increased this power to about 80% ($P \leq .05$). A reduction in cover from 12 to 6% could be detected with 80% probability with only 2 transects, while a cover reduction to 10% could only be detected with 40% probability using 10 transects ($P \leq .05$). Artificial populations provide a valuable mechanism for quantitatively evaluating field sampling designs.**

**Key Words: Short-grass steppe, vegetation measurement, Type II error, sample size, hypothesis testing, basal cover, disturbance.**

The purpose of vegetation monitoring is to determine if significant ecologically important changes have occurred over time. It is also important to differentiate between ecological importance and statistical significance (Yoccoz 1991). To avoid such a misunderstanding, monitoring designs should clearly specify what constitutes an ecologically important vegetation change, and monitoring methods must be selected so that changes of this magnitude can be observed with acceptable error rates.

Acceptable error rates, themselves, should be a function of the ecological consequences of change, as has been noted in the evolving concept of ecological risk assessment (U.S. Environmental Protection Agency 1992). If vegetation changes have large relative ecological importance (or large implications for management), then acceptable error rates must be smaller than when changes have lesser consequences.

Monitoring designs should be stable, powerful, robust, and cost-effective if they are to detect ecologically important vegetation changes with acceptable error (Larsen and Marx 1981). Stable designs have an acceptable risk of a false conclusion of vegetation change; that is, Type-I statistical error is acceptable. Powerful designs have an acceptable likelihood of detecting vegetation change, given known rates of Type-I error; that is, Type-II statistical error is acceptable. Robust methods are those that produce data that are not influenced by extraneous factors (Whysong and Brady 1987). For example, frequency is not a robust measure because it is dependent on plant size and shape (Bonham 1989). Lastly, cost-effective methods are those sufficient to meet these 3 criteria within available funding limitations.

The monitoring problem in natural resource management is one of how to design stable, powerful, robust, and economical inventory methods that will detect ecologically important changes with acceptable error rates. Several characteristics of the monitoring problem, including selection of desired magnitude of change to detect and acceptable risks of Type-I error, have been widely addressed (Cook and Stubbendieck 1986). Estimating the power of different methods, on the other hand, has been considered infrequently because doing so is infeasible using traditional field experiments. The cost of creating treatments is high and numerous replications are needed to ensure adequate replication.

One approach for studying Type-II error rates of monitoring designs is by employing simulation models with known distributions. Our objective was to evaluate point data from line transects, called point-line (Bonham 1989), with respect to power, using this procedure. The qualitative merits of point-line sampling are outlined in texts on vegetation sampling (Heady et al. 1959).

## Methods

A rigorous evaluation of the point-line transect technique for monitoring changes in basal cover requires large sample sizes and known values of cover and the spatial distribution of plants, as well as plant sizes (Bonham 1989). Investigations based on field data are formidable and costly. Thus, computer simulations (Turbo Pascal, version 6.0) were used because they allowed controlled measurements of known population values with a large number of replications.

Graphic computer models were developed to represent both the point-line transect sampling method and vegetation characteristics of a representative shortgrass plant community situated at the U.S. Army's Pinon Canyon Maneuver Site, about 60 km northeast of Trinidad, Colo. (Shaw et al. 1989). For simulation purpos-

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es, the community was defined in terms of the dominant species, blue grama (*Bouteloua gracilis* (H.B.K.)Lag.), with an initial basal cover of 12%. Plant shape was assumed to be circular. Two mean plant sizes, 8 and 12 cm in diameter, were used to parameterize the simulated community, but no statistical differences were found between them and the data were combined (Mitchell et al. 1994).

Simulated communities were initially created that had random, moderately-, and highly-contagious distributions. Both random and nonrandom disturbance patterns were likewise evaluated. However, preliminary analyses showed that no significant differences were caused by plant distribution or disturbance pattern, at scales considered in these analyses, and only the randomly distributed communities were used in this study (Mitchell et al. 1994). Disturbance treatment effects were combined.

The effect of disturbance was assumed to be one-tailed. That is, military commanders (not unlike other rangeland managers) are primarily concerned about monitoring whether abundance of beneficial vegetation has decreased from that found on sites in satisfactory condition. Once a site has been placed in an undesirable state, the manager would be interested in monitoring the success of recovery efforts, another 1-tailed test. A 1-sided hypothesis provides an advantage over a 2-sided test if values in only 1 direction from $H_0$ are meaningful because its critical value is closer to the population mean (Larsen and Marx 1981), thus increasing the test's power.

The concept of a management objective based upon 2 condition states, satisfactory and unsatisfactory, is almost 50 years old (Ellison 1949), but is the focus of renewed interest in terms of warning lines between healthy and at-risk states of rangeland health (Committee on Rangeland Classification 1994). Of course, when more than 2 condition states are possible, and movement can be in both directions, a 2-tailed test is appropriate.

A scale of 1 $cm^2$ per pixel was used to generate vegetation models and cover measurements. At this scale, each graphic screen represented a community of 10.24 by 7.68 m. Therefore, a simulated vegetation community large enough for inclusion of a 100-m transect was represented by 11 separate, but linked, graphic screens.

All simulation trials began with the initial population cover value of 12%. Binomial (hit-miss) data were recorded from 100 points systematically located at 1-m intervals along transects following the procedure described for training lands under control of the U.S. Army (Tazik et al. 1992).

The simulation model used 1 computer screen pixel to represent a sample point. Such an approach facilitated basal cover estimation because observations were always dichotomous; that is, each pixel was either totally covered by a plant or is not covered at all. This corresponds to the assumed field situation in which the point is dimensionless, thereby providing nominal-scale data fitting a binomial distribution.

Ten thousand randomly located permanent transects from each of 10 independent simulated blue grama populations with the same cover (12%) were used to obtain estimates of basal cover. The populations were then reduced in basal cover by removing individual, random plants. Each new population was sampled for basal cover using the same 10,000 permanently located transects. The disturbance and resampling process was repeated until reduced populations of 10%, 8%, 6%, 4%, and 2% were obtained.

The power of the point-line transect method was estimated using 10 different sample sizes (numbers of transects grouped into a sample), ranging from n = 1 to n = 10. Grouping of transects assumed homogeneity among simulated communities.

Precision of basal cover estimates was estimated using confidence intervals derived directly from distributions of 10,000 sample replicates for each set of estimates. Areas under distribution curves from sampling-disturbance-resampling iterations were then directly measured to estimate the power of the technique to detect reductions in basal cover for each vegetation condition (Tanke and Bonham 1985). Power curves were used to summarize these data.

## Results and Discussion

### Accuracy and Precision

Sample means of plant basal cover were estimated with an accuracy of less than 0.5% ($P \leq 0.05$) for simulated populations with a range of 2% to 12% basal cover. The high level of accuracy was obtained because sample means were calculated from extremely large samples relative to any sample collected in field studies.

Expectedly, as the number of transects grouped into a sample increased, the range in estimated mean cover decreased and the proportion of estimates falling closer to the true mean increased. For example, when 1 transect was used to estimate basal cover from the initial population (12%), the estimates for $\mu$ ranged from 0% to 25% while approximately one-half of them fell between 10% and 14% (Fig. 1). If 10 transects were grouped, the range of estimates for the initial population narrowed to 0% to 17% and 19 out of 20 were within ± 2% of 12% (Fig. 2).

The resulting sampling distributions (1-tailed test) means a manager would have to estimate a basal cover of ≤ 6% before inferring that cover had decreased when using 1 transect, but would make the same judgment when cover decreased to 10% with 10 transects ($P \leq 0.05$).

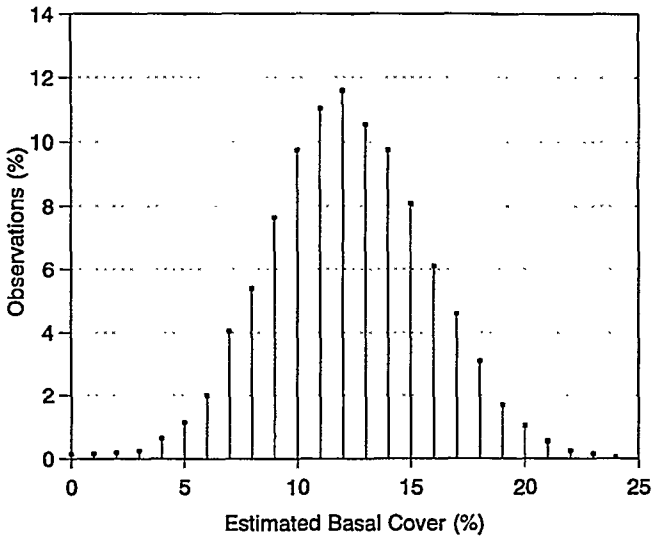


**Fig. 1. Sampling distribution of basal cover estimates of a simulated blue grama population with a true population cover of 12%. Derived from Monte Carlo analysis from a single 100-m, point-line transect (100 points).**

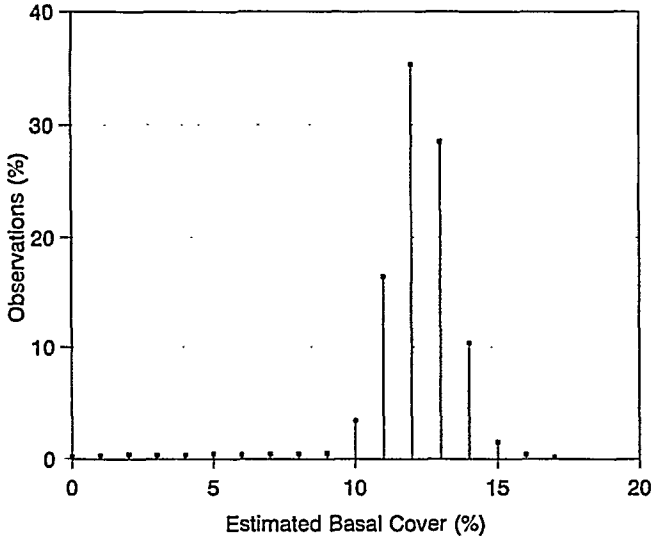


Fig. 2. Sampling distribution of basal cover estimates of a simulated blue grama population with a true population cover of 12%. Derived from Monte Carlo analysis from three 100-m, point-line transects (100 points each). Cover values classified to nearest percent.

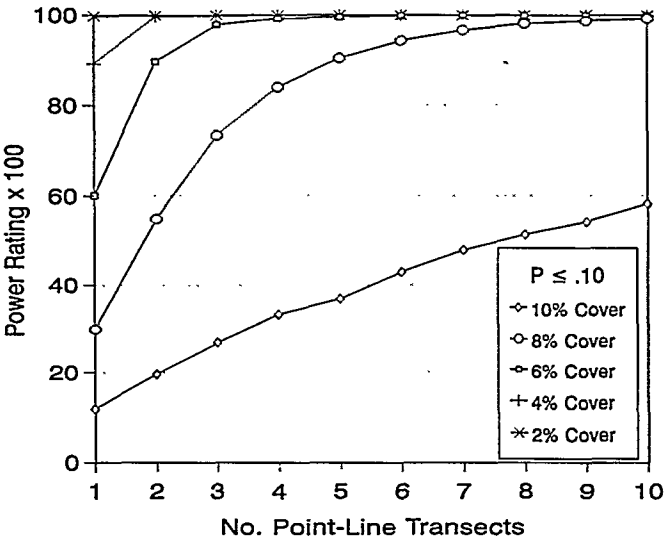


Fig. 4. Power curves for decreases in basal cover from a simulated blue grama population (μ = 12%) to 10%, 8%, 6%, 4%, and 2% cover. $P \leq 0.10$. Standard error of all means ≤ 0.5%.

## Power

The power of the monitoring design increased as the acceptable rate of Type-I error became larger, sample precision increased (expressed through increased sample size), and the minimum detectable change in basal cover increased.

*Type-I Error.* Consider the situation described above with an initial basal cover of 12% and a sample size of one transect, giving a rejection region of ≤ 6% cover for the probability of a Type-I error of $\alpha = .05$. Under these conditions the probability of detecting a 50% decrease in basal cover to 6% was 42% (Fig. 3). If the allowable Type-I error was increased to $\alpha = .086$, or about 10% for the null population (rejection region ≤ 7% basal cover), then the probability of detecting the same change increased to approximately 59% (Fig. 4). As the number of transects in the sample approached 5, the differences in power due to varying acceptable level of Type-I error became much less important.

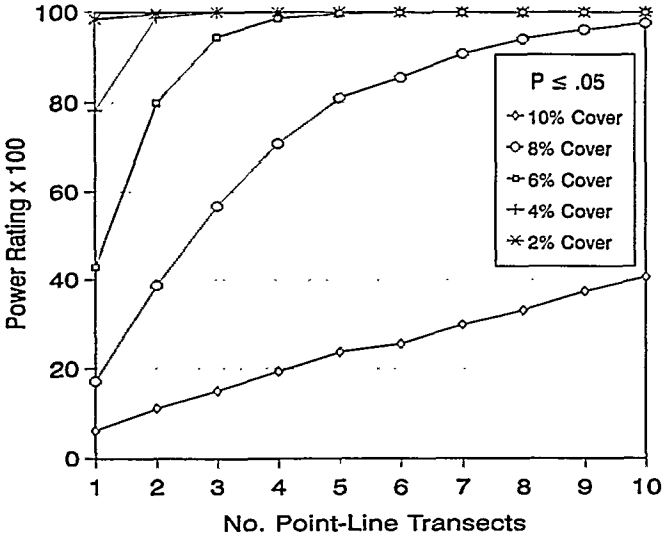


Fig. 3. Power curves for decreases in basal cover from a simulated blue grama population (μ = 12%) to 10%, 8%, 6%, 4%, and 2% cover. $P \leq 0.05$. Standard error of all means ≤ 0.5%.

*Sample Size.* Sample size is an important consideration on military training lands because sample allocation of the Army's land condition analysis program is based upon population size (land area) rather than population variance (Tazik et al. 1992). As depicted in figures 3 and 4, the power of the point-line method was plainly affected by the number of transects used to estimate basal cover. The relationship between power and sample size was logarithmic.

*Minimum Detectable Change.* As the degree of change to be detected increased, the power of the point-line method to distinguish it increased measurably. For instance, when 3 transects were grouped as a sample and given an acceptable Type-I Error of $\alpha = .05$, the power of detecting a 2% decrease in basal cover was less than 15%, while the power of detecting a 4% change slightly greater than one-half. The loss of one-half of the original cover (12% to 6%) could be discerned more than 9 times out of 10 (Fig. 3).

Of the variables affecting the power of the point-line method, only increased sample size requires greater cost to attain greater power. Its tradeoff is between cost-effectiveness and power rather than stability or sensitivity and power.

The logarithmic relationship between sample size and minimum acceptable detectable change, shown in Figures 3 and 4, provides some insight for those designing vegetation monitoring systems: That is, if relatively small changes in species abundance are important to observe, additional observations tend to equally increase the monitoring system's power. Thus, their value stays somewhat constant as the sample size increases. However, when larger changes in cover must occur before they can be detected, each added observation contributes less to the monitoring sys-

tem's power.

For a given sample size, increasing the minimum acceptable detectable change will enhance statistical power to a greater extent than allowing the Type-I error probability to increase. Therefore, when planning a monitoring program, one will generally maximize the power of estimates from point-line data by allowing for the largest possible minimum detectable change.

## Conclusions

Appropriateness of the point-line transect sampling design for monitoring changes in plant cover can be evaluated by considering power and robustness of the design given desired Type-I statistical error and the minimum detectable change. Careful thought should be given to the ecological consequences of both Type-I and Type-II statistical errors and appropriate rates of error then assigned. In some circumstances the ecological consequences of wrongly concluding change in cover when none has occurred (Type-I error) are equivalent to the consequences of failing to detect change (Type-II error). Under such conditions, the errors must be equally appraised in designing the monitoring system.

In evaluating monitoring designs, Type-I error rates are assigned based on knowledge of the baseline population and the ecological consequences of error. Type-II error rates are then determined by reference to the power curves generated from simulation models. Power curves are then used to determine sample sizes necessary to satisfy accuracy and risk requirements. Simulation modeling provides a way to select measurement and monitoring methodology for plant basal cover. Budgetary constraints usually are primary in dictating magnitudes of change possible to detect and error rates are often set without ecological considerations. Good monitoring practice, on the other hand, would dictate that ecological considerations have a major influence on error rates of a monitoring design.

Tools are now available to plan monitoring designs to ensure that the proper tradeoffs are made between Type-I error, power, desired detectable change, and sample size. Failure to use these tools may result in monitoring designs which are incapable of meeting monitoring objectives. Specifically, monitoring designs may not have a reasonable probability of detecting important ecological changes. Poorly planned monitoring designs will not provide decision makers the information they need to protect ecological resources. Properly designed monitoring systems, on the other hand, will provide the data that land managers require to respond to changes in ecosystems and help insure that wise management decisions are made.

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# Book Reviews

**China's Pastoral Region.** Sheep and wool, minority nationalities, rangeland degradation, and sustainable development. By John W.Longworth and Gregory J. Williamson. 1993. CAB International, Wallingford, Oxon, UK. 350 p. US$85.50 hardbound. ISBN 0 85198 890 3.

*China's Pastoral Region* is a book that gets you thinking about the future.

The impressions and implications left by the book transcend its detailed technical content much as cumulative impressions of China transcend the details of daily life there. The book is a survey of the past, present, and future of many aspects of livestock management, agricultural marketing, economic development, and governmental policy involving China's rangelands. It is a product of a cooperative research project of the Australian Centre for International Agricultural Research (ACIAR). The project involved researchers from Australia's University of Queensland, and from China's Institute of Rural Development (Academy of Social Sciences) and Institute of Agricultural Economics (Academy of Agricultural Sciences). The book is subtitled *Sheep and Wool, Minority Nationalities, Rangeland Degradation and Sustainable Development,* and it focuses on an ambitious, holistic analysis of these 4 interrelated considerations in the rangeland region of China.

Following a detailed table of contents, separate lists of figures, tables and plates and maps, and a brief introduction, the book is organized into 4 parts. The 3 chapters of Part 1 outline the research project, discuss characteristics of the pastoral region, and describe the Chinese sheep and wool scene. Part 2 consists of 3 chapters, each a provincial case study. Nine chapters, each a county case study, comprise Part 3. In Part 4, which the authors entitle *The Big Picture,* 2 chapters summarize constraints to development in the pastoral area, and considerations for the future. A list of references and a detailed index follow Part 4.

The challenge of a research project to investigate the many facets of life related to Chinese rangelands is one that many researchers might find overwhelming. But the book describes a well-conceived research plan and an approach involving a combination of methods of data collection, including considerable field investigation. The resulting 230 pages of case studies of Parts 2 and 3 are an impressively detailed blend of demographic, socio-economic, agro-pastoral, marketing, and policy information. Many tables and figures are included on everything from climatic data to marketing statistics to livestock numbers. The rapid changes occurring in some parts of China today, combined with the often inertial quality of range-livestock economies make for interesting speculation of how rapidly the survey data will become outdated. The historical, methodological and philosophical contents of Parts 1 and 4 should age well.

In its rural sociological approach and basic message, the idea that *range* management is actually *people* management is manifest in *China's Pastoral Region.* In view of China's recent political history and current reality, this good old extension axiom carries some heavy-handed implications. In fact, the euphemized philosophical discussions in *China's Pastoral Region* have some heavy political overtones. Some will find reassurance that knowledgeable, well-meaning professionals like the authors can formulate holistic carrot-and-stick strategies to manage people, that is, *resources,* for societal objectives in the face of an immense and growing population. Others may sense external paternalistic manipulation encouraging the threat of force, loss of individual freedom, breeding restrictions—a kind of husbandry applied 1 level up the food chain. They may view ominously the authors' closing statement that policy changes are needed at all levels of Chinese government to "*create a milieu in which local communities are prepared to accept and to enforce restrictions on short-term individual behaviour in the interests of long-term socially desirable outcomes.*"

The underlying fears of most of course are that the problems China faces, most rooted in overpopulation, foreshadow our own problems—that the problems we see in the developing China are not our past but our future. In a future world of people management, any country based on individual freedom is a developing country. China may benefit from Western ecological insights, pastoral experience, and holistic thinking. But the idea of 2 Australian authors offering China the advice on policy quoted above seems curious; the Chinese are way out in front on this one.

If people management does have a brighter future than range management, then the *real* future for the upwardly mobile in a managed future will be for people to manage the people who manage the range. Such second-level managers are politicians and bureaucrats and social engineers, and in the managed future the authors prescribe, their career prospects are bright enough to make me ponder a career change. As I said, *China's Pastoral Region* is a book that gets you thinking about the future.—*David L. Scarnecchia,* Washington State University, Pullman, Washington.

**Structure and Functioning of Seminatural Meadows.** Edited by M. Rychnovska. 1993. Elsevier Science Publishers, Amsterdam, The Netherlands. Available in the U.S. from Elsevier Science Publishing, Madison Square Station, New York, N.Y. 386 p. US$206.00 hardbound. ISBN 0-444-98669-3 (Elsevier).

This book is a summary of results of a 1972–1985 field project of the Man and the Biosphere Programme which investigated the functioning of grasslands. The study was conducted on mesophytic grasslands of the Zdarske Vrchy Landscape Reserve, in submontane Central Europe, in what was then Czechoslovakia. The project was designed as a comprehensive ecological study of grassland processes and functioning. In approach and style it is reminiscent of the International Biological Programme (IBP) work on grasslands. Also, the book (Number 27 in the series *Developments in Agricultural and Managed-Forest Ecology* ) resembles IBP publications in style and format.

The 20 major chapters of the book provide detailed coverage of wide array subjects in grassland ecology, including, plant-water relationships, nutrient cycling, above- and below-ground biomass dynamics, grassland microorganisms, photosynthesis, fertility, grassland consumers, and use and management of grasslands. Each contributed chapter is written by one or more individual authors whose names are found only in the table of contents, and not with the individual chapters. Little other information about the contributing authors is given. The book has a detailed index and an oddly formatted table of contents. Most of the contents of

the book have been published previously in journals and other outlets; these previous publications make up a much of the bibliography.

In presentation, *Structure and Functioning of Seminatural Meadows* is technical at the level of a major ecological journal. It is a translation, presumably from Czech, and some minor misspellings and typographical errors escaped editing. What some readers might find more distracting is some imprecision of interpretation that is difficult to avoid in translation. It has not been wholly avoided here, but then occasional imprecision of description is not limited to translated books. Acronyms are abundant, and sometimes confusing, especially in the parts of the book reporting results of field research. These parts of the book, often apparently taken from journal papers with little additional editing, are less readable than the synthesis and interpretation parts of the book. On balance, the book is reasonably readable.

A systems philosophy pervades the book. Strongly emphasized is the role of grasslands within larger natural and agricultural landscapes. The sustainable utility, ecological merit, and economic value of managed grasslands are advocated. But the book contains almost nothing on grazing by ungulates.

The separation of pure grassland ecology from applied grassland science involving livestock grazing should seem familiar to North American scientists. Still, those involved in either modeling or field research will find a wealth of data on grassland processes in this book, much of it relevant to North American grasslands.—*David L. Scarnecchia,* Washington State University, Pullman, Washington.

**When Indians Became Cowboys.** Native Peoples and Cattle Ranching in the American West. By Peter Iverson. 1994. University of Oklahoma Press, Norman. 266 p. US$24.95 cloth. ISBN 0-8061-1867-9.

This is not a novel about cowboys and Indians. Although many segments of this book report anecdotal events in the lives of individuals or groups in a lively and often humorous vein, it remains a scholarly treatment of an aspect of the life of American Indians and development of the Western cattle industry. It commences with the introduction of cattle and horses into the Indian culture in what is now the southwestern United States and continues through today.

The author is a professor of history at Arizona State University. He is an authority on American Indians and has more than a passing acquaintantship with cattle ranching. The word order in the title correctly captures his treatment of events. However, for many readers, both ranchers and non-ranchers, a reversal of word order to "When Cowboys (Anglo Ranchers) Became Indians" might be equally appropriate.

The first 3 chapters provide a brief, but well documented, treatment of early Indian culture, the introduction of cattle into that culture and the early intrusion upon Indian land associated with expansion of the cattle industry. the 2 themes of "allotment" and "leasing" and their prominent role in constraining development of Indian ranching are introduced in Chapter 3. The era of the great open range was relatively short from approximately 1867 to around the turn of the century. By the early 1900s, the Indian nations had signed treaties and become confined to reservations. Commencing the parallel with today's ranchers, the author writes, "The Anglo-American rancher, had he even read the plaintive words of Seattle of the Suquamish, could not have imagined they could possibly have been applied to him. how could he see commonality with a people whose best days appeared to be in the past rather than in the future?"

The next 2 chapters treat Indian cattle ranching in 2 regions; the Northern Plains and in Oklahoma and the Southwest. Chapters 5 and 6 treat the era of the New Deal and post WWII. They chronicle the policies of the Bureau of Indian Affairs and the impact of their inconsistent interpretation on Indian lives and development of an Indian cattle industry.

The concluding chapter has a couple of major themes. The first, as implied in the title, relates how ranching became central to the Indian culture of the American West. The second, and surely the more poignant for those of us who are not Indians, is captured in the passage, "In sum, the ranchers are more like Indians of old, surrounded by a society that knows little about them and cares less, except when it has other priorities for their land."

Quite apart from one's interest in Indian history or culture, those with an interest in cattle ranching, particularly in public land states, will be intrigued by the historical parallels developed in this book.—*LeRoy Rogers*, Washington State University, Pullman, Washington.