

Interactions Among Western Ragweed and Other Sandhills Species After Drought

Patrick E. Reece,¹ Joe E. Brummer,² Brian K. Northup,³
Ann E. Koehler,⁴ and Lowell E. Moser⁵

Authors are ¹Professor, University of Nebraska, Panhandle Research and Extension Center, 4502 Ave I, Scottsbluff, NE 69361;

²Research Scientist, Colorado State University, Western Colorado Research Center, P.O. Box 598, Gunnison, CO 81230;

³Ecologist, USDA, Agricultural Research Service, Grazinglands Research Laboratory, 7207 W Cheyenne St, El Reno, OK 73036;

⁴Rangeland Ecology Research Analyst, University of Nebraska, Panhandle Research and Extension Center, 4502 Ave I, Scottsbluff, NE 69361; and ⁵Professor, University of Nebraska, 352 Keim Hall, Lincoln, NE 68583.

Abstract

Interannual differences in yield and species composition of herbaceous vegetation on semiarid rangelands are common and often related to variations in precipitation regime. Interspecific interactions that occur after drought-induced population fluxes of western ragweed (*Ambrosia psilostachya* D.C.) were evaluated by removing western ragweed or associated species from 1-m² quadrats at weekly intervals beginning in early May, June, or July 1991 or 1992 on high-seral sandhills prairie in Nebraska. The composite of peak standing crops for ragweed and each group of associated species was 77% greater during May–October 1991 (2 252 kg·ha⁻¹) compared with 1992 (1 275 kg·ha⁻¹) when April and May precipitation was 98 mm below average and a late frost occurred. Mean levels of western ragweed herbage up to 436 kg·ha⁻¹ had no effect on associated species in 1991 when above average precipitation occurred throughout the growing season. In contrast, when an unusually dry spring occurred in 1992, relatively small mean levels of ragweed (189 kg·ha⁻¹) reduced end-of-season standing herbage of rhizomatous C₄ grasses on control plots by about 21% (137 kg·ha⁻¹) with little effect on other associated species, regardless of when treatments were initiated. Within a given year, western ragweed density was seasonally constant, similar among treatments, and independent of preceding-year species composition. Severe defoliation of western ragweed had little effect on subsequent-year populations, indicating an ability to maintain primordia for several years with limited plant growth. Because western ragweed is not a strong competitor in the presence of vigorous graminoids, deferring use of June- or July-grazed pasture until after July in the subsequent year can minimize increases in western ragweed.

Resumen

Diferencias en el rendimiento interanual y la composición de las especies de vegetación herbácea en praderas semi-áridas son común y frecuentemente relacionados con la variedad del régimen de precipitación. Interrrelación interespecífica que ocurre después del cambio continuamente provocado por la sequía en la ambrosía del oeste (*Ambrosia psilostachya* D.C.) fueron evaluadas con quitar la ambrosía del oeste y especies asociadas de 1-m² en intervalos cada semana empezando en mayo, junio, o julio de 1991 o 1992 en praderas de alto crecimiento en Nebraska. El compuesto de cosechas de ambrosía en su punto máximo y cada grupo de especies asociadas fue 77% mayor durante mayo-octubre de 1991 (2,252 kg ha⁻¹) comparado con 1992 (1,275 kg ha⁻¹) cuando la precipitación en abril y mayo fue 98 mm menos del promedio y ocurrió una helada tardía. El promedio de ambrosía del oeste hasta 436 kg ha⁻¹ no tuvo ningún efecto en especies asociadas en 1991 cuando ocurrió precipitación más allá del promedio durante el período de crecimiento. En contraposición, cuando ocurrió una sequía durante la primavera en 1992, relativamente pequeños niveles de ambrosía (189 kg ha⁻¹) redujeron la cosecha al fin de la temporada de zacate rizomato C₄ en terrenos controlados por aproximadamente 21% (137 kg ha⁻¹) con poco efecto en otras especies asociadas, sin tomar en cuenta cuando empezó el tratamiento. Durante cada año, la densidad de la ambrosía del oeste se mantuvo constante cada temporada, similar entre tratamientos, e independientemente de la composición de los años siguientes. Defoliación severa de ambrosía del oeste tuvo un pequeño efecto la población de los años siguientes, indicando la capacidad de mantener el primigenio por varios años con limitación en el crecimiento de la planta. La ambrosía del oeste no tiene un competidor fuerte en la presencia de zacate vigoroso, el uso distinto en los pastos en junio o julio hasta después de julio en los años siguientes puede disminuir el aumento de ambrosía del oeste.

Key Words: *Ambrosia psilostachya*, interspecific competition, seasonal herbage distribution, shoot density, subsequent-year effects

Introduction

Western ragweed (*Ambrosia psilostachya* D.C.) is one of the most widely distributed (GPFA 1986) and abundant native forbs on rangelands in the Great Plains (Vermeire and Gillen 2000). It forms extensive clonal populations (Salzman 1985; Salzman and Parker 1985) with creeping and often deep

Research was partially supported by funds provided through the Hatch Act and the Anna H. Elliott Fund, University of Nebraska Foundation. A contribution of the University of Nebraska Agricultural Research Division, Lincoln, Nebraska Journal Series No. 14287.

Correspondence: Dr Patrick E. Reece, University of Nebraska, Panhandle Research and Extension Center, 4502 Ave I, Scottsbluff, NE 69361. Email: preece@unl.edu

Manuscript received 17 October 2003; manuscript accepted 8 April 2004.

Table 1. Codominant species of each category of species associated with western ragweed.

	C ₄ rhizomatous grasses
Prairie sandreed	<i>Calamovilfa longifolia</i> (Hook.) Scribn.
Sand bluestem	<i>Andropogon hallii</i> Hack.
Switchgrass	<i>Panicum virgatum</i> L.
	C ₄ bunchgrasses
Little bluestem	<i>Schizachyrium scoparium</i> (Michx.) Nash
Blue grama	<i>Bouteloua gracilis</i> (H.B.K.) Lag. ex Griffiths
Sand dropseed	<i>Sporobolus cryptandrus</i> (Torr.) A. Gray
	Sedges
Sun sedge	<i>Carex heliophila</i> Mack.
Schweinitz flatsedge	<i>Cyperus schweinitzii</i> Torr.
	C ₃ grasses
Needle and thread	<i>Stipa comata</i> Trin. and Rupr.
Prairie junegrass	<i>Koeleria pyramidata</i> (Lam.) Beauv.
	Other forbs
Stiff sunflower	<i>Helianthus rigidus</i> (Cass.) Desf. ssp. <i>subrhomboideus</i> (Rydb.) Heiser
Purple prairie clover	<i>Dalea purpurea</i> Vent.
Narrowleaf puccoon	<i>Lithospermum incisum</i> Lehm.

rootstocks (Weaver 1958; GPFA 1986). Relative palatability of western ragweed herbage is low for cattle, bison, and deer (Fahnestock and Knapp 1993; Northup 1993; Fahnestock and Knapp 1994; Oretaga et al 1997). However, seeds of western ragweed are considered an excellent protein source for gallinaceous bird species (Boren et al 1995). Additionally, over 130 insect species have been collected from western ragweed plants in North America (Goeden and Ricker 1985), which may enhance diet quality of small mammals and ground-nesting birds. Although increases in western ragweed may be desirable for wildlife, an abundance of this species in tallgrass or sandhills prairie is generally considered an indication of overgrazing (Vermeire and Gillen 2000). In spite of its potential impact, herbage relationships among this rhizomatous forb and associated species have not been quantified for semiarid sandhills prairies.

The Nebraska Sandhills encompass about 4.9 million contiguous hectares, and other similar sandhills prairies are widely distributed throughout the Great Plains. Population fluxes of western ragweed often occur between drought and the return of predrought conditions on high-seral sandhills prairie. Western ragweed appears to have the ability to rapidly respond to increased availability of soil water and nutrients resulting from drought and/or grazing-induced reductions in the vigor (Reece et al 1996) or tiller density (Reece et al 2002) of associated species. We hypothesized that western ragweed is a weak competitor with a disproportionately high potential for herbage production early in the growing season compared with associated species. Our objectives were to quantify interspecific herbage relationships and determine the role of shoot recruitment and growth potential in western ragweed herbage production and repopulation.

Methods

Study Site

This study was conducted on high-seral sandhills prairie (Table 1) at the University of Nebraska, Gudmundsen Sandhills Laboratory (GSL), near Whitman, Nebraska (42°07'N, 101°43'W, elevation 1 049 m). All sites were in pastures used exclusively for dormant-season grazing (October–March) at moderate stocking rates (32 AUD•ha⁻¹) since 1985. Soils are Valentine fine sands (mixed, mesic typic Ustipsamments).

Precipitation and air temperature data were measured and recorded by an automated weather station at the GSL headquarters. These data were used to determine plant-year precipitation, the moisture potentially available to plants during the growing season. It includes precipitation received during the preceding dormant season (October–March) plus that received during the current growing season (April–September). Plant year is identified by the year of the active growing season. The 15-year average plant-year precipitation at GSL was 455 mm.

Data Collection

This study was initiated the first week of May 1991. Eighteen 1-m² quadrats were randomly located and permanently marked in relatively homogeneous plant communities at 8 sites in each of 3 pastures. Nine quadrats were randomly selected for each treatment year, 1991 or 1992, at each site. A 3 × 3 factorial array of defoliation treatments (removal of western ragweed, removal of associated species, or nonclipped control) and initial treatment application dates (10 May, 10 June, or 10 July) were randomly assigned to each set of 9 quadrats. Defoliation treatments were applied to the entire 1-m² area by clipping target species at ground level at weekly intervals throughout the growing season. Vegetation responses were measured in the interior 0.5-m² area of each quadrat to minimize the likelihood of clonal support from western ragweed plants outside the treatment area (Salzman 1985; Salzman and Parker 1985).

Western ragweed density was measured in the western-ragweed-removal, associated-species-removal, and respective control plots when clipping was initiated in May, June, or July. End-of-season western ragweed density was measured on associated-species-removal and control plots in early October. Subsequent-year western ragweed density was measured in all quadrats in mid-June the year after treatments were applied.

Standing herbage of target species was collected on vegetation removal plots when defoliation treatments were initiated. Herbage removed at subsequent weekly clippings was discarded. End-of-season western ragweed herbage was measured on associated-species-removal and control plots in early October. End-of-season associated species herbage measurements were made on ragweed-removal and control plots. Herbage was oven dried at 60°C to a constant weight and weighed to estimate dry matter production. To estimate total annual production, we calculated the composite peak herbage by adding the peak standing herbage for western ragweed and each group of associated species (Table 1), regardless of when the peak occurred (eg, when defoliation treatments were initiated in May, June, or July, or during the end-of-season harvest in October). This value was used because herbage

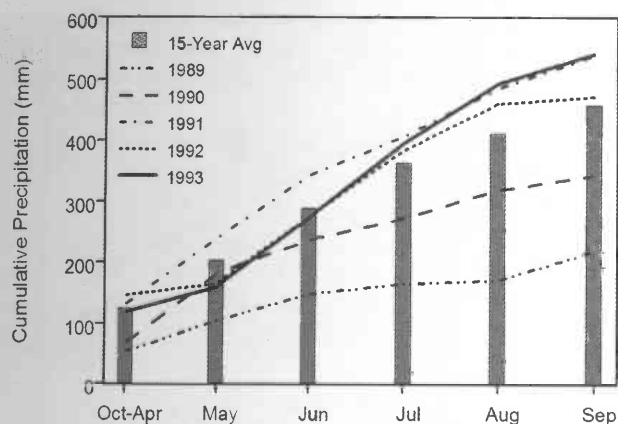


Figure 1. Cumulative plant-year (October–September) precipitation for the 1989–1993 growing seasons and the 15-year average at the Gudmundsen Sandhills Laboratory near Whitman, Nebraska.

production peaks at different times of the growing season for different species.

Statistical Analysis

Experimental units were 0.5-m^2 quadrats centrally placed in the $1 \times 1\text{-m}$ treated areas. Data were analyzed as a randomized complete block using the general linear models procedure (SAS 2002). Level of probability selected for significance was $P \leq 0.05$. The least squares means procedure within SAS (2002) was used for mean separation. Regression equations (SAS 2002) describing the relationship between end-of-season western ragweed herbage and density were fit to experimental units within treatment dates and years. Equations describing the effect of initial date of associated species removal on end-of-season standing crop of western ragweed were fit to pasture means within years (regression procedure, SAS 2002). The stepwise regression procedure (SAS 2002) was used to evaluate relationships between western ragweed density and preceding-year or current-year herbage produced by groups of associated species (Table 1). Stepwise regression was also used to determine if relationships occurred between subsequent-year western ragweed density and preceding-year ragweed density, mean shoot weight, or end-of-season herbage.

Results and Discussion

Based on field observations, relatively high frequencies of western ragweed occurred in the Nebraska Sandhills after prolonged drought from 1988 to 1990, similar to observations reported by Bovey et al (1966) and Berg et al (1997). During this study, plant-year precipitation was 54% and 26% below average in 1989 and 1990, respectively, whereas it was 17% and 3% above average in 1991 and 1992, respectively (Fig. 1). Western ragweed density on control plots ranged from 12 to 90-m^{-2} in 1991 and 18 to 152-m^{-2} in 1992. End-of-season western ragweed herbage on control plots ranged from 36 to $611\text{ kg}\cdot\text{ha}^{-1}$ in 1991 and from 22 to $544\text{ kg}\cdot\text{ha}^{-1}$ in 1992.

Composite peak herbage was 43% lower in 1992 ($1\,275\text{ kg}\cdot\text{ha}^{-1}$) than in 1991 ($2\,252\text{ kg}\cdot\text{ha}^{-1}$; Fig. 2) following an

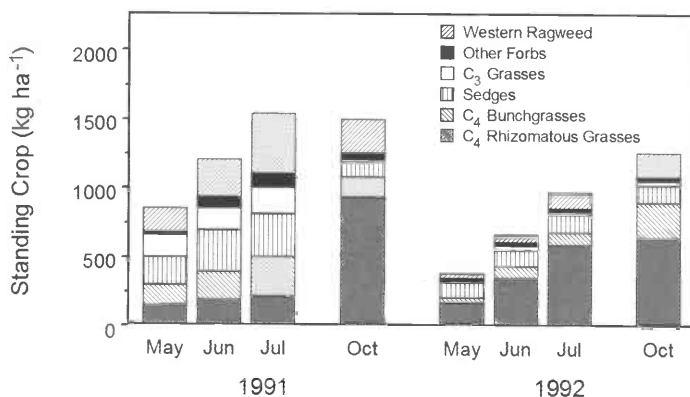


Figure 2. Seasonal patterns in standing herbage of western ragweed and associated species from initial harvests on vegetation removal plots initiated in early May, June, or July and end-of-season (early October) herbage harvested from control plots.

unusually dry April and May and a relatively late spring frost in 1992. Herbage production on sandhills prairies in this region is measurably greater in response to spring precipitation compared with summer precipitation (Dahl 1963). Precipitation during April and May 1991 was about 14% above the 15-year average for GSL and 116 mm above April–May precipitation in 1992. Additionally, plants had 3 more weeks of uninterrupted spring growth in 1991 than in 1992 because of differences in the date of last frost (5 and 26 May, respectively).

Seasonal Standing Crop Patterns

During early May to early July, western ragweed and groups of associated species produced more herbage in 1991 compared with 1992, except for rhizomatous C_4 grasses, which were about twice as productive in 1992 compared with 1991 (Table 2). All species, except C_3 grasses, contributed to increases in total standing crop from early May to early July 1991 (Fig. 2). Cool-season grass herbage was near peak standing crop in early May and remained relatively constant during May and June in both years. Increases in total herbage from May to July 1992 were primarily from rhizomatous C_4 grasses (Fig. 2).

Western ragweed standing crop increased about $4.5\text{ kg}\cdot\text{ha}^{-1}\cdot\text{d}^{-1}$ from early May to early July in 1991 and about $1.3\text{ kg}\cdot\text{ha}^{-1}\cdot\text{d}^{-1}$ in 1992 (Fig. 2). However, mean density of

Table 2. Herbage (mean \pm SE) produced by western ragweed and associated species averaged over May, June, and July sample dates for 1991 and 1992.

Species	1991 ¹ ($\text{kg}\cdot\text{ha}^{-1}$)	1992 ¹ ($\text{kg}\cdot\text{ha}^{-1}$)
Western ragweed	294 ± 16	69 ± 6
Other forbs	69 ± 4	19 ± 2
C_3 grasses	171 ± 6	26 ± 4
Sedges	274 ± 10	119 ± 7
C_4 bunchgrasses	214 ± 11	73 ± 6
C_4 rhizomatous grasses	180 ± 6	369 ± 24

¹Year effects were significant ($P < 0.0001$) for western ragweed and all groups of associated species.

Table 3. End-of-season herbage of warm-season rhizomatous grasses for western ragweed removal and paired control treatments when removal started in early May, June, or July 1991 or 1992.

Month	1991 ¹			1992 ¹		
	Removal (kg·ha ⁻¹)	Control (kg·ha ⁻¹)	P	Removal (kg·ha ⁻¹)	Control (kg·ha ⁻¹)	P
May	883	953	0.28	789	634	0.02
June	1 037	962	0.24	799	667	0.04
July	856	860	0.96	759	634	0.05

¹Year by treatment interaction effects were significant, $P = 0.01$. Standard errors ranged from 5% to 8% of the mean. Probability (P) of differences between western ragweed removal treatments and paired controls refer to comparisons within years and months.

western ragweed was 42% greater ($P < 0.0001$) in 1992 ($71 \cdot \text{m}^{-2}$) compared with 1991 ($50 \cdot \text{m}^{-2}$). In contrast to seasonal population declines reported for tallgrass and mixed prairies (Vermeire and Gillen 2000), density of western ragweed in this study was relatively constant during the growing season and after killing frost in October. Consequently, seasonal increases in standing herbage of western ragweed were primarily the result of increases in mean shoot weight in both years.

Standing crop of western ragweed and most associated species declined from early July to October in 1991. In contrast, rhizomatous C_4 grass herbage increased by about $710 \text{ kg} \cdot \text{ha}^{-1}$ during this period (Fig. 2), and its contribution to total standing crop increased from 14% to 62%. The unusually large increase in rhizomatous C_4 grass herbage corresponded to relatively high percentages of sand bluestem (*Andropogon hallii* Hack.) and prairie sandreed (*Calamovilfa longifolia* [Hook.] Scribn.) reproductive tillers, which are heavier than vegetative tillers (Hendrickson et al 1998; Reece et al 1999). In 1992, western ragweed and C_4 bunchgrass herbage increased by 72% and 173%, respectively, whereas little change occurred in other associated species from early July to October. Warm-season grasses accounted for about 72% of the herbage harvested in October in both years.

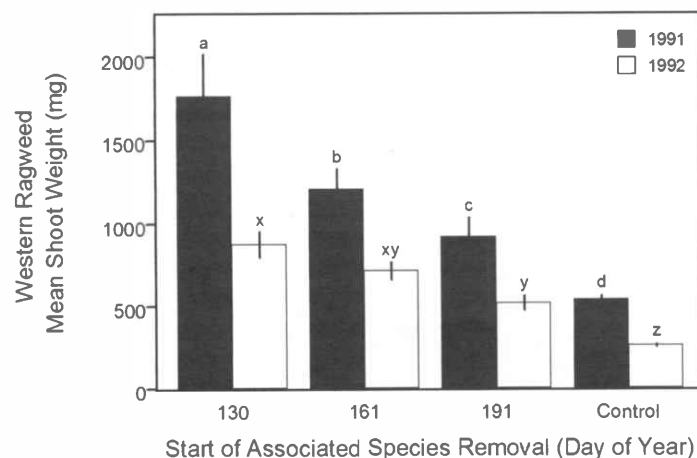


Figure 3. End-of-season shoot weight (mean \pm SE) of western ragweed for control and associated species removal treatments beginning on 3 dates in 1991 and 1992. Within years, means with the same letter are not different ($P > 0.05$).

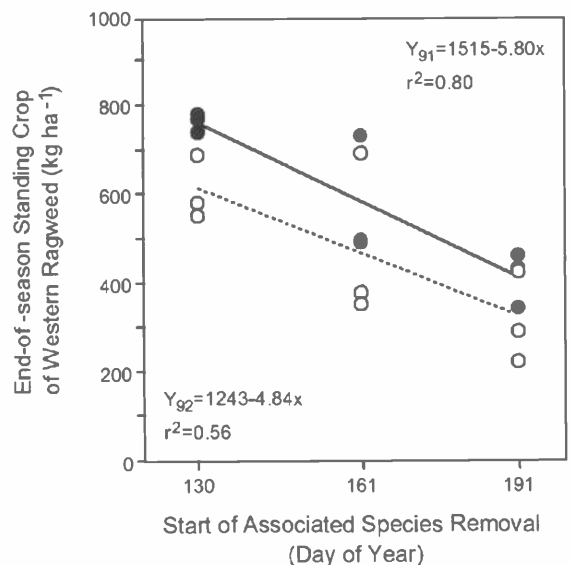


Figure 4. Response of end-of-season standing crop of western ragweed to removal of associated species beginning on 3 dates in 1991 (filled circle) or 1992 (open circle).

Effects of Western Ragweed Removal on Associated Species

Mean levels of western ragweed herbage production up to $436 \text{ kg} \cdot \text{ha}^{-1}$ (Fig. 2) had no measurable effect on the yield of associated species in 1991 (Table 3) when above-average cumulative precipitation occurred throughout the growing season (Fig. 1). In contrast, when a dry spring occurred in 1992, relatively small amounts of western ragweed ($189 \text{ kg} \cdot \text{ha}^{-1}$) on control plots (October) reduced end-of-season standing crop of rhizomatous C_4 grasses by about 21% or $137 \text{ kg} \cdot \text{ha}^{-1}$ compared with western ragweed-removal treatments (Table 3).

Competition between western ragweed and associated species for limited soil water was most likely to occur during April and May of 1992 when precipitation was 98 mm below the 15-year average. The relatively wide dispersion of sedges and C_3 grasses in warm-season grass dominated communities and limited growth of C_4 grasses in April and May may explain the lack of western ragweed effects on cool-season species in the sandhills. Tiller emergence of rhizomatous C_4 grasses occurs primarily from April to mid-June. From 65% to 85% of prairie sandreed tillers emerge by the end of May (Cullan 1998; Hendrickson et al 2000; Reece et al 2002). If interspecific interference reduced tiller emergence and corresponding end-of-season standing crop, yield responses of rhizomatous grasses, expressed as a percentage of paired controls (Table 3), should have declined as initial date of western ragweed removal was delayed. However, increases were relatively constant, ranging from 20% to 24% of paired controls, indicating measurable competitive effects did not occur until after 10 July. The apparent lack of effect of a dry spring on tiller emergence is consistent with a concurrent study at GSL in which rate of prairie sandreed tiller emergence and tiller number were poorly correlated with short- and long-term precipitation totals (Hendrickson et al 2000).

Table 4. Linear relationship ($y = a + bx$) between end-of-season western ragweed herbage ($\text{kg}\cdot\text{ha}^{-1}$) and density ($\text{No}\cdot\text{m}^{-2}$) in 1991 and 1992, with and without removal of associated species near Whitman, Nebraska.

Associated species removal	<i>n</i>	1991 ¹			1992 ¹		
		<i>a</i>	<i>b</i> ± SE	<i>r</i> ²	<i>a</i>	<i>b</i> ± SE	<i>r</i> ²
June	24	184	6.5 ± 1.6	0.45	141	4.6 ± 0.9	0.57
July	24	149	5.2 ± 1.2	0.48	64	4.0 ± 0.8	0.51
Control	72	69	3.7 ± 0.5	0.40	-27	3.1 ± 0.3	0.66

¹All regression equations are significant, $P \leq 0.01$.

Competitive effects of western ragweed that occurred after 10 July may have been linked to epic events of tiller mortality that are common in rhizomatous graminoids during the growing season (Callaghan 1976; de Kroon et al 1992; Reece et al 2002). For example, Reece et al (2002) found that under relatively dry conditions, densities of prairie sandreed tillers declined 25%–64% during July or August. Mortality primarily occurs in small tillers that may be more susceptible to interspecific interference. Above average precipitation from June through August 1992 may not have eliminated the potential for competition for soil water given the low water holding capacity of sandy soils and relatively large amounts of C_4 grass leaf area in July and August. The inability of rhizomatous C_4 grasses to compensate for competitive effects when above average precipitation occurred during July and August 1992 suggests that herbage production potential was reduced, perhaps because of increased rates of tiller mortality during the summer.

Effects of Associated Species Removal on Western Ragweed

Associated species accounted for 72%–81% of the standing crop from May to July 1991 and 89%–91% of standing crop from May to July 1992 (Fig. 2). Western ragweed biomass increased in response to removal of associated vegetation (Fig. 3). Complete defoliation of associated species at weekly intervals may have increased the availability of soil water and nutrients, thereby reducing any effects of interspecific competition on western ragweed. Delaying removal of associated species (ie, release from interspecific competition) decreased western ragweed herbage at constant and similar rates in both years (Fig. 4; $P > 0.05$).

Yield response of western ragweed to removal of associated species in May, June, or July provided insight into how timing of summer grazing may affect herbage production by western ragweed. Mean end-of-season ragweed herbage on control plots was $247 \text{ kg}\cdot\text{ha}^{-1}$ in 1991 and $189 \text{ kg}\cdot\text{ha}^{-1}$ in 1992 (Fig. 2). Based on the extrapolation of the regression lines in Fig. 4, severe defoliation of associated species after July would cause little or no increase in current-year western ragweed herbage.

Removal of associated species had no effect on ragweed density during the current growing season. Within a given year, western ragweed density accounted for 40%–48% of the variation in end-of-season ragweed standing crop in 1991 and 51%–66% of the variation in 1992 on control plots and on June or July associated-species-removal plots (Table 4). Progressively larger intercept and slope coefficients (Table 4) when associated

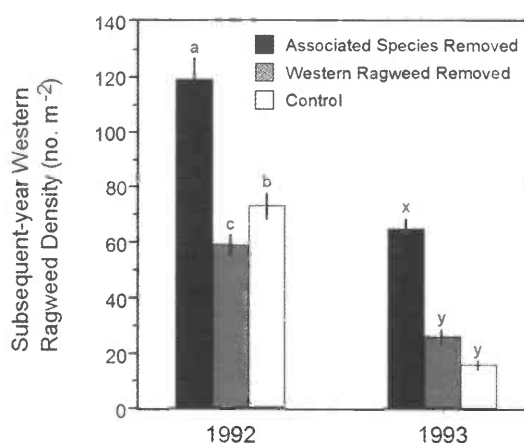


Figure 5. Subsequent-year western ragweed densities (mean ± SE) in mid-June 1992 and 1993, about 1 year after treatments were applied in 1991 or 1992, respectively. Data for the 3 treatment initiation dates did not differ ($P > 0.05$) and were pooled. Within years, means with the same letter are not different ($P > 0.05$).

species were removed earlier corresponded to increases in mean western ragweed shoot weights (Fig. 3). End-of-season western ragweed herbage was poorly correlated ($r^2 < 0.25$) with density on May removal plots because some ragweed shoots grew disproportionately large. After removal of associated species in May, mean weight of western ragweed shoots on individual plots ranged from 641–5 888 mg in 1991 and 366–1 934 mg in 1992.

During a concurrent study at GSL (Brummer et al 1994), increases in western ragweed density and herbage production corresponded to declines in total organic reserves of prairie sandreed and sand bluestem in paddocks grazed heavily during July or multiple times during June, July, and/or August 1988–1991 (Reece et al 1996). However, total organic reserves of the grass species in dormant-season grazed paddocks were similar to nongrazed paddocks, indicating that drought-induced increases in western ragweed were primarily the result of reduced basal area of grasses (Reece et al 2002), rather than vigor.

Subsequent-year Western Ragweed Density

Large increases in herbage production by western ragweed generally preceded increases in subsequent-year western ragweed densities. Removal of associated species increased subsequent-year western ragweed densities by 59% in 1992 and 306% in 1993 compared with control plots (Fig. 5). However, posttreatment populations of individual clones were not clearly related ($r^2 < 0.25$) to preceding-year species composition. Other factors may have contributed to this apparent lack of relationship. For example, phytophagous insects lay more eggs on large compared with small western ragweed plants (Reznik 1985), possibly impacting their subsequent contribution to repopulation. Although not measured, probable micro-environmental modifications included increased exposure to sunlight, warmer soil temperatures, and greater variation in diurnal air and soil temperature patterns. Wan et al (2002) reported progressive and relatively large annual increases in the density of western ragweed in year-long artificially warmed tallgrass prairie in Oklahoma.

Without damaging plants, it was not possible to determine if shoots originated from rhizomes or seeds. However, vegetatively propagated clones share the same genetic material and are likely to be more uniform than plants produced from seed. In this study plots were widely distributed over 24 sites, yet within plots initial western ragweed densities and plant heights were relatively uniform. This suggests that most repopulation was from buds supported by a network of rhizomes (Salzman 1985; Salzman and Parker 1985). The similarity of posttreatment populations on control and ragweed-removal plots, where seed production was eliminated, supports this interpretation. Additionally, viable western ragweed seed was not observed in extensive seedbank surveys at GSL in 1990 and 1991 (Pérez et al 1998). They suggested that absence of viable seeds for many species may have resulted from reduced seed rain caused by prolonged drought and/or seed predation by mammals, birds, and/or granivorous invertebrates. Pérez et al (1998) reported limited occurrence of large seeded species in the seedbank and relatively high percentages of damaged seed in all collections.

The ability of western ragweed to produce densities similar to control plots after complete defoliation (Fig. 5) indicated this species can maintain primordia for at least 2 years with limited plant growth. Selective defoliation of this species by phytophagous insects used for biological control (Goeden and Ricker 1985) may be required for several years before declines in ragweed populations would be expected.

Management Considerations

Relatively low palatability, high potential for spring growth, and the ability to maintain primordia when herbage production is limited make western ragweed ecologically valuable for stabilizing sandhills prairie when drought and/or overgrazing occur. As an indigenous forb, western ragweed and associated species were in dynamic equilibrium on the high-seral sandhills prairie sites in this study. Relatively low shoot weights of western ragweed on control plots compared with the robust shoots that developed when associated species were removed clearly indicated the competitive inferiority of western ragweed in the presence of vigorous graminoids.

The competitive effect of western ragweed on rhizomatous C_4 grasses after an unusually dry spring in 1992 was unexpected because these grasses are traditionally considered relatively drought tolerant. Additionally, vigor of rhizomatous grasses should have been relatively high because pastures were grazed only after killing frost for 7 years (Reece et al 1996). The majority of western ragweed shoots tend to develop in microsites that are relatively favorable for plant growth (Salzman 1985; Salzman and Parker 1985). The size and number of favorable microsites probably increased because of drought-induced mortality in graminoids that occurred before our study was initiated. Shoots of western ragweed were most abundant in openings between bunchgrasses where rhizomatous C_4 grass tillers were often in close proximity.

Economic and ecological thresholds for western ragweed on semiarid sandhills prairie appear to be inseparable from precipitation regime and grazing history. Defining thresholds strictly by shoot density or standing crop of western ragweed would be unreliable. Lack of competitive effects from western ragweed when above average precipitation occurred in this and

other studies (Launchbaugh 1967; Vermeire and Gillen 2000) indicated economic thresholds for control of western ragweed have limited utility. Yield responses of graminoids to western ragweed control on semiarid, mid- to high-seral sandhills prairie are likely to be inconsistent and too small to recover the costs of chemical control.

Increases in subsequent-year western ragweed populations are most likely to occur on summer-grazed pastures compared with nongrazed (Gillen et al 1991) or dormant-season-grazed pastures (Brummer et al 1994). Heavy grazing during July is most likely to reduce vigor of dominant grasses (Reece et al 1996), and the regrowth potential of graminoids is limited after July (Reece et al 2001). If increases in subsequent-year density of western ragweed are linked to microenvironmental increases in temperature (Wan et al 2002), management practices that maintain uniformly distributed residual herbage may limit population increases. Reducing stocking rates and/or periodically deferring grazing until after killing frost in the fall will increase residual herbage and enhance the vigor of palatable species (Reece et al 1996).

Acknowledgments

The authors would like to thank Gordon Moeller and Bryan Hurst for technical assistance and Sharon Holman for preparation of the manuscript. We appreciate the numerous constructive comments by R.L. Gillen and 2 anonymous reviewers.

Literature Cited

- BERG, W. A., J. A. BRADFORD, AND P. L. SIMS. 1997. Long-term soil nitrogen and vegetation change on sandhill rangeland. *Journal of Range Management* 50:482-486.
- BOREN, J. C., R. L. LOCHMILLER, D. M. LESLIE, JR., AND D. M. ENGLE. 1995. Amino acid concentrations in seed of preferred forages of bobwhites. *Journal of Range Management* 48:141-144.
- BOVEY, R. W., M. K. MCCARTY, AND F. S. DAVIS. 1966. Perennial ragweed on western Nebraska rangeland. *Journal of Range Management* 19:220-222.
- BRUMMER, J. E., P. E. REECE, J. T. NICHOLS, AND R. K. ENGEL. 1994. Western ragweed response to date and frequency of grazing sandhills vegetation. *Society for Range Management Abstracts for Annual Meetings* 47:63.
- CALLAGHAN, T. V. 1976. Growth and population dynamics of *Carex bigelowii* in an alpine environment: strategies of growth and population dynamics of tundra plants. *Oikos* 27:402-413.
- CULLAN, A. P. 1998. Grazing date by stocking rate effects on prairie sandreed [MS thesis]. Lincoln, NE: University of Nebraska. 69 p.
- DAHL, B. E. 1963. Soil moisture as a predictive index to forage yield for the sandhills range type. *Journal of Range Management* 16:128-132.
- DE KROON, H., T. HARA, AND R. KWANT. 1992. Size hierarchies of shoots and clones in clonal herb monoculture: do clonal and non-clonal plants compete differently? *Oikos* 63:410-419.
- FAHNESTOCK, J. T., AND A. K. KNAPP. 1993. Water relations and growth of tallgrass prairie forbs in response to selective grass herbivory by bison. *International Journal of Plant Science* 154:432-440.
- FAHNESTOCK, J. T., AND A. K. KNAPP. 1994. Plant response to selective grazing by bison: interactions between light, herbivory and water stress. *Vegetation* 115:123-131.
- GILLEN, R. L., F. T. MCCOLLUM, M. E. HODGES, J. E. BRUMMER, AND K. W. TATE. 1991. Plant community responses to short duration grazing in tallgrass prairie. *Journal of Range Management* 44:124-128.
- GOEDEN, R. D., AND D. W. RICKER. 1985. The life history of *Ophraella notulata* (F.) on western ragweed, *Ambrosia psilostachya* De Candolle, in southern California (Coleoptera: Chrysomelidae). *Pan-Pacific Entomologist* 61:32-37.

- GREAT PLAINS FLORA ASSOCIATION (GPFA). 1986. Flora of the Great Plains. Lawrence, KS: University Press of Kansas. 1392 p.
- HENDRICKSON, J. R., L. E. MOSER, K. J. MOORE, AND S. S. WALLER. 1998. Morphological development of 2 warm-season grasses in the Nebraska Sandhills. *Journal of Range Management* 51:456–462.
- HENDRICKSON, J. R., L. E. MOSER, AND P. E. REECE. 2000. Tiller recruitment patterns and biennial tiller production in prairie sandreed. *Journal of Range Management* 53:537–543.
- LAUNCHBAUGH, J. L. 1967. Vegetation relationships associated with intensity of summer grazing on a clay upland range site in the Kansas 20 to 24 inch precipitation zone. Kansas Agricultural Experiment Station Bulletin No. 154. Manhattan, KS.
- NORTHUP, B. K. 1993. Utilization of native forages of the Nebraska Sandhills by yearling cattle [PhD dissertation]. Lincoln, NE: University of Nebraska. 328 p.
- ORTEGA, I. M., S. SOLTERO-GARDEA, F. C. BRYANT, AND D. L. DRAWE. 1997. Evaluating grazing strategies for cattle: deer forage dynamics. *Journal of Range Management* 50:615–621.
- PÉREZ, C. J., S. S. WALLER, L. E. MOSER, J. L. STUBBENDIECK, AND A. A. STEUTER. 1998. Seedbank characteristics of a Nebraska Sandhills prairie. *Journal of Range Management* 51:55–62.
- REECE, P. E., J. E. BRUMMER, R. K. ENGLE, AND B. K. NORTHUP. 1996. Grazing date and frequency effects on prairie sandreed and sand bluestem. *Journal of Range Management* 49:112–116.
- REECE, P. E., T. L. HOLMAN, AND K. J. MOORE. 1999. Late-summer forage on prairie sandreed dominated rangeland after spring defoliation. *Journal of Range Management* 52:228–234.
- REECE, P. E., J. S. NIXON, L. E. MOSER, AND S. S. WALLER. 2002. Seasonal dynamics of prairie sandreed rhizome development. *Journal of Range Management* 55: 182–187.
- REECE, P. E., J. D. VOLESKY, AND W. H. SCHACHT. 2001. Cover for wildlife after summer grazing on sandhills rangeland. *Journal of Range Management* 54: 126–131.
- REZNIK, S. Y. 1985. Factors of oviposition selectivity in *Zygogramma suturalis* (Coleoptera, Chrysomelidae). *Zoologicheskii Zhurnal* 64:234–244.
- SALZMAN, A. G. 1985. Habitat selection in a clonal plant. *Science* 228:603–604.
- SALZMAN, A. G., AND M. A. PARKER. 1985. Neighbors ameliorate local salinity stress for a rhizomatous plant in a heterogeneous environment. *Oecologia* 65:273–277.
- SAS. 2002. SAS Online Doc®. Version 8. Cary, NC: SAS Institute, Inc.
- VERMEIRE, L. T., AND R. L. GILLEN. 2000. Western ragweed effects on herbaceous standing crop in Great Plains grasslands. *Journal of Range Management* 53: 335–341.
- WAN, S., T. YUAN, S. BOWDISH, L. WALLACE, S. D. RUSSELL, AND Y. LUO. 2002. Response of an allergenic species, *Ambrosia psilostachya* (Asteraceae), to experimental warming and clipping: implications for public health. *American Journal of Botany* 89:1843–1846.
- WEAVER, J. E. 1958. Classification of root systems of forbs of grassland and consideration of their significance. *Ecology* 39:393–401.