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Overstory-understory relationships for broom snakeweed-blue grama grasslands

KIRK C. MCDANIEL, L. ALLEN TORELL, AND JOHN W. BAIN

Authors are professor, Dep. Range and Animal Sci.; associate professor and former graduate research assistant, Dep. Agr. Econ. and Agr. Bus., New Mexico State University, Las Cruces 88003.

Abstract

Data collected over a 11-year period at 2 study areas near Vaughn and Roswell, N.M. were used to define equations that relate grass biomass to the amount of broom snakeweed (*Gutierrezia sarothrae* [Pursh] Britt. & Rusby) occupying blue grama (*Bouteloua gracilis* [H.B.K. Lag]) rangeland over time. A 5 parameter sigmoidal growth equation and a negative exponential equation best expressed the relationship between understory grass biomass and overstory broom snakeweed biomass. Explanatory variables included realized precipitation during the second (April to June) and third (July to September) quarters, which coincides primarily with warm-season grass growth. Minimum suppression of grass biomass occurred with complete elimination of broom snakeweed, suggesting control strategies with high overstory mortality will likely be most beneficial to understory production.

Key Words: herbage production, *Gutierrezia sarothrae, Bouteloua gracilis* weed control, range improvement

Overstory-understory relationships have been defined for many woody and herbaceous plants common on western rangelands (Bartlett and Betters 1983, Ffolliot and Clary 1972). Published overstory-understory equations include linear, logarithmic, quadratic, cubic and various nonlinear, exponential functional forms (Ffolliot 1983, McPherson 1992, Scanlan 1992). In general, the relationship between herbaceous production and woody cover has been found to be a downward-sloping curve that is either convex to the origin or S-shaped over the relevant range (Jameson 1967). The convex shape, reported to be appropriate for numerous overstory species (Jameson 1967, Hull and Klomp 1974, Ffolliot 1983, Pieper 1990) suggests marginal suppression of herbaceous biomass declines as overstory cover increases, and implies that the first woody plants to invade an area suppress herbaceous production the most. Similarly, a sigmoid shaped curve implies a light or scattered stand of overstory species results in little if any suppression of understory production until a threshold level is eventually reached, and grass yield then rapidly declines (Scifres et al. 1982, Jameson 1967).

Several studies have investigated competitive relationships between broom snakeweed (*Gutierrezia sarothrae* [Pursh] Britt. & Rusby), an undesirable woody weed, and associated grasses growing on rangeland (Campbell and Bomberger 1934, Gardner 1951, McDaniel and Sosebee 1988). Ueckert (1979) and McDaniel et al. (1982) found that thinning a heavy stand of broom snakeweed by 25%, 50%, or 75% did not greatly increase grass yield, whereas complete removal of the weed resulted in a grass production increase from 200% to 400%, suggesting some type of nonlinear relationship between overstory broom snakeweed cover and understory grass production.

To define overstory-understory relationships for an economic analysis of broom snakeweed control, Carpenter et al. (1991) used a linear equation to relate expected grass production to broom snakeweed canopy cover. Variables reported to influence grass production included snakeweed cover, summer rainfall, and soil type (site shifters). For a similar economic analysis, Torell et al. (1990) used a logarithmic model to define overstory-understory relationships with explanatory variables defined to be broom snakeweed yield, climatic conditions, and site characteristics. A shortcoming noted by Torell et al. was that the logarithmic model overestimated grass production when broom snakeweed biomass was near zero. A problem with the linear estimation is other research (McDaniel et al. 1982 and Ueckert 1979) suggests the correct broom snakeweed-understory relationship is curvilinear.

The purpose of this study was to define equations expressing the overstory-understory relationship for broom snakeweed growing on blue grama (*Bouteloua gracilis* (H.B.K. Lag])-dominated grasslands in central New Mexico. Model estimation is provided from broom snakeweed and grass biomass data collected over an 11-year period at 2 permanent study sites near Vaughn and Roswell, N.M.

Methods

Equation Development and Definition

Equation estimation was based on concepts developed by Jameson (1967) and Ffolliot (1983). Jameson suggested a 5-parameter transition sigmoidal growth curve (adapted from Grosenbaugh 1965) as an appropriate general model for defining overstory-understory relationships. Depending on parameter estimates, the nonlinear function defined by Jameson will either be convex to the origin or S-shaped over the relevant range. Ffolliot (1983) indicated a simpler negative exponential equation was adequate for nearly all overstory-understory relationships. With either approach, the rate of decline in herbaceous standing crop as cover or yield of woody plants increases is influenced by climate and other site-specific factors. Broom snakeweed and grass yield are known to vary by location, especially with growing season moisture (McDaniel 1989); seasonal precipitation patterns were considered on a site specific basis for our model estimation.

General specification of the sigmoidal growth curve and the negative exponential curve are:

$$Y = H + A(1-e^{-BX})^{M+1} + \sum \alpha_1 R_i; \text{ (sigmoid equation)} \quad (1)$$

$$Y = a + be^{-cX} + \sum \alpha_1 R_i; \text{ (exponential equation)} \quad (2)$$

The dependent variable (Y) is understory or grass production (kg/ha). The independent variable (X) defines overstory produc-

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tion (kg/ha) on the area, and the R_is define rainfall conditions during specific quarters of the year (e.g., R_2 = cm of rainfall during the 2nd quarter: April, May, and June). The upper and lower asymptotes shift up or down depending on rainfall conditions.

For the sigmoid curve defined by Equation 1, $H + \Sigma \alpha_i R_i$ defines the upper asymptote and $H + A + \Sigma \alpha_i R_i$ is the lower asymptote. Understory production will approach this lower asymptote as overstory yield is maximized. Because increasing overstory canopy decreases understory herbage production, the estimated value of parameter A will be negative. Parameter B provides the necessary curvature for the model and M adjusts the inflection point. The curve will have a sigmoid or S shape for $M + 1 > 1$, and will be convex to the origin throughout the relevant range when $0 < M + 1 \leq 1$. When $M + 1 = 1$, the equation reduces to the simpler exponential function (Equation 2). The flexibility of this equation is unique and especially useful for estimating overstory-understory relationships.

For Equation 2, the parameters $a + b + \Sigma \alpha_i R_i$ define the upper asymptote and $a + \Sigma \alpha_i R_i$ define the lower asymptote. The parameter c defines the exponential rate at which overstory vegetation suppresses grass production. The curve will be convex to the origin throughout the relevant range.

Equation Estimation

In addition to the nonlinear models defined by Equations 1 and 2, other functional forms (including linear through fourth-order polynomial models) were estimated. The best functional form was chosen based on standard goodness-of-fit criteria including highest R^2, minimum root mean square error (RMSE) and analysis of residuals. The R^2 was computed as $1 - \Sigma (y - \hat{y})^2 / \Sigma (y - \bar{y})^2$ (Kvalseth 1985). Regression equations were estimated using appropriate linear and nonlinear regression routines found in SAS (1985).

Various rainfall variables (R_is) were defined to estimate how seasonal rainfall patterns influence grass production. Rainfall exerted a significant ($p<0.001$) influence on grass production only during the 2nd (April–June) and 3rd quarters (July–September) when blue grama (*Bouteloua gracilis* [Willd. ex H.B.K.] lag. ex Griffiths) and other warm-season grasses were actively growing. Similar to the findings of Carpenter et al. (1991), fall and winter rainfall did not influence the production of warm-season grasses dominating the research sites.

Data Sources

Field studies were established at 2 locations on New Mexico's central plains grassland region, about 56 km northwest of Roswell and 28 km southeast of Vaughn. The region is characterized by cool dry winters and warm moist summers. Long-term annual precipitation is about 30 cm at Roswell and 27 cm at Vaughn, about 65% occurring between July and September.

Broom snakeweed growing in association with blue grama forms the vegetational mosaic of both areas. Broom snakeweed is the dominant overstory plant, with occasional scatterings of walking stick cholla (*Opuntia imbricata* [Harr.] DC.). Common warm-season grasses in addition to blue grama include black grama (*Bouteloua eriopoda* [Torr.] Torr.), sideoats grama (*Bouteloua curtipendula* [Michx.] Torr.) and buffalograss (*Buchloe dactyloides* [Nutt.] Engelm). Few annual or perennial broadleaf species occurred at either site. Soil at the Roswell site is a Hogadero gravelly loam (loamy-skeletal, mixed mesic Aridic Calciustoll); and soil at the Vaughn site is a Pastura gravelly loam (loamy, mixed shallow Ustollic Paleorthid). Both sites occur on undulating shallow limestone hills.

Broom snakeweed and grass biomass data were acquired from 2 separate experimental areas established at each study site in 1979 and 1983. Results from these experiments have been reported in part elsewhere and were designed to compare various herbicides for broom snakeweed control and to determine the subsequent grass response. In the 1979 experiment, 1 untreated and 12 herbicide-treated plots were established at both locations. Herbicides were applied using a trail-mounted sprayer to plots (19.2-by-42 m) arranged in randomized complete blocks with 2 replications. Broom snakeweed and grass biomass data collected in October 1979 and 1980 were reported by McDaniel (1984). In general, treatments provided varying degrees of control success; therefore, a wide range of broom snakeweed biomass levels could be compared with understory grass production.

Drought conditions in 1980 and early 1981 caused broom snakeweed to largely die out at both locations; thus grass and snakeweed production data were collected for 2 years from the 1979 herbicide-treated plots. However, broom snakeweed biomass and density data were collected continually from 1979 to 1989 in October on untreated plots (McDaniel 1989).

Broom snakeweed had reestablished by 1983 and a second herbicide control experiment was initiated at both sites near the 1979 study areas. The objective of this experiment (previously reported by McDaniel and Duncan 1987) was to compare 3 rates of picloram (4-amino-3,5,6-trichloro-2-pyridinecarboxylic acid) and metsulfuron {2-[[[[(4-methoxy-6-methyl-1,3,5-triazin-2-yl)amino]carbonyl]amino]sulfonyl]benzoic acid} for broom snakeweed control in fall and spring. Again, varying broom snakeweed control levels resulted, depending on the herbicide used and rate of herbicide applied.

Plot size and vegetation sampling were identical for the 1979 and

Table 1. Precipitation (cm) by quarters from 1979 to 1989 near Vaughn and Roswell, N.M.

	Vaughn Study Area					Roswell Study Area				
	Jan.–Mar.	Apr.–Jun.	Jul.–Sep.	Oct.–Dec.	Total	Jan.–Mar.	Apr.–Jun.	Jul.–Sep.	Oct.–Dec.	Total
1979	4.3	18.0	10.9	4.1	37.4	3.3	16.3	12.6	5.4	37.8
1980	1.8	3.5	8.7	0.7	14.7	1.5	7.2	14.1	1.2	24.0
1981	1.7	4.8	11.6	4.1	22.2	1.6	10.1	16.5	3.8	31.9
1982	2.1	2.0	20.1	4.7	28.9	2.5	1.6	24.0	3.9	32.0
1983	4.5	3.3	12.1	7.6	27.6	6.1	11.7	6.4	7.1	31.3
1984	1.8	5.8	14.0	10.3	31.8	2.9	11.0	17.6	14.6	46.1
1985	5.0	12.6	16.6	12.4	46.5	7.4	14.6	11.9	11.4	45.3
1986	2.8	14.2	8.5	13.1	38.6	8.4	11.7	19.9	19.9	60.0
1987	5.6	9.7	19.4	5.8	40.5	6.9	16.0	9.8	4.1	36.8
1988	1.5	10.8	31.2	2.7	46.1	5.3	11.3	15.3	4.7	36.6
1989	1.6	3.5	14.8	1.5	21.4	2.5	3.6	16.7	0.8	23.6
Study Period	3.0	8.0	15.3	6.1	32.3	4.4	10.4	15.0	7.0	36.8
Normal	2.6	5.3	14.4	4.2	26.5	2.9	6.7	16.0	4.5	30.1

Source: NOAA (Various issues).

1983 experiments. Broom snakeweed was counted and then clipped and bagged separately from grass to a 2.5-cm stubble height in five, 0.2-m^2 frames along each of 2 lines located diagonally across each plot. Clipped material was oven dried before weighing. Field sampling for the second experiment was completed in September or early October each year from 1984 to 1989. Lines were relocated each year to avoid clipping previously sampled quadrats.

Data used in the regression analyses reported here include observations from both the 1979 and 1983 experiments at Vaughn and Roswell. Regression equations were estimated with data separated or combined by experiments and by sites. As expected, herbicide-treated areas usually had less broom snakeweed biomass and higher grass biomass than untreated plots. However, at each research site, areas having similar snakeweed biomass generally had comparable levels of grass production (McDaniel and Duncan 1987).

Results and Discussion

Broom Snakeweed Growth and Rainfall Conditions

During the 11-year study period (1979–1989), annual rainfall near Vaughn and Roswell was substantially below the long-term average only during 1 year (Table 1); thus, environmental conditions were generally favorable for broom snakeweed survival and growth. In 1980, only about half the normal rainfall was received at Vaughn and rainfall was about 80% of normal near Roswell. This low rainfall caused significant broom snakeweed death throughout much of New Mexico (McDaniel 1989) and a decline in yield at both study sites (Fig. 1). By the first quarter (January–March) of

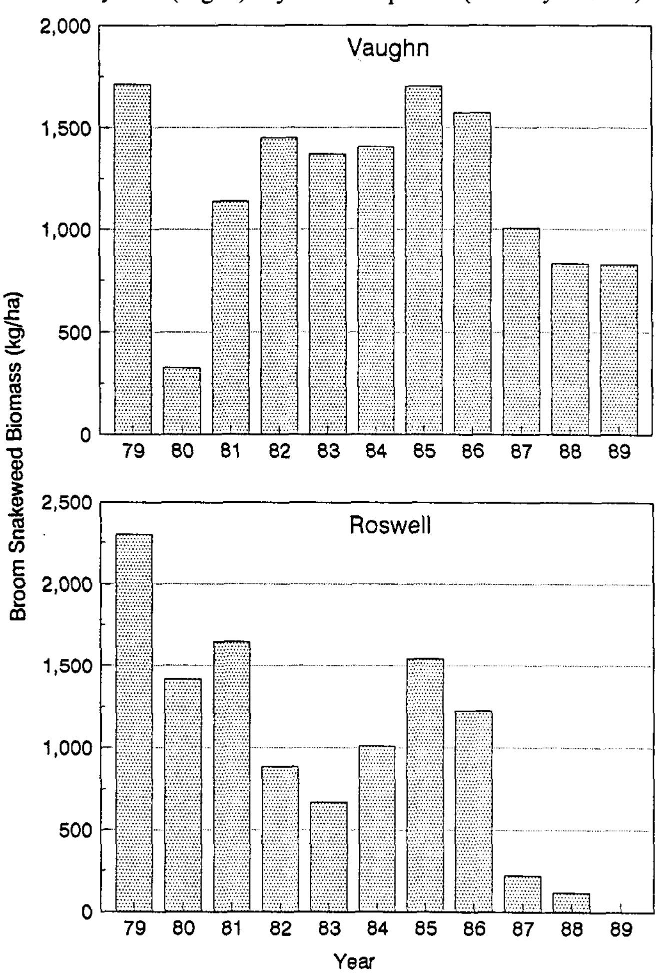

Fig. 1. Broom snakeweed biomass near Vaughn and Roswell, N.M. 1979–1989.

1981, nearly all the mature broom snakeweed plants on both sites were dead, presumably because of drought (data not shown). During the second (April–June) and third (July–September) quarters of 1981, rainfall was near or above normal at Vaughn and Roswell and many seedlings (first-year plants) were counted on untreated study plots in October 1981 (88/m^2 and 115/m^2 at Vaughn and Roswell, respectively). About 75% of the seedlings died within 2 years but the surviving plants matured and comprised the generation of broom snakeweed on the sites from late 1981 to 1989 (McDaniel 1989). During the study, 1981 was the only year that a large number of propagules were counted.

Broom snakeweed biomass remained relatively constant on untreated study plots at Vaughn from 1982 to 1986. After this time some natural mortality occurred and production declined slightly from 1987 to 1989 (Fig. 1). At the Roswell site in 1987, broom snakeweed root borers *(Crossidius pulchellus)* eliminated most of the plants. These native beetles mainly attack mature broom snakeweed and can kill plants over broad areas under certain circumstances (Richman and Huddleston 1981). By 1989, broom snakeweed died out completely at the Roswell site.

Overstory-Understory Relationships

The sigmoid (Equation 1) and exponential (Equation 2) equations described the relationship between broom snakeweed and grass biomass equally well (Table 2). Both models produced nearly identical R^2 values for both research sites and when data were combined across sites. Other linear and polynomial model specifications did not fit the data as well (results of the alternative models are not reported).

The exponential and sigmoid models produced similar downward sloping, convex curves, because M+1 was estimated to be near or less than 1 for each sigmoid equation (Table 2). Parameter estimates were slightly different between sites but overstory and understory biomass were found to be inversely related, as expected. When data were combined by year across sites, 61% of the variability in grass biomass (Y, kg/ha) was attributed to variation in broom snakeweed biomass (X, kg/ha) and rainfall conditions.

Growing season (2nd and 3rd quarter) precipitation was significant ($P<0.001$) for all equations. During April, May, or June, 1 cm of precipitation added about 20 kg/ha to grass biomass, as indicated by the combined regression coefficients (Table 2). Precipitation during July, August, or September added slightly less to grass biomass, about 16 kg/ha at the Vaughn site and 11 kg/ha at the Roswell site. Including fall and winter rainfall did not contribute significantly to the amount of grass biomass at either site. This was expected because warm-season grasses dominated the understory layer. Although grasses were not separated by species to allow direct evaluation, blue grama biomass was most important, as this plant comprised more than 75% of the herbaceous component by weight at both sites (McDaniel and Duncan 1987). Pieper (1990) reported blue grama biomass to be highly negatively related to overstory piñon-juniper canopy because the grass appears to be relatively intolerant to shade or other competitive interactions.

Estimated curves exhibit diminishing marginal suppression of grass production as snakeweed biomass increases (Fig. 2). The curves are steepest at zero where a marginal suppression of about 2.6 kg/ha of grass biomass per 1.0 kg/ha increase in snakeweed biomass occurs. At 200 and 400 kg/ha of broom snakeweed, corresponding marginal suppression of grass biomass was about 0.9 and 0.5 kg/ha, respectively. At 600 kg/ha of snakeweed biomass, the curve flattens and only a 0.35 kg/ha suppression of grass biomass per unit change in snakeweed biomass occurs. Grass biomass averaged across years and sites was 667 kg/ha without broom snakeweed, and 212 kg/ha with an average snakeweed biomass of 600 kg/ha.

Response of grass understory at Roswell to increasing snake-

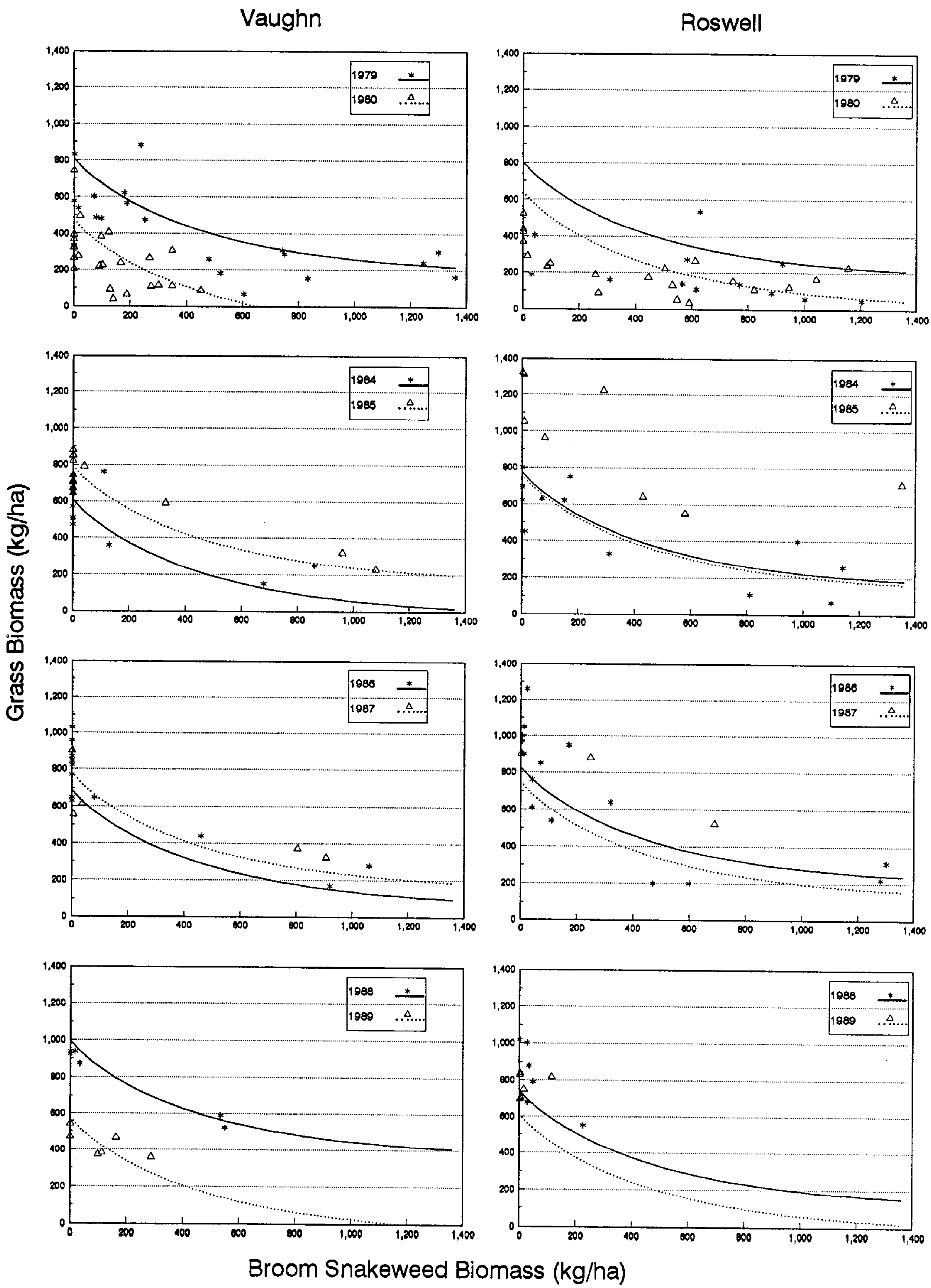

Fig. 2. Observed (*, Δ) broom snakeweed and grass biomass compared with predicted values using the combined data, sigmoid model at the Vaughn and Roswell study sites during selected years.

Table 2. Estimated equations defining overstory-understory relationships for the Vaughn and Roswell study sites.

Equation	n	R^2	RMSE[a]	Estimated Equation
Sigmoid				
Vaughn	104	.68	151.2	$\hat{Y} = 278 - 569\,(1 - e^{-.0015X})^{0.601} + 17.8\,R_2 + 16.0R_3$ (53.2)[b](151.9) (.0016)(.267) (2.86) (2.67)
Roswell	100	.59	231.9	$\hat{Y} = 367 - 698\,(1 - e^{-.0023X})^{1.027} + 22.7\,R_2 + 10.9R_3$ (187.7)(94.2) (.0013)(.566)(6.94) (9.31)
Combined	204	.61	195.0	$\hat{Y} = 258 - 629\,(1 - e^{-.0020X})^{0.881} + 20.5\,R_2 + 16.6R_3$ (59.8)(64.4) (.0008)(.284) (3.01) (3.02)
Exponential				
Vaughn	104	.68	151.3	$\hat{Y} - 242 - 503e^{-.0031X} + 17.9R_2 + 16.2R_3$ (84.8) (59.8) (.0010)(2.87) (2.68)
Roswell	100	.59	230.7	$\hat{Y} - 333 - 701e^{-.0022X} + 22.8R_2 + 11.0R_3$ (185.5) (72.7) (.0006)(6.82) (9.23)
Combined	204	.61	194.5	$\hat{Y} - 363 - 615e^{-.0022X} + 20.6R_2 + 16.6R_3$ (76.5) (47.4) (.0005)(3.00) (3.01)

[a]Root mean square error.
[b]Numbers in brackets are the asymptotic standard error of the estimate.

weed biomass differed slightly from the response at Vaughn. Plots of data (Fig. 2) showed the equations to underestimate grass biomass during some years and overestimate grass biomass during other years, especially at the Roswell site. Predicted changes in grass biomass were adequately explained by rainfall variation, but other unknown factors were also important.

Management Implications

Year-to-year variation in climatic conditions and the amount of broom snakeweed present substantially influences the availability of usable forage for livestock on southwestern rangelands (Pieper and McDaniel 1990). The unfavorable combination of drought and high broom snakeweed biomass can nearly eliminate grazing capacity, as was the case on the Vaughn and Roswell study sites during 1980 and 1989 (Fig. 2). Conversely, when broom snakeweed is eliminated grass biomass can increase dramatically, especially when rainfall conditions are favorable. This wide variability in understory production makes stocking rate decisions difficult. Uncertainty about rainfall, and severity and duration of broom snakeweed occupation creates a tradeoff between the increased returns that could be made by increasing stocking rate when conditions are favorable, versus losses that might occur as conditions change for the worse. Quantifying overstory-understory relationships is thus crucial for improved management decisions.

The overstory-understory relationship for the broom snakeweed and blue grama-dominated grasslands we studied had the same negative curvilinear shape that had been observed for many other woody and herbaceous plants (Ffolliot 1983). As indicated by this downward-sloping convex shape, the first overstory plants to invade an area suppress understory production the most, implying that control strategies resulting in high overstory mortality will be the most economically efficient (Tanaka and Workman 1988). Further, leaving some overstory canopy to meet other resource objectives may be high cost in terms of the additional understory production that could be obtained by completly removing these plants.

Broom snakeweed populations have been described as cyclic over time and rapid changes in plant numbers were noted in New Mexico between 1970 and the present (Pieper and McDaniel 1990). Reductions in herbaceous and broom snakeweed biomass by drought followed by above-average fall-spring precipitation appears to favor broom snakeweed establishment. During this 11-year study, seedlings were only noted once (1981) following drought and suggest elimination of an early-age stand of broom snakeweed should be emphasized in a management program.

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