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LONG-TERM FORAGE PRODUCTION OF NORTH AMERICAN SHORTGRASS STEPPE[1]

W. K. LAUENROTH
Department of Range Science and Natural Resource Ecology Laboratory,
Colorado State University, Fort Collins, Colorado 80523 USA

O. E. SALA
Department of Ecology, Faculty of Agronomy, University of Buenos Aires,
Avenue San Martín 4453, Buenos Aires 1417, Argentina

Abstract. We evaluated the relationship between annual forage production and annual and seasonal precipitation and temperature at a shortgrass steppe site in north-central Colorado using a long-term data set (52 yr). We also constructed a relationship between forage production and aboveground net primary production (ANPP). Precipitation fluctuated randomly, but temperature had clear warming and cooling trends including a 17-yr warming trend from 1974 to 1990.

Forage production was significantly related to both annual and seasonal precipitation but not temperature. Precipitation events between 15 and 30 mm accounted for most of the variability in production because they accounted for most of the variability in precipitation and because they wetted the soil layers that have the largest effect on production. Forage production amplified variability in annual precipitation.

Production showed time lags of several years in responding to increases in precipitation. Change in vegetation structure has a characteristic response time, which contrains production responses in wet years. Constraint caused by vegetation structure is the reason why regional ANPP–precipitation models have a steeper slope than long-term models and point out a weakness of exchanging space for time in predicting production patterns.

Key words: aboveground net primary production; forage production; population-ecosystem interactions; shortgrass steppe; spatial variability; temporal variability; water use efficiency.

INTRODUCTION

The relationship between forage production and precipitation in semiarid regions has been widely used to explain the variability in production at individual sites through time (e.g., Smoliak 1986), and spatially at the regional (e.g., Sala et al. 1988) and the global scales (e.g., Lauenroth 1979). Because of the fundamental nature of the relationship between water availability and plant production (Noy-Meir 1973), rain use efficiency (annual aboveground net primary production [ANPP] divided by annual rainfall) has been proposed as a unifying concept in arid-land ecology (Le Houérou 1984).

The reason precipitation has such large explanatory power for net primary production in arid and semiarid regions is because it is both low and variable (Bailey 1979). For example, in the shortgrass region of the Great Plains of North America there are <60 d each year with detectable precipitation (>2 mm) and <20 d with >6 mm of precipitation (Lauenroth and Milchunas 1991). Thus, the normal condition of the soil in semiarid regions is dry. This dry background condition is interrupted by infrequent wet periods. Sala et al. (1992) analyzed 33 yr of climatic data for the Central Plains Experimental Range (CPER) in north-central Colorado and found that annual precipitation was almost twice as variable (CV = 31%) as potential evapotranspiration (CV = 18%). Under such conditions it is not surprising that statistical relationships between precipitation and ANPP are often reported (Rutherford 1980, Le Houérou 1984).

The objectives of this study were: (1) to evaluate the utility of the relationship between precipitation and net primary production to explain interannual variability in forage production, (2) to assess the major sources of interannual variability in forage production, and (3) to compare our long-term site-specific relationship between precipitation and production with a similar regional relationship. This work focuses on the CPER in the northern portion of the North American shortgrass steppe (Lauenroth and Milchunas 1991). We report on a long-term data set collected from 1939 to 1990.

METHODS

The CPER is located in north-central Colorado, North America, in the precipitation shadow of the Rocky Mountains, ≈40 km south of Cheyenne, Wyoming (40°49′ N, 104°46′ W). Annual precipitation was 321 ± 98 mm (mean ± 1 SD) over the 52 yr from 1939 to 1990 (Table 1). Annual temperature averaged 8.6

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TABLE 1. Annual forage production, aboveground net primary production (ANPP), precipitation, and air temperature data for the Central Plains Experimental Range in north-central Colorado for 1939–1990.

	Production (g/m^2)					Precipitation (mm)					
	Forage air-dry mass			$\mathrm{ANPP}_{\mathrm{FE}}$* (oven-dry mass)	$\mathrm{ANPP}_{\mathrm{OD}}$† (oven-dry mass)	Event size class					
Year	Mean	SD	No. est			<5	5–15	15–30	>30	Total	Temp (°C)
1939	50	12.1	11		84					117	9.30
1940			0			74	76	106	83	339	8.85
1941	74	11.3	10		102	6	0	0	0	325	8.43
1942	123	33.3	7		139	0	0	0	0	371	8.07
1943	123	32.6	13		140	80	159	137	115	490	8.80
1944	75	24.2	7		103	48	64	55	38	205	8.29
1945	66	19.5	7		96	56	133	98	0	288	8.00
1946	67	15.2	9		97	42	148	106	0	296	8.77
1947	96	25.9	9		119	67	117	84	70	338	8.26
1948	50	14.5	10		84	100	93	0	0	193	8.42
1949	82	13.4	8		109	95	169	76	0	341	8.56
1950	54	20.7	18		87	77	163	0	59	299	8.63
1951	70	16.9	13		99	80	126	89	35	330	7.74
1952	95	24.8	5		118	61	130	162	0	353	8.82
1953	73	13.6	8		102	56	88	103	54	301	9.38
1954	22	4.3	6		62	62	45	15	0	122	9.92
1955	32	4.8	4		70	89	74	133	31	328	8.21
1956	50	13.0	4		84	40	117	15	72	244	8.94
1957	64	23.7	19		94	85	182	77	71	415	8.29
1958	77	20.7	19		104	97	155	79	0	331	8.71
1959	83	13.5	10		109	68	146	56	37	307	8.40
1960	57	8.1	14		89	66	109	0	0	175	8.44
1961	76	16.5	10		104	81	152	136	36	404	8.20
1962	81	16.3	10		107	59	134	165	41	399	8.20
1963	80	12.3	6		107	59	86	155	38	338	8.50
1964	25	4.4	6		65	43	65	0	0	107	7.64
1965	48	12.2	6		82	51	193	83	44	371	7.63
1966	49	11.9	6		83	52	120	36	85	292	7.77
1967	90	12.4	3		115	70	174	177	167	588	7.62
1968	77	26.0	6		105	61	161	76	36	333	7.69
1969	86	25.1	5		112	5	167	139	35	417	7.89
1970	72	18.7	6	115	101	70	101	71	0	242	8.02
1971	73	8.4	6	74	102	56	92	114	0	262	8.16
1972	24	4.4	7	85	64	72	181	55	67	374	8.32
1973	68	14.8	16	64	98	68	120	53	34	275	8.36
1974	22	5.7	13	55	63	43	91	64	70	268	9.30
1975	63	20.7	31	55	94	75	73	142	34	324	8.88
1976	44	12.0	28		80	83	135	42	0	261	9.42
1977	27	9.1	35		67	57	108	83	0	248	9.92
1978	37	16.2	30		74	78	46	126	42	292	9.08
1979	88	28.6	22		113	90	184	184	36	494	8.94
1980			0			62	138	116	45	360	9.60
1981	128	50.4	16		143	77	122	162	36	397	10.09
1982	117	17.7	12		135	74	106	139	155	475	9.17
1983	91	29.5	16	164	115	61	127	167	73	428	9.02
1984	103	37.4	8	108	124	85	152	100	70	407	9.81
1985	84	10.7	8	128	110	119	128	74	0	321	9.07
1986	55	5.1	3	119	88	108	157	0	0	265	10.92
1987	63	4.8	8	62	94	107	167	57	0	332	10.52
1988	57	6.8	8	90	90	76	80	92	86	335	10.23
1989	55	5.7	6	82	87	72	109	75	44	300	9.93
1990	58	4.7	6	110	90	96	158	104	0	357	10.21
Mean	66		11	94	97	54	119	99	44	321	8.6
SE	29		8	32	21	19	43	58	39	98	0.6
CV (%)	44			34	22	29	36	59	88	31	7

* Field estimates of ANPP from the Central Plains Experimental Range.

† Eq. 1 [$\mathrm{ANPP}_{\mathrm{OD}} = 46 + 0.76(\text{Forage Production})$] converts from air-dry forage production to oven-dry ANPP.

± 0.6°C over the same time period (Table 1) (Kittel 1990). The climate of the CPER is typical of midcontinental semiarid sites in the temperate zone except for the large influence of the Rocky Mountains 60 km to the west. Maxima in precipitation and temperature occur in June, July, and August, and minima occur in December, January, and February.

The vegetation is representative of the northern portion of the shortgrass steppe (Lauenroth and Milchunas 1991). Most locations at the CPER, regardless of past grazing history, are dominated by the perennial bunchgrass *Bouteloua gracilis* H.B.K. Lag ex Griffiths, which accounts for ≈90% of both basal cover and forage production (Milchunas et al. 1989). Associated species include *Buchloë dactyloides* (Nutt.) Engelm, *Opuntia polyacantha* Haw, *Sphaeralcea coccinea* (Pursh) Rydb, and *Carex eleocharis* Bailey. Nomenclature follows the Great Plains Flora Association (1986).

Forage production was estimated annually from 1939 to 1990 (except 1940 and 1980), although the same pastures were not sampled every year (Table 1). Because of the importance of *B. gracilis* at the CPER, most locations are similar in species composition. The standard deviations of forage production (Table 1) provide an indication of the variability among locations sampled. Samples were collected by harvesting live and attached-dead biomass of grasses, sedges, and forbs from 0.19-m^2 (2 ft^2) quadrats at the end of the growing season. *O. polyacantha* was not harvested. This method has been shown to provide good estimates of aboveground net primary production (ANPP) for ecosystems such as the shortgrass steppe in which the species that account for the majority of production have similar phenologies (Lauenroth et al. 1986). An exception to this procedure occurred in the data for the years 1969–1972, in which masses were visually estimated but not harvested. The average number of locations sampled was 11 with a range of 3 in 1967 to 35 in 1977; no sampling was done in 1940 or 1980 (Table 1). The data presented here represent an average over the locations sampled each year. All masses are expressed on an airdry basis.

While the lack of identical sampling locations and number of locations from year to year limits the utility of the data set for some purposes, it nevertheless is valuable for an analysis of the relationship between precipitation and forage production. The reason for this is that such relationships have been shown to be sufficiently robust to be detectable even in variable data sets (Lauenroth 1979, Le Houérou 1984, Le Houérou et al. 1988). Furthermore, these data are important because very few similar data sets exist for temperate grasslands. The most important assumption for this analysis is that the estimates of forage production (airdry basis) for each year are proportional to ANPP (ovendry basis). We tested this assumption by evaluating the relationship between estimates of average forage production and estimates of ANPP.

Forage production was significantly ($F = 4.66$; df = 1,12; $P = .05$; $r^2 = 0.28$) and positively related to ANPP by the equation:

$$\text{ANPP} = 46 + 0.76(\text{Forage Production}). \quad (1)$$

This relationship was established using 14 yr in which estimates of both ANPP and forage production were available (Table 1). Results for both forage production and ANPP are presented (Table 1).

RESULTS

The climate at the CPER is representative of sites in semiarid regions with relatively high variability in precipitation from year to year (CV = 31%) and relatively low variability in temperature (CV = 7%) (Table 1; Fig. 1A, B). Twenty-three of the 52 observations of annual precipitation were below the mean with no more than three of the low values occurring in consecutive years (Fig. 1B). By contrast, every year from 1959 to 1973 had an annual temperature below the mean (Fig. 1A). Annual temperature has been increasing since 1967, and each of the years from 1974 to 1990 had temperatures above the mean. Results from a runs test indicated that the temperature deviations were not random but that the precipitation deviations were random (Draper and Smith 1966). Maximum temperature deviations were ≤2.5°C and positive; maximum precipitation deviations were >200 mm and were both positive and negative.

Forage production was even more variable than precipitation (Table 1, Fig. 1C). Average forage production was 66 g/m^2 (ANPP = 97 g/m^2) with a CV of 44%. Twenty-four of the observations were below the mean and 27 were at or above the mean. The data clearly indicated that the interannual variability in forage production was as much a result of departures above the long-term average as below. The longest runs in deviations were positive and occurred between 1967–1971 and 1981–1985.

Forage production following years with very low precipitation showed a clear lag in recovery (Fig. 1). For example, precipitation in 1954 was 200 mm below the long-term mean, and forage production was 40 g/m^2 below the mean (Fig. 1, Table 1). While precipitation was above or near the mean in two of the following three years, forage production did not recover to average or above until 1958. A similar sequence was observed following the very dry year of 1964.

Long-term forage production at the CPER was significantly ($P \leq .05$) related to annual precipitation, growing season precipitation, a linear combination of annual precipitation and annual temperature, and the ratio of annual precipitation to annual potential evapotranspiration (data not shown). Forage production was significantly ($F = 30.83$; df = 1,48; $P < .001$; $r^2 = 0.39$) related to annual precipitation by the equation:

$$\text{Forage Production} = 13 + 0.172(\text{Annual Precipitation}). \quad (2)$$

The intercept was not significantly different from zero. The corresponding model using growing season precipitation where the growing season is defined from April through September was:

$$\text{Forage Production} = 17 + 0.210(\text{Growing Season Precipitation}). \quad (3)$$

This model was also significant ($F = 29.52$; df = 1,39;

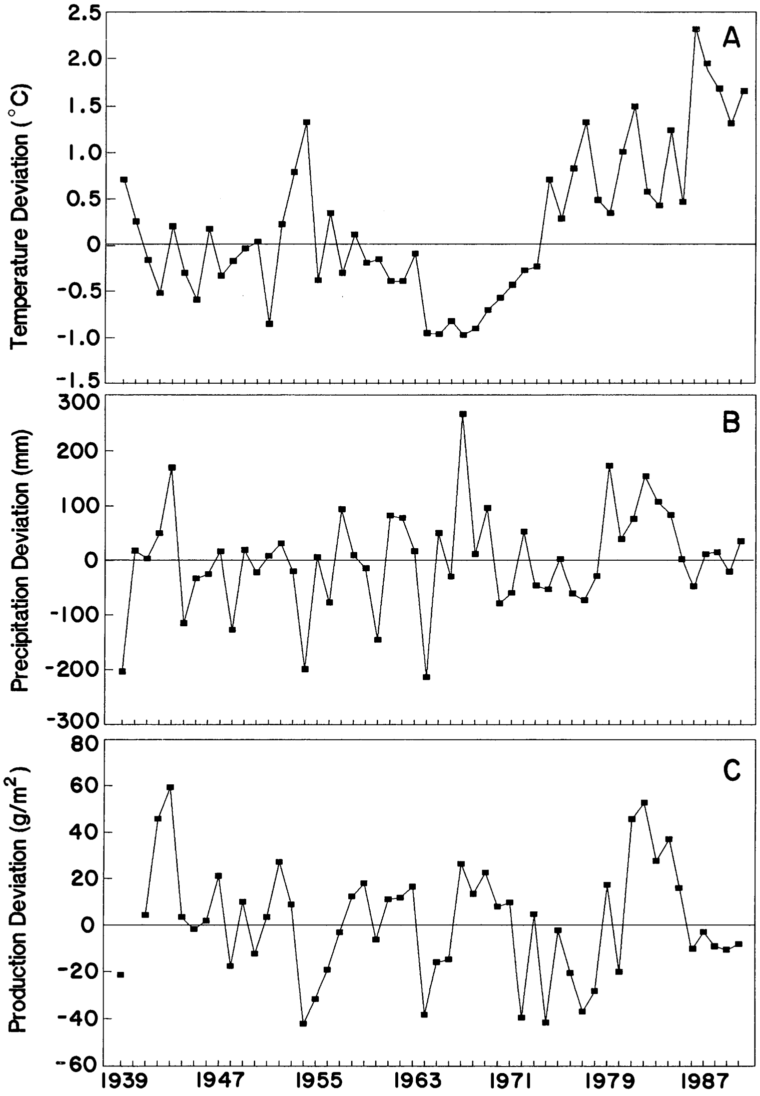

FIG. 1. Deviations of annual values from the long-term average for the period 1939–1990 for temperature (A), precipitation (B), and forage production, measured as live and attached-dead air-dry biomass at the end of the growing season for grasses, sedges, and forbs (C) for the Central Plains Experimental Range in north-central Colorado.

$P < .001$; $r^2 = 0.43$). The intercept again was not significantly different from zero.

Precipitation events are very likely not equivalent in their effects on ecosystem processes such as ANPP (Sala and Lauenroth 1982). Most past analyses have focused on the timing of precipitation using seasonal, water year, or monthly precipitation as independent variables (e.g., Smoliak 1986). We tested the idea that dividing growing season precipitation into events of different sizes would provide a more powerful explanation of the variability in production than could be obtained with all events lumped. The resulting model was:

$$\begin{aligned}\text{Forage Production}\\ &= 13.4 + 0.26(\mathrm{PPT}_{30}) + 0.13(\mathrm{PPT}_{15})\\ &\quad + 0.19(\mathrm{PPT}_5) + 0.05(\mathrm{PPT}_{>30}), \qquad (4)\end{aligned}$$

in which PPT_{30} was the amount of growing season precipitation that was received in events between 15 and 30 mm, PPT_{15} events between 5 and 15 mm, PPT_5 events <5 mm, and $\mathrm{PPT}_{>30}$ all events >30 mm (Table 1). This model was significant ($F = 7.72$; df = 4,37; $P < .001$; $r^2 = 0.45$), even though PPT_{30} was overwhelmingly the most important explanatory variable. A model with just PPT_{30} had an r^2 of 0.33 compared to the value of the full model of 0.45.

DISCUSSION

The relationship between precipitation and forage production explained between 39 and 45% of the variability in production over the 52 yr of observation. In many cases the deviations from the relationships were as interesting as the instances of good fit. For example, the dry years of 1954 and 1964 were followed by years of low forage production despite the fact that in both cases precipitation following the dry year was normal or above (Table 1). Such a lag in the recovery of forage production following a drought is likely the result of an interaction among population, community, and ecosystem processes (Webb et al. 1978). The structure of the vegetation, as reflected in abundance of life-forms and species and in the density of seeds and tillers, provides a constraint within which normal fluctuations in precipitation cause bounded fluctuations in production. Drought conditions can result in plant or tiller mortality thus decreasing the capability of the current vegetation to respond to high resource availability. The data for 1954 and 1964 suggest a several-year lag in recovery. An extreme example of this phenomenon was documented for the major drought that occurred in the 1930s (Weaver and Albertson 1944).

Semiarid regions are widely thought of as especially variable in environmental conditions and biological responses (Noy-Meir 1973, Bailey 1979), and the shortgrass steppe is no exception (Coupland 1958, Wiens 1974). Fluctuation in precipitation is the principal cause of variability in grassland environments (Coupland 1958, Wiens 1974). Over the 52 yr of observation at the CPER, precipitation ranged from nearly 70% below the long-term mean to 80% above it (Fig. 1). Observations included 3 yr of severe drought ($<50\%$ of the mean) and three very wet years ($>150\%$ of the mean). To a large extent the very wet and dry years occurred as isolated instances. As an example of the extremes in this semiarid environment, the driest year in the record (1964; 104 mm) was followed 3 yr later by the wettest year in the record (1967; 588 mm).

The ideas of vegetation structure constraint on ANPP and time lags to recovery suggest that ANPP should be less variable than annual precipitation. However, forage production not only reflected but amplified the variability in precipitation (Table 1). Le Houérou et al. (1988) evaluated 77 data sets with 895 pairs of production and rainfall and reported a mean difference in variability of production over precipitation of 44%. The reason for the greater variability of annual forage production than annual precipitation is likely related to the intraseasonal variability in water availability that occurs for a particular amount of annual precipitation. Wet years within which the increased precipitation is synchronous with the long-term pattern of precipitation are likely to be more productive than years that are wet because of very early and very late precipitation. Sala and Lauenroth (1982) speculated that small precipitation events should have a larger per unit effect on ecosystem dynamics than large events because of their potential to activate processes related to mineral nutrient supply. The most productive years should be those in which small precipitation events that stimulate mineral nutrient availability are followed by large events that stimulate plant production processes.

Arid and semiarid regions receive precipitation only 10–50 d/yr and only 5–6 of these events are sufficiently large to affect biotic processes (Noy-Meir 1973). The CPER receives an average of 32 precipitation events during the May through August growing season, most of which are small (Sala and Lauenroth 1982). Over the 52 yr of data collection, 17% of growing season precipitation was received in events <5 mm, 36% in events between 5 and 15 mm, 30% between 15 and 30 mm, and 17% in events >30 mm. According to our analysis, events in the range of 15–30 mm accounted for a larger fraction of the variability in primary production than other sizes (Eq. 4). We suggest that this is the combined effect of accounting for a large portion of the variability in precipitation as well as wetting the soil layers that are most effective in promoting production. Water from events in the 15–30 mm and larger size classes penetrate deeper into the soil than the more frequent events of <15 mm. Water from lower layers is lost only via transpiration since there is no deep percolation in this site, and evaporation only affects upper soil layers (Sala et al. 1992).

The concepts of a constraint on primary production by vegetation structure and time lags in responding to favorable conditions suggest an explanation for the difference in slope between the long-term model developed here and a regional model developed by Sala et al. (1988). Their analysis of the relationship between ANPP and annual precipitation for the Central Grasslands of the U.S. has a much steeper slope than the long-term relationship developed for the CPER (Fig. 2). At the maximum value of precipitation observed for the CPER, the prediction of the regional model was was significantly ($P < .05$) higher than the estimate of the long-term model (300 vs. 130 g/m^2). The magnitude if this difference decreased as annual precipitation approached the mean (Fig. 2). The Sala et al. (1988) regional model utilizes the ANPP of an ecosystem with a different vegetation structure at each value of precipitation. By contrast, the long-term model relates annual precipitation and ANPP for the same vegetation structure through time. If we assume the vegetation at a site is adapted to conditions in the neighborhood of modal water availability, we should expect that life-form and species composition constraints will limit responses to both very wet and dry conditions. Further, changes in vegetation structure can be slow and are mediated by changes in processes that range from expansion of the biomass or numbers of individuals of extant species to migration of new species (Tilman 1988, Coffin and Lauenroth 1990). These vegetation structure constraints on ANPP explain why, under dry conditions, the regional model underestimates ANPP and under wet conditions, overestimates ANPP.

The differences between regional and temporal models point out a weakness of exchanging space for time. Regional models predict the response of a set of dif-

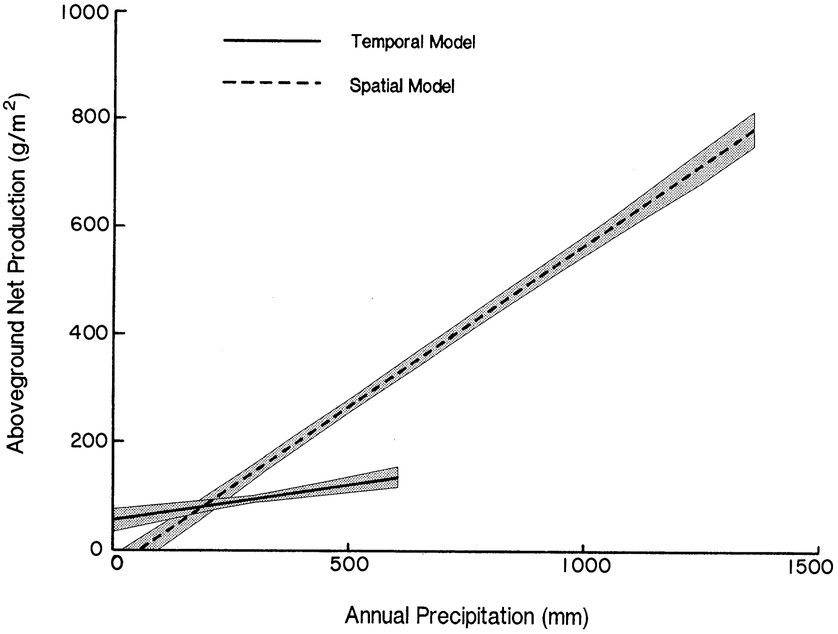

FIG. 2. Relationships between aboveground net primary production (g/m^2) and annual precipitation (mm) for a regional model (Sala et al. 1988) for the Central Grassland Region of the U.S. and for the long-term model from this work for the Central Plains Experimental Range. Shaded areas represent 95% confidence intervals. Regional model ANPP = −34 + 0.60(Ann. Precipitation). Long-term model ANPP = 56 + 0.13(Ann. Precipitation).

ferent ecosystems to spatial patterns in annual precipitation while temporal models predict responses of a single ecosystem to a time series of precipitation. Predictions of the effects of climate change on ANPP, based upon regional models, may contain important sources of previously unrecognized error. A better understanding of the characteristic response times of different ecosystems to changes in climate will be required if we are to make such predictions.

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