Climate Change and Grasslands: Unexpected Consequences of Extreme Rainfall Patterns

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Abstract

Climatic variability is an inherent feature of grasslands, with large fluctuations in temperatures combined with precipitation regimes characterized by floods and severe drought occurring within and between years. Global climate models and emerging data indicate that extremes in precipitation regimes are increasing worldwide. Thus, variability in temporal patterns of water availability in grasslands, as directly influenced by altered precipitation patterns and indirectly by forecast increases in temperature, will likely increase in the future. Analyses of long-term relationships between grassland productivity and rainfall patterns coupled with experimental manipulations of precipitation inputs have yielded a number of surprising insights regarding how these grasslands will respond to future more extreme climates. Long-term data and experiments have shown that even in relatively mesic grasslands, water availability limits aboveground productivity in most years. Thus, most grasslands will be sensitive to climate change. Sensitivity can be influenced by dormant season soil moisture conditions as well as by within-season precipitation patterns. Surprisingly, increases in precipitation extremes (larger rainfall events with longer intervening dry periods) during the growing season reduced productivity in mesic grasslands but increased production in semi-arid grasslands. Understanding interactions between rainfall amount and its distribution in grasslands is key to forecasting responses to climate change.

Key words: Aboveground net primary production, forage production, grasslands, extreme rainfall regimes, precipitation variability

1. Introduction

Grasslands provide a wide variety of ecosystem services globally, with forage production for livestock of primary economic importance, and high biodiversity and C sequestration of key ecological value (Daily 1997). Climatic means, and variation around those means, are major factors controlling the structural and functional dynamics of the major grasslands worldwide. Formed by climate changes originating during the Miocene-Pliocene transition (Axelrod 1985), the present day distribution and ecological attributes of grasslands are determined primarily by regional temperature and precipitation gradients (Sala *et al.* 1988), and interactions with fire and grazing (Knapp *et al.* 1998). Both the mean and extremes of precipitation (e.g., floods and droughts) can strongly affect ecosystem processes in grasslands and on a continental scale, interannual variability in precipitation may affect productivity more in grasslands than in most other biomes in North America (Axelrod 1985, Knapp & Smith 2001). Consequently, changes in rainfall and temperature, predicted as a result of global climate change, are expected to directly and rapidly impact grasslands by affecting individual organisms, community composition and ecosystem processes (Weltzin *et al.* 2003).

Altered rainfall patterns and increased temperatures are components of most global climate change predictions. The Inter-governmental Panel on Climate Change has long suggested that potential increases in temporal variability in rainfall will impact biotic responses and processes in grasslands as well as most other ecosystems more than changes in annual precipitation quantity alone (Houghton *et al.* 1996, IPCC 2007). In particular, forecast more variable or extreme rainfall regimes are expected to be characterized by larger individual storms from high energy convective weather systems (increased heavy rainfall days) combined with longer intervening dry periods (Easterling 2000, Groisman *et al.* 1999, IPCC 2007). Recent trends in precipitation worldwide confirm that these rainfall patterns are becoming widespread (Dore 2005, Huntington 2006).

The sensitivity of grassland ecosystems to the changes in temperature and rainfall variability predicted by global climate models (GCMs) poses important questions for the future productivity and sustainability of these ecologically and agriculturally important ecosystems. For example, how will changes in precipitation variability (i.e., the timing of rainfall events) affect aboveground plant productivity (the primary determinant of economic value for these ecosystems)? Because grasslands occur on every continent but Antarctica, and by some estimates former or current grass dominated ecosystems cover up to 40% of the terrestrial land surface and are responsible for 30-35% of global terrestrial net primary production (Field *et al.* 1998), a second important issue to address is whether or not grasslands will respond similarly to this global-scale change in climate and if not, what are the key factors determining differential sensitivity of grassland type to more extreme rainfall regimes.

Grasslands are excellent model ecosystems for conducting manipulative experiments because they are tractable and respond relatively rapidly. Grasslands are also well represented in the US Long-term Ecological Research network and have been the focus on several long-term experiments worldwide. As a result, these systems have been well-studied and abundant long-term data are available. The objectives of this paper are to synthesize data and results from three related studies, one retrospective and two experimental, to explore the consequences of increasingly extreme rainfall regimes in grasslands and to better understand the mechanisms behind these responses. Although a wide array of data are available from these studies, our focus will be in responses in aboveground net primary production since this represents forage production for livestock and food production.

2. Methods

Retrospective analyses - We used two long-term data sets that included daily rainfall and aboveground net primary production (ANPP) data from grasslands in North America and South Africa to assess the generality of precipitation – ANPP relationships (Knapp *et al.* 2006). Specifically, the sites were the Konza Prairie Biological Station (KPBS) in northeastern Kansas, USA (39° 05'N, 96° 35'W), and the Ukulinga Research Farm (URF) near Pietermaritzburg, South Africa (29° 24'E, 30° 24' S).

The KPBS is a 3,487 ha grassland ecosystem where native perennial C_4 grasses (*Andropogon gerardii* and *Sorghastrum nutans*) account for the majority of herbaceous primary productivity (Briggs and Knapp 1995). The climate is continental with cold winters, and a maximum mean monthly air temperature in July of 27°C. Annual precipitation averages 857 mm/year, with most falling from convective storms during the April-September growing season. Soils across KPBS are fine textured, silty clay loams.

Although KPBS includes watersheds that are exposed to a variety of fire frequencies and grazing treatments, for this analysis we focused on a 15-yr data set from an ungrazed watershed that was burned annually in the spring each year. ANPP was estimated in this watershed at 2-week intervals throughout the growing season by harvesting all aboveground biomass at ground level from 20 0.1 m^2 quadrats.

The URF experimental site is also a C_4 grassland (dominated by *Themeda triandra* and *Heteropogon contortus* in frequently burned sites) with scattered C_3 trees in areas protected from fire. Long-term mean annual precipitation is 838 mm, mostly falling during the summer (mid-September – March). Summers are warm with a mean monthly maximum of 26.4 °C in February, and winters are mild with occasional frost. Soils are derived from shales and are fine textured. There has been no large ungulate grazing at this site for > 50 yrs (Knapp *et al.* 2006).

Several treatments are included in the long-term experimental plots at URF, but for this study we focused on the annual early spring fire treatment, which is mowed at the end of the growing season (typically in March). To estimate total ANPP, whole-plot samples or subsamples of biomass harvested with mowing were collected, dried and weighed.

For this comparative analysis, 15 continuous years of ANPP were available for KPBS, but ANPP data were not collected in all years of the study at URF. However, 24 years of data were available and corresponding climatic data are from on-site weather stations were available at both sites. This permitted us to assess relationships between interannual variability in precipitation regimes and ANPP in grasslands with similar fire and grazing histories on two continents.

Experimental rainfall manipulations – We have manipulated growing season rainfall regimes under field condition in native grasslands with two related experiments. The Rainfall Manipulation Plots (RaMPs) experiment is a long-term study at the KPBS in Kansas (USA). This study has been complemented by a short-term Great Plains Grasslands experiment that encompasses a broad gradient in mean annual precipitation across the grasslands of the Great Plains of the US.

The RaMPs experiment addresses two elements of climate change scenarios that have not been assessed simultaneously in other experimental studies; – (1) increased variability in growing season rainfall patterns, including more severe seasonal droughts and larger individual storm events, and (2) interactions between two abiotic factors (temperature and precipitation) that are strongly coupled to one another at all hierarchical levels – via the energy budgets of organisms and ecosystems.

The RaMPs facility was designed for replicated, experimental alteration of the timing and quantity of precipitation inputs into undisturbed grassland, using natural rainfall collected at the site (Fay *et al.* 2000). Subplots nested within the larger rainfall manipulation plots are exposed to elevated temperatures maintained by IR lamps. The four treatments imposed are (1) ambient rainfall patterns and temperatures, (2) rainfall patterns altered such that dry intervals between naturally occurring rain events are increased by 50% with concurrent increases in the quantity of rain per event (but with no change in total growing season precipitation), (3) canopy and soil temperatures elevated with overhead infrared lamps by ca. 2.0, and (4) both warming and rainfall treatments combined. Total annual rainfall quantity is allowed to vary naturally among years in this study. We will focus only on the rainfall manipulation treatments for this paper.

In the Great Plains Grasslands (GPG) experiment, we investigated the impacts of a shift to more extreme rainfall patterns on three distinct C_4-dominated grassland ecosystems that span a broad precipitation gradient in the US. Consistent with the RaMPs experiment, we defined extreme precipitation regimes (from an intra-annual perspective) as a shift from extant rainfall patterns to regimes characterized by fewer, but larger events with extended intervening dry periods between events. The Great Plains is an ideal location to test the generality of ecosystem responses to this predicted shift in extreme rainfall patterns because it is characterized by a strong west-east precipitation gradient (320 to 830 mm) that results in three moisture-driven ecosystem types – the semi-arid steppe, the mixed grass prairie, and the mesic tallgrass prairie. We manipulated the distribution of rainfall during the growing season in NE Colorado, Central Kansas), and Eastern KS via rainout shelters The 30 yr mean quantity of growing season rainfall was added to plots at each site distributed as 12-, 6-, or 4- events. Duration of the dry interval between events was 10-, 20-, or 30-days, respectively. The locations for this experiment were the KPBS (tallgrass prairie; Manhattan, KS, USA) at the mesic end of the gradient and the Shortgrass Steppe Long-Term Ecological Research Site (semi-arid steppe; Nunn, CO) at the xeric end.

In both of the RaMPs and GPG experimental studies, ANPP was measured at the end of the growing season by harvesting biomass from 0.1 m^2 quadrats. Biomass was sorted by growth form and dead biomass from previous years was also separated to allow for an estimate of current year aboveground biomass production.

3. Results

Retrospective analyses – The focus on our analysis of the two long-term ANPP – precipitation data sets was on growing season rainfall, the distribution of that rainfall (early vs. late in the season), and its impact on interannual variability in ANPP. Overall, total growing season precipitation was a strong driver of ANPP at both sites over the 15 and 24-yr records. Moreover, the slopes of the relationship between growing season precipitation and ANPP did not differ between the South African and North American sites (Knapp *et al.* 2006). In contrast, the two sites differed markedly in the effect of early vs. late growing season precipitation on ANPP (Fig. 1). Precipitation that fell during the first half of the growing season was a strong predictor of annual ANPP in South Africa, whereas this relationship was not significant at the North American site. In contrast, rainfall that fell late in the season had a similar impact on annual ANPP at both sites (Fig. 1). Thus, the South African site was much more responsive to rainfall in the first half of the growing season than the North American site.

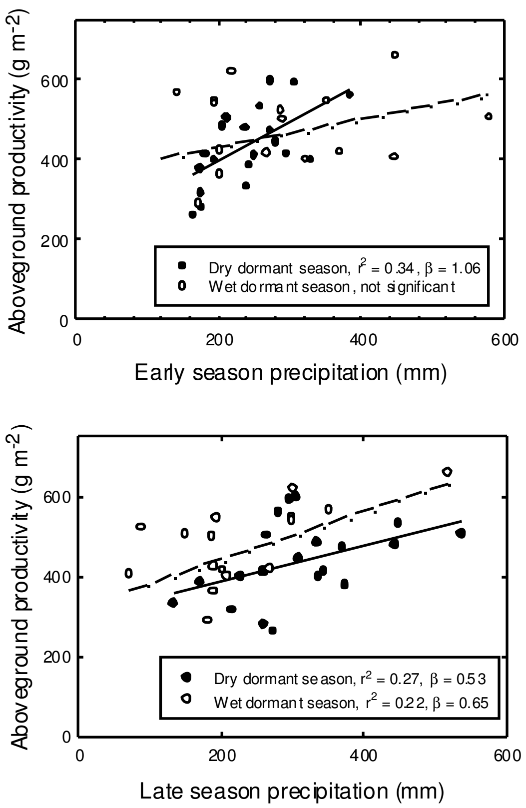

Figure 1. *Top: Relationship between interannual variability in annual aboveground net primary production and precipitation falling during the first half of the growing season for grassland sites burned annually in the spring at the Ukulinga Research Farm in South Africa (solid line, filled symbols) and the Konza Prairie Biological Station in Kansas, USA (open symbols). Only the relationship at URF was significant (URF:* $r^2 = 0.34$*,* $\beta = 1.06$*,* $P \leq 0.001$*; KPBS:* $P = 0.098$*). Bottom: Relationship between annual aboveground net primary production and precipitation falling during the latter half of the growing season. The relationship was significant for URF (*$r^2 = 0.27$*,* $\beta = 0.53$*,* $P = 0.002$*), and marginally significant for KPBS (*$r^2 = 0.22$*,* $\beta = 0.65$*,* $P = 0.056$*). Figures modified from Knapp et al. (2006).*

Experimental rainfall manipulations – By altering the number of growing season rainfall events, their size and the interval between them, without altering total growing season rainfall amounts, we simulated a predicted climate change scenario of more extreme rainfall patterns in native grassland ecosystems. These alterations in rainfall patterns directly affected soil moisture dynamics that, in turn, influenced plant, community and ecosystem structure and function. In both experimental studies, soil moisture dynamics played a key role in determining responses in short- and long-term ecosystem function (ANPP). Data from the long-term RaMPs experiment at the KPBS indicated that the altered precipitation regime results in patterns of soil water availability markedly more variable than the typical present-day regime, with the soil surface layers remaining dry for longer periods and deeper soil layers being recharged more often (Knapp *et al.* 2002). Results from the RaMPs also showed that both mean soil moisture and measures of its temporal variability (i.e., the temporal coefficient of variation in soil moisture) were strongpredictors of ANPP. As expected, over the several year of the experiment, increased mean soil moisture was related to increased ANPP, but increased variability in soil moisture led to decreased ANPP.

Of particular importance for this assessment of sensitivity are analyses conducted separately for the ambient and altered treatments within the RaMPs experiment. The strong relationship between soil water content and ANPP for all data combined was driven primarily by the altered treatment (Fig. 2). However, across the 7 years of the study, there was no statistically significant relationship between soil water content and ANPP for plots exposed to the ambient rainfall regime, but there was a strong relationship between soil moisture and ANPP for the altered treatment plots. This may, in part, be due to the wider range of data for soil water content and ANPP in the altered (more extreme rainfall patterns) than the ambient treatments (Fig. 2).

For the GPG experiment, a shift to fewer but larger events significantly increased ANPP by 30% in the most arid end of the gradient whereas a redistribution of rainfall from 12- to 4- events caused an 18% reduction in ANPP in the most mesic grassland. Although the GPG study was conducted over only 1-yr, ANPP responses in the mesic grassland were consistent with past results from the RaMPs experiment (Knapp *et al.* 2002). This was also true for the semi-arid grassland, where a previous study in another year at the same site yielded a similar response (White *et al.* 2008). Similar to the RaMPs results, soil water content was strongly influenced by the experimental alteration in rainfall patterns in this experiment and these alterations were consistent with ANPP responses. Mean soil water content in the top 20 cm of the soil profile was increased by 19% in the arid grassland as the number of events was decreased from 12 events, whereas mean soil water content was reduced by 20% with a shift to fewer but larger rainfall events (more extreme regime) in the mesic grassland.

4. Discussion

Comparative retrospective analyses of long-term ANPP-precipitation data in the two grasslands in North America and South Africa yielded two important results. First, relationships between ANPP and total growing season precipitation were quite similar overall (Knapp *et al.* 2006). Second, the effect of the timing of growing season rainfall (sub-divided as rainfall occurring in the first half *vs.* the second half of the growing season) differed strongly between these two grasslands (Fig. 1), with the South African grassland more sensitive to both early and late season rainfall inputs, whereas the North American grassland was sensitive only to late season rainfall. This differential sensitivity is likely due to the characteristics of the dormant season in these grasslands.

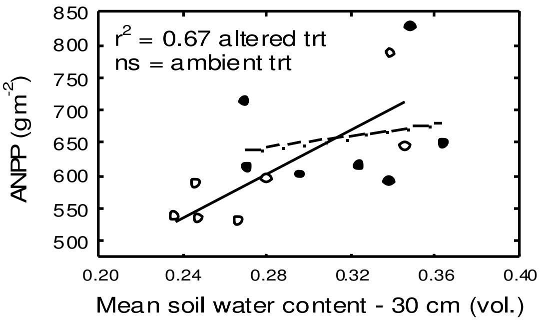

Figure 2. *Relationship between aboveground net primary production (ANPP) and mean soil water content during the growing season over 7 years in the RaMPs experiment in a mesic grassland in Kansas USA (Fay et al. 2000). The ambient treatment represents natural rainfall patterns and the altered treatment is for plots in which the intervals (number of days) between rain events was lengthened by 50% and individual storms were combined so that fewer rain events occurred but they were larger in size. For both treatments, the total quantity of rain input to the plots was identical, just the pattern differed.*

Although dormant season precipitation is similar in both regions (ca. 25% of annual), dormant season temperatures in sub-tropical South Africa are much higher than in temperate North America. Warm temperatures and low precipitation in South Africa result in a large deficit in the overall ecosystem water balance during the dormant season and thus very low levels of soil moisture. Indeed, soil moisture limitation, not temperature, defines the growing season for most warm, lowland South African savannas and grasslands. Because soil moisture is low early in the growing season, these grasslands are very sensitive in interannual variability in inputs at this time of year. In contrast, in the North American grassland studied (KPBS), evaporative demand is lower than precipitation inputs during the winter and soil water content may increase during the late winter and early spring prior to green-up with warm temperatures (Knapp *et al.* 1998). Thus, the growing season in this temperate grassland is defined primarily by temperature with high springtime levels of soil water leading to reduced sensitivity to rainfall inputs at this time. These differences in dormant season soil water are fundamentally important for explaining the differential sensitivity of these two grasslands to the timing of rainfall during the growing season. Differential sensitivity to early vs. later season precipitation amounts suggests that although shifts in overall precipitation quantity may affect ANPP equivalently in both ecosystems, alterations in seasonal precipitation patterns may have different effects on ANPP. In particular, future alterations in early season rainfall regimes will affect South African grasslands more so than North American systems.

Results from the RaMPs experiment indicate that increased sensitivity of ANPP to interannual variability in precipitation quantity can also be increased by more extreme rainfall patterns within the growing season (Fig. 2). This link between intra- and interannual variability is driven by years in which more extreme rainfall treatments lead to large reduction in mean soil water content and consequent reductions in ANPP. Thus, from an economic and food production perspective, more extreme rainfall regimes with the growing season, even with no change in annual quantity or interannual variability, will lead to an increased frequency of years with low forage production, at least in relatively mesic grasslands.

Results from the GPG experiment along a 600 km precipitation-productivity gradient demonstrate that sensitivity of grassland ecosystems to more extreme within growing season rainfall regimes is widespread. However, responses of ANPP to these forecast more extreme rainfall regimes appear to be contingent on grassland type. At the mesic end of the gradient, longer dry intervals between events led to extended periods of below-average soil water content that reduced ANPP by 18%. The opposite response was observed at the dry end (semi-arid steppe), where a shift to fewer, but larger, events led to extended periods of above-average soil water content and resulted in a 30% increase in ANPP.

The inverse responses of these grasslands are likely due to differences in average soil water conditions in semi-arid vs. mesic grasslands. At the low end of the precipitation gradient, semi-arid shortgrass steppe is characterized by chronically low levels of soil water availability and extended periods of intense water stress. While small rain events intermittently alleviate these conditions and improve plant water relations (Sala and Lauenroth 1982), high evaporative demand rapidly returns water from the soil to the atmosphere. This pattern of precipitation input and soil water availability changes with a shift to larger, less frequent events (extreme rainfall patterns). Here, large quantities of water are input into the ecosystem in relatively short periods of time, increasing the amount and duration of water available in the soil for plant uptake. In mesic grasslands, where relatively abundant soil water availability usually occurs and soil and plant water stress is minimal for substantial portions of the growing season, relatively frequent rainfall events consistently maintain most ecosystem processes in a relatively unstressed state by maintaining high soil water levels. A shift to more extreme events creates long periods of evapotranspiration in the absence of rainfall and these are conditions that deplete soil water to stress levels greater than what is typically experienced today.

These results highlight the difficulties in extending inferences from single site experiments to whole ecosystems or biomes as well as demonstrating the complexity inherent in predicting how terrestrial ecosystems worldwide will respond to more extreme climate conditions. As this experiment shows, even within a relatively uniform biome type, ANPP responses differed in both magnitude and direction in response to increased rainfall extremes, but no change in annual amount.

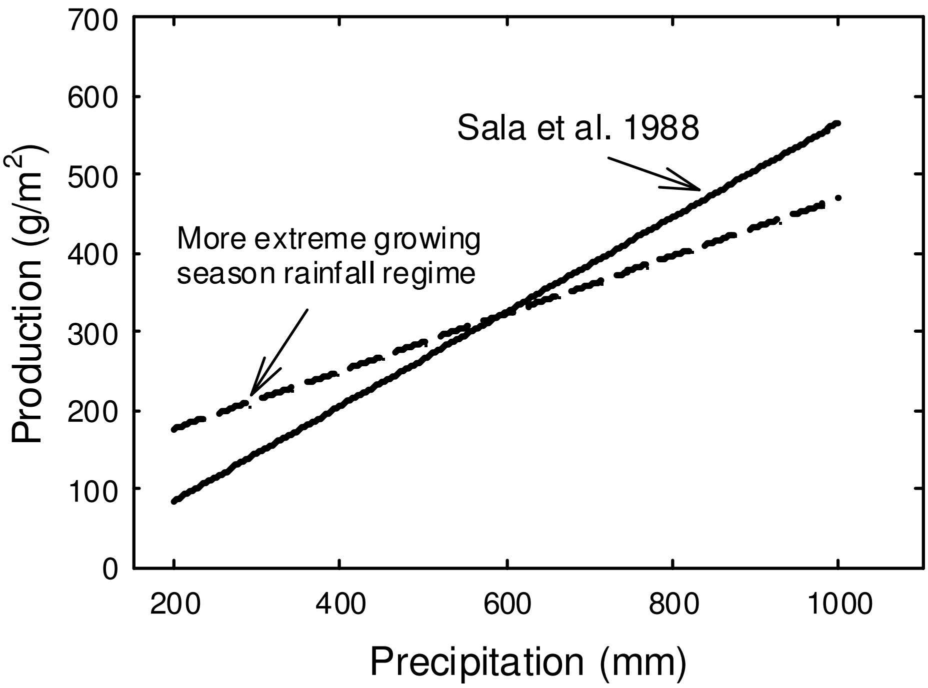

Figure 3. *Projected change in the regional relationship between annual precipitation and aboveground production for grasslands that span the Great Plains of the US. The solid line is from Sala et al (1988) based on observational field data. The dashed line depicts the qualitative change expected if semi-arid and mesic grasslands respond to more extreme rainfall regimes consistent with experimental field manipulations.*

These opposing responses on a single grassland biome to widely forecast shift in rainfall patterns, with some regions of the biome experiencing greater water limitations while water stress in others will be alleviated, have important implications for regional patterns of forage production. Sala and Lauenroth (1982) published regional scale relationships between ANPP and precipitation for North America that is widely-used but that may require modification with more extreme rainfall regimes (Fig. 3). Of course, the new relationship proposed in Figure 3 for more extreme rainfall regimes is based on a very limited number of sites. This reinforces the need for more research to be conducted in the area of climate extremes and ecosystem responses. In summary, the results presented here highlight some of the more surprising consequences that an increase in extremes in rainfall regimes may have for grasslands, as well as some important lessons to be considered for coping with the future of grasslands and the services they provide (Table 1). Of particular need is research in more intensively managed grasslands from those that are grazed by domestic livestock to row-crop ecosystems in formerly grassland sites. How

Table 1. *Summary of key lessons learned from research focused on understanding how changing rainfall patterns (an increase in the variability or extremes of rainfall regimes) will impact grasslands, with implications for forage/food production.*

1. Alterations in rainfall patterns in grasslands to more extreme within-season regimes can either decrease or increase forage production, even with no change in precipitation amount.
2. Increases or decreases in forge production in response to more extreme rainfall patterns are contingent on the seasonal average levels of soil moisture for grasslands, with mesic grasslands responding negatively and more arid grasslands positively.
3. Dormant season soil moisture may either mitigate or exacerbate responses of forage production in grasslands to changes in climate.
4. The sensitivity of grassland forage production to interannual variability in rainfall amount may be increased by more extreme within season rainfall regimes.
5. Because most grasslands are heavily managed and many have been converted to row-crop agriculture for food production, research is needed to determine how these highly managed ecosystems respond to more extreme climate regimes.

management interacts with forecast more extreme climate regimes to influence food production and other ecosystem services represents a significant knowledge gap in our understanding of climate change – ecosystem relationships.

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