Intra-seasonal precipitation patterns and above-ground productivity in three perennial grasslands

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Summary

1. Relationships between above-ground net primary productivity (ANPP) of grasslands and annual precipitation are often weak at the site level, with much of the inter-annual variation in ANPP left unexplained. A potential reason for this is that the distribution of precipitation within a growing season affects productivity in addition to the total amount.

2. We analysed long-term ANPP data for three southern African temperate grasslands (mean annual precipitation ranging from 538 mm to 798 mm) to determine the effects of precipitation event size, number and spacing relative to seasonal totals.

3. Ungrazed, non-manipulated treatments at each site showed contrasting results despite sharing a common, dominant species. At the driest site, a model combining average event size and number of events per growing season provided a substantially better fit to the ANPP data than precipitation amount (seasonal total). At the wettest site, the interval between events was the most important precipitation variable. Precipitation distribution was not important at the intermediate site where amount was the best predictor of ANPP. A limit to the size of precipitation events efficiently utilized for ANPP was evident for the driest site only.

4. At each site, experimental treatments that altered species composition and soil fertility had little effect on precipitation–ANPP relationships. The lack of consistency in the relative importance of the precipitation variables among sites suggests that local, edaphic factors modify precipitation–ANPP relationships.

5. This analysis demonstrates that the distribution and size of precipitation events can affect ANPP independent of precipitation amount. As altered precipitation regimes are forecast by global climate models, the sensitivity of ecosystems to precipitation distribution should be considered when predicting responses to climate change.

6. While mean values of precipitation, and other ecosystem drivers, are typically used to predict function at the level of whole ecosystems, our results show that more complex measures of environmental variability may be required to understand ecosystem function, and to increase the accuracy of predictions of ecosystem responses to global change.

Key-words: C₄ grasslands, climate change, fertilization, net primary production, precipitation, species composition.

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Introduction

Determining the controls on net primary productivity, a fundamental process in all ecosystems, is one of the founding goals of ecosystem ecology. The above-ground net primary productivity (ANPP) of grasslands has been relatively well studied, with inter-annual variation in ANPP widely regarded to be primarily determined by inter-annual variation in precipitation quantity. Regional-scale meta-analyses, relating mean peak biomass of sites to mean annual precipitation, have confirmed this relationship for most of the grassland and savanna regions of the world (Deshmukh 1984; Le Houérou et al. 1988; Risser 1988; Sala et al. 1988; McNaughton et al. 1993; Epstein et al. 1997; Ojima et al. 1999; Ni 2004). While these analyses may be useful for predicting
regional scale effects of projected global change (e.g. Burke et al. 1991), site-specific analyses are required to predict the effects of global change at the local scale and to gain a mechanistic understanding of how precipitation affects ecosystem function. Indeed, long-term experiments at the site level have generated sufficient data to allow for more mechanistic assessments of the effect of annual precipitation on ANPP for perennial grasslands around the world (Smoliak 1986; Le Houërou et al. 1988; Lauenroth & Sala 1992; Briggs & Knapp 1995; Knapp et al. 1998; Jobbagy & Sala 2000; O’Connor et al. 2001; Chidumayo 2003; Knapp et al. 2006; Nippert et al. 2006). However, while most precipitation-ANPP relationships are significant at the site level, much of the variation in ANPP is not accounted for, even in long-term studies, and relationships often appear nonlinear.

A potential reason for poor relationships between precipitation and ANPP is that the distribution of precipitation within a growing season affects ANPP independent of the total amount. It has long been suggested that the majority of plant productivity occurs in the form of short-duration pulses following rainfall events, at least for semi-arid and arid systems (Noy-Meir 1973). There is likely to be an optimal distribution of such pulses for ANPP, i.e. an optimal distribution of precipitation event sizes and of the intervals between them. For example, Lauenroth & Sala (1992) found that precipitation events of 15 mm to 30 mm were responsible for most of the effect of precipitation on ANPP for a short grass steppe site (although the potential importance of small events < 5 mm has also been emphasized; Sala & Lauenroth 1982). For mesic tallgrass prairie, Knapp et al. (2002) found that extending the intervals between precipitation events – without changing the total precipitation for the season – reduced ANPP by about 10% over 4 years in a rainfall manipulation experiment. The optimal distribution of events sizes and intervals is likely to vary from one ecosystem to the next, or even between different communities in the same system, depending on rates of run-off, infiltration, evapotranspiration and the ability of dominant species to tolerate water stress between events. Global climate change models predict not only changes in annual precipitation (Houghton et al. 2001) but also increases in ‘extreme events’, with precipitation more likely to fall in larger but less frequent events (Gordon et al. 1992; Easterling et al. 2000; Meehl et al. 2005). Analyses of long-term climate data from regions throughout the world indicate that such increases in extreme precipitation regimes have already begun (Karl et al. 1995; Groisman et al. 1999; Plummer et al. 1999; Easterling et al. 2000; Domonkos 2003). These changes warrant more detailed investigation of the effects of precipitation distribution patterns on productivity.

To determine whether the distribution of precipitation does affect ANPP independent of precipitation amount, we analysed long-term ANPP data for three grasslands dominated by C₄ perennials, each differing in mean annual precipitation and soil type. At all three sites low soil water, not low temperature, determines the dormant season (empty bucket systems sensu Knapp et al. 2006). Standing biomass was removed every year at each site, eliminating any potential effects of carried-over biomass (Knapp & Seastedt 1986; O’Connor et al. 2001; Haddad et al. 2002; Chidumayo 2003) which allowed for a focused analysis of the effects of current season precipitation. In addition, treatments originally implemented at each site to address rangeland management questions have created communities differing remarkably in species composition and soil fertility. These long-term data were used to address three questions: (i) does the distribution of precipitation affect ANPP independent of amount, (ii) does this effect differ between different grassland ecosystems, and (iii) does this effect differ within an ecosystem, due to differences in species composition and soil fertility?

**Methods**

**SITE AND DATA DESCRIPTIONS**

Long-term data for ANPP and precipitation were obtained from three sites in South Africa, referred to as Bloemfontein, Towoomba and Ukulinga. Data for Bloemfontein are from a long-term experiment established in 1977 at an agricultural research farm (Sydenham) near Bloemfontein and in 1995 at the campus of the University of the Free State, 5 km away (26°15'E, 28°50'S, altitude 1350 m a.s.l.). The same experimental design was used at both sites, and both had similar soils (a sandy clay loam) and the same C₄ grass community (soils and species composition for each site are described in more detail by O’Connor et al. 2001 and Snyman 2000). Data from both locations were treated as a single set. Mean monthly temperatures on the campus ranged from 17 °C in July to 33 °C in January. Three treatments were established in 1977 with the goal of maintaining plant communities representing vegetation in good, moderate and poor states, as would be created by grazing regimes of increasing intensity. The medium and poor condition communities were created and maintained by removing certain species by hand. The existing (ungrazed) vegetation at the start of the experiment was considered in good condition and left unchanged. Few individuals had to be removed after the first few years. There were three replicates of each treatment, each consisting of a 2 × 15 m² plot (treatments were randomly assigned to plots). ANPP was estimated as peak standing biomass, measured by clipping the above-ground biomass of eight 0.25-m² quadrats, placed randomly in each plot, to a height of 3 cm at the end of each growing season. Entire plots were subsequently cut to the same height in July each year, before the start of the next growing season.

Results are presented for the good condition and poor condition plots only, as those for the moderate condition plots were similar to those for the good condition plots. The good condition plots (referred
treatment received an annual total of 151.4 kg N ha\(^{-1}\) in productivity, referred to as the P2N3 treatment. This treatment received the greatest increase of all the treatments over the study period. This treatment was observed within a few years of commencement of the treatments, and the various treatments now represent ecosystems differing markedly in nutrient availability, productivity and species composition (Fynn & O’Connor 2005). There were three replicate 2.7 \times 9.1 \text{ m}^2 plots per treatment. ANPP was measured twice each year, in December (the middle of the growing season) and in February (towards the end of the season), by mowing a 2.1-m strip in each plot. Mowed material was weighed fresh, and this weight converted to dry mass using a subsample dried to constant mass.

Analyses were restricted to data from the control and the treatment receiving the most N and P, referred to as the N3P treatment, which had the highest mean ANPP of all the treatments over the study period. This treatment received an annual total of 211.7 kg N ha\(^{-1}\) as NH\(_4\)NO\(_3\) applied bi-annually and 28 kg P ha\(^{-1}\) as phosphate applied annually. The control plots were dominated by *Themeda triandra* and *Tristachya leucothrix* Nees, and the N3P plots by *Panicum maximum* with *Eragrostis curvula* Schrad. (Nees) subdominant (Le Roux & Mentis 1986; Fynn & O’Connor 2005). Daily precipitation data was collected on site. Due to missing data, information from only 30 growing seasons could be used (1950–63, 1965–79, 1997/98 and 1999/2000).

### Precipitation Variables

The effect of precipitation amount was evaluated using growing season totals. The effect of precipitation distribution was evaluated using three variables: average precipitation event size, number of precipitation events and the average interval between precipitation events over a growing season. Average event size and event number together determine precipitation amount. However these variables may affect ANPP independent of amount, and of each other, depending on how efficiently primary producers utilize events of various sizes, and how vulnerable they are to infrequent rainfall events. Event number is related to average interval as fewer events will always result in longer intervals. However, average interval provides a more direct measure of the (temporal) spacing of precipitation events and was included in analyses for a better estimate of this effect. For analyses where event size appeared to be important, an additional variable was calculated by ‘capping’ events to 25 mm (i.e. setting all events > 25 mm to 25 mm and recalculating seasonal totals). Fifty-millimetre capped totals were calculated in a similar way. This was done to determine if there was a saturating effect of event size (that would occur if substantial run-off or infiltration below the rooting zone followed large events).

For Bloemfontein the growing season was arbitrarily defined as the 1 September to 30 April, for Towoomba as the 1 September to the end of the month of cutting, and for Ukulinga from the 1 September to the date...
Ages were therefore calculated as geometric means.

Growing season averages were calculated for the duration of these growing seasons. A precipitation event was defined as all precipitation ≥ 1 mm falling on consecutive days. Precipitation intervals were calculated as the number of days between events.

The distributions of events and intervals were strongly skewed to the right for each growing season (and when combined for all seasons; Fig. 1). Growing season averages were therefore calculated as geometric means.

**Statistical Analyses**

Simple linear regressions were used to test the effect of seasonal total for each treatment at each site. As seasonal total was often correlated with precipitation distribution variables, the independent effects of the various variables were not tested together in a single model. Instead separate models were used to evaluate the effects of either seasonal total or precipitation distribution. Models for each treatment at each site were then compared on the basis of linearity, outliers and the corrected Akaike’s Information Criterion (AICc). Outliers were judged using the standardized DFFITS statistic. DFFITS is calculated by refitting models after removing a particular datum, and indicates how much the partial regression coefficients in a model change (in standardized units) when an outlier is excluded. AICc estimates the likelihood that a model is correct, given the data, relative to alternative models. The AICc for each model was calculated from the mean square error of a least squares regression, and these values were used to calculate the relative likelihood of the particular models under comparison, following Burnham & Anderson (2002). The relative likelihood is the probability that a particular model, in a set of compared models, provides the best fit to the data. Two multiple regression models were used to test for the effect of precipitation distribution: one combining average event size and event number, and one combining average event size and average interval. Event number and average interval were not tested together as these variables were always correlated. Average event size and event number, and average event size and average interval, were not correlated in any of the analyses, and variance inflation factors were never greater than 1.1. The inclusion of an interaction term did not improve the fit of any of these models. All analyses were performed using Statistica v 6.1 (Statsoft Inc., Tulsa, USA).

**Results**

Mean annual precipitation across the three sites varied from amounts typical of semi-arid to mesic grasslands (Table 1). The ranking of the sites according to precipitation amount reflected differences in precipitation distribution: Ukulinga, with the highest precipitation, had the most precipitation events but the smallest average event sizes and the shortest intervals between events (Fig. 2). Bloemfontein, the driest site, was the opposite, and Towoomba was intermediate. At each site, inter-annual variation in ANPP was large and the CV of ANPP always greater than that of the total annual precipitation (Table 1). Bloemfontein had the greatest inter-annual variation in precipitation, although the CV of ANPP was no greater than that at Towoomba, where the CV of precipitation was lower. The poor condition plots at Bloemfontein had greatly reduced ANPP and rain use efficiency (RUE, sensu Le Houèrou 1984), and showed greater inter-annual variation in these. Ukulinga had the greatest ANPP, the least inter-annual variation in ANPP and the greatest RUE. At both Towoomba and Ukulinga, fertilization with N and P increased productivity, by almost 280% above that of the control plots at Towoomba and 75% at Ukulinga. Fertilization also increased inter-annual variability in ANPP, particularly at Ukulinga.

Productivity of the control plots at each site showed different responses to precipitation distribution, with precipitation distribution variables providing a better fit to the ANPP data than precipitation amount at Bloemfontein and Ukulinga, but not at Towoomba (Fig. 3). At Bloemfontein, the driest site, incorporating the effects of event size and event number provided the best model (Table 2). While precipitation amount

![Fig. 1](image-url)
showed a linear effect on ANPP, a large outlier resulted in a relatively poor fit. The multiple regression combining event size and number could account for the low ANPP in the outlier year, and explained more of the variation in ANPP. Standardized parameter estimates were similar for each variable, and maximum productivity was only obtained in years with both large events and many events. Event size and interval produced a weaker model revealing little effect of the spacing of precipitation events. Capping precipitation to 25 cm produced a model similar to event size plus event number, and better than precipitation amount ($r^2$ improved from 0.46 to 0.66 and no clear outliers). At Towoomba, the site with intermediate precipitation, precipitation amount had a linear effect on ANPP with no outliers (Table 2). Neither of the precipitation distribution models provided a substantial improvement to this model, although event size alone gave a similar fit with an almost identical AICc. Capping event sizes to 25 mm or 50 mm did not improve on the amount model. The effect of precipitation amount at Ukulinga, the wettest site, was weak (Table 2). Event size plus event number improved on the amount model, again accounting for a large outlier. The event size plus interval model showed an even greater improvement and clearly provided the best fit. Standardized parameter estimates indicated a greater effect of interval than event size.
Differences in productivity–precipitation relationships between the various treatments at each site were comparatively small. For the poor condition plots at Bloemfontein, event size plus event number again provided the best fit, but less of the inter-annual variation in the ANPP could be explained. Precipitation amount again contained an outlier and appeared to be nonlinear, with ANPP often well above average in years with average rainfall. Capping events to 25 mm improved on the amount model only slightly, while capping to 50 mm produced a substantial improvement ($r^2$ increased from 0.32 to 0.42 and the relationship was more linear). At Towoomba, ANPP for the fertilized plots was similar to that for the control plots in dry years, but consistently greater in wet years (resulting in the substantially greater mean and variance). Precipitation amount had a strong linear effect on ANPP, with an $r^2$ value more than twice that for the control plots (Table 2). Capping event sizes to 25 mm or 50 mm did not improve on this model, and event size alone did not produce as good a fit. The greater and more variable ANPP of the fertilized plots at Ukulinga also resulted from greater maximum values, relative to the control plots. However, greater productivity did not necessarily occur in the wettest years, and precipitation amount provided a very poor fit to the ANPP data (Table 2). The precipitation distribution models provided large improvements, although $r^2$ was still low. A model with interval alone provided as good a fit as the combination of event size and interval.

### Discussion

Patterns of precipitation events within a growing season are complex and the variables used to quantify them are likely to be correlated with the amount of precipitation, as was the case in this study. This precludes a simple test of the relative importance of amount and distribution, such as estimating their effects in a multiple regression model. However, the comparison of alternate models using a suitable criterion such as AIC – an approach now gaining popularity in ecology (Johnson & Omland 2004; Richards 2005) – revealed that variation in precipitation event sizes, numbers and intervals can explain inter-annual variation in ANPP better than seasonal precipitation totals.

The control plots at each site in this study differed substantially in their precipitation–ANPP relationships, with event sizes important at the driest site, the spacing of events important at the wettest site and neither important at the intermediate site. These

<table>
<thead>
<tr>
<th>Model terms</th>
<th>$r^2$</th>
<th>Relative likelihood</th>
<th>Outlier</th>
</tr>
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<td></td>
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<tr>
<td>Control</td>
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Precipitation distribution and ANPP differences occurred despite a common dominant species (*T. triandra*) at all three sites. Likewise results for the fertilized plots at Towoomba and Ukulinga differed, despite both being dominated by *P. maximum*. Furthermore, large changes in species composition created by the various treatments had little effect on model selection within sites. The importance of precipitation distribution relative to amount, and of the precipitation variables relative to each other, therefore appears to be more a function of edaphic factors (such as soil texture, depth or fertility) than species composition. These results also indicate that certain species are able to dominate grass communities in environments with very different rainfall regimes.

At Towoomba, the efficiency with which primary producers utilized precipitation was affected little by the distribution of the precipitation. The relatively sandy soil at this site has a high infiltration rate (194 mm h\(^{-1}\)) for the control plots; Donaldson *et al.* 1984) and run-off is likely to be minimal, even following large precipitation events, allowing primary producers access to most of the precipitation that falls. The strong relationship between event size and ANPP observed for the control plots, as well as the lack of an effect of capping large events, suggests that larger events are actually required for maximum productivity. Infiltration to deeper soil layers may therefore be necessary for the dominant species to obtain maximum productivity. The lack of effect of event number and average interval revealed that the spacing of events is not important under the current climate regime. Either rates of evapotranspiration are low enough to prevent significant drying of the soil between events, or the dominant species tolerate water stress well and maintain most of their biomass when soils dry between events. Low rates of evapotranspiration seem unlikely as the site experiences hot temperatures during the summer. Furthermore, the lack of effect of precipitation distribution was most evident for the fertilized plots where productivity is greater and rates of transpiration presumably higher. The particularly strong relationship between ANPP and precipitation amount for the fertilized plots was the result of far greater productivity in wet years. This may have been a consequence of the altered species composition as *P. maximum* (the dominant species) can grow very rapidly when nutrients and water are readily available (Pretorius *et al.* 1974; Healey *et al.* 1998).

At Bloemfontein and Ukulinga, precipitation distribution variables provided a better fit to the ANPP data than precipitation amount, but for different reasons. At Bloemfontein, both larger events and many events were required for maximum productivity. This may indicate that a threshold of soil water at a certain depth is required for optimal growth (with the threshold only reached after a large number of small events, or a few large events). Wilting during the growing season occurs regularly at this site (Snyman 1998) but as the average interval between events did not affect ANPP, the dominant species are presumably tolerant of this. Tolerance of water stress by the dominant primary producers therefore appears to be an important factor at both Bloemfontein and Towoomba, buffering productivity against the negative effects of long-precipitation intervals.

In contrast to Towoomba, an upper limit to the size of events that contributed effectively to ANPP was evident at Bloemfontein. The main reason for the relatively weak effect of precipitation amount, for the control plots, was an outlier season that contained a few large events resulting in a large seasonal total but only moderate ANPP. As capping precipitation to 25 mm greatly improved the relationship between amount and ANPP, the limit to the size of events that can be effectively utilized actually appears to be much lower than many of the events recorded. The effect of event size on ANPP at Bloemfontein therefore appears to be twofold: larger event sizes up to about 25 mm increase growth and therefore RUE, but event sizes above about 25 mm are less effective and reduce RUE. The lower RUE for the poor condition plots reflects the inability of the dominant species to effectively utilize precipitation in most years (Snyman 1998, 1999). This also explains the weaker relationship between precipitation and ANPP. The lower RUE was mainly a result of lower basal cover, not species composition, as differences in ANPP per unit basal cover between the good and poor condition plots are much less than the differences in ANPP alone (Wiegand *et al.* 2004).

The potential importance of the spacing of precipitation events was revealed for Ukulinga, the site with the highest precipitation and the shortest intervals between precipitation events. The low proportion of inter-annual variation in ANPP that could be explained for the Ukulinga plots is probably a result of the high frequency of events preventing water shortages in most growing seasons. This would result in high productivity in most years and can explain the low inter-annual variation in ANPP (for the control plots) and the weak relationships between precipitation amount and ANPP. Only when an unusually long interval between events occurs would water stress develop and productivity slow (thus the relatively strong effect of average interval on ANPP). For the control plots, the effect of event size suggests that larger events are required to eliminate water stress following a longer interval. These results indicate that the dominant species in the control plots at Ukulinga do not tolerate water stress well – the opposite conclusion to that reached for Bloemfontein and Towoomba, despite all three sites sharing a common dominant species. A potential explanation for this is that water stress is more severe at Ukulinga, when it does occur. The soil at Ukulinga is relatively shallow and this may limit storage of precipitation between events. Furthermore, greater clay content may result in lower soil water potentials even with moderate drying. Rates of evapotranspiration may also be higher at Ukulinga, given that productivity is higher.

The results for the control plots at Ukulinga are consistent with those found at the Konza Prairie Biology
At Towoomba the apparent lack of effect of large events and long intervals suggest that productivity will be little affected by larger but less frequent precipitation events. An obvious caveat is that climate change may bring larger events and fewer events than were ever experienced in the duration of this study (Nippert et al. 2006). While there must be an upper limit to the size of events that can be effectively utilized, it was not evident in these data. The lack of an effect of capping events indicates that even events > 50 mm make a significant contribution to ANPP. Furthermore, the growing season with largest average event size also had the largest control plot ANPP. At Bloemfontein, increases in the frequency of large events, or larger individual events, can be expected to reduce RUE. The results for the poor condition plots suggest that heavy grazing will not change this response qualitatively. For Ukulinga, reductions in RUE are also likely, as a smaller number of precipitation events will result in longer intervals and a greater frequency of periods of water stress.

Huxman et al. (2004) found that RUE converges to a similar minimum during dry years, for a wide range of ecosystems representing most terrestrial biomes. Our results contrast with Huxman et al. in that there was not a decrease in average RUE with mean annual precipitation across the three sites studied (Table 1), nor convergence to a similar RUE in dry years for all the plots included in our analyses (data not shown). Broad patterns that emerge from comparisons across large gradients in productivity and mean annual precipitation may overshadow site-level effects of precipitation distribution or site-specific factors on RUE. However, our results do show that these effects can be large enough to create substantial differences in RUE between ecosystems within the same biome and, for prediction at the site level, may be more important than broad-scale comparisons.

Conclusions

Annual or seasonal totals of precipitation provide a simple and convenient means to evaluate the effect of precipitation on ANPP, but the more complex effects of precipitation distribution should not be overlooked, particularly considering the predictions of global climate change models. Our results show a variety of effects of precipitation distribution, with the size of precipitation events being important at the driest site considered, and the spacing of events important at the mesic site. Differences between sites were greater than differences within sites created by changes in species composition and soil fertility. Clearly this generalization needs to be tested elsewhere (Knapp et al. 2004). Such studies can only improve our understanding of the determinants of ANPP, and allow for more robust predictions of ecosystem responses to global climate change.

Acknowledgements

Biomass data for Towoomba were obtained from Scholes (1998) and daily precipitation data from the South African Weather Service (http://www.weathersa.co.za). Biomass and precipitation data for Ukulinga were obtained from Richard Fynn, Grassland Sciences, School of Biological and Conservation Science, University of KwaZulu-Natal.

References


Precipitation distribution and ANPP


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